Context-dependent movement, task-relevant sensory filtering and approaches to Parkinson's training

by

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Abstract

People with Parkinson's disease experience motor symptoms that are affected by sensory information in the environment. Sensory attenuation is a phenomenon that describes the modulation of sensory input caused by motor intent. This appears to be altered in Parkinson's and may index important sensorimotor processes underpinning Parkinsonian symptoms. Seemingly disparate results in sensory attenuation experiments are reconciled with an emphasis on task-relevance in the modulation of sensory input.

Additionally, findings from original psychophysics and motor learning experiments are presented. A Cornsweet illusion task is used to elucidate context-dependent perception, which increases with age. Adaptation effects also occur in response to contextual cue manipulation, with implications further afield for training techniques. The subsequent motor learning experiment altered sensory information availability during a pegboard task. The results demonstrated that altered sensory input prompts strategy change, but no unique enhancements in motor skill performance. An interdisciplinary approach is then used critique some of the broader themes in neuroscience that relate to the questions explored in this thesis.

Collectively, this work illuminates the dual effect of basal ganglia dysfunction in Parkinson's disease: a reduced capacity to filter task-relevant signals harms the ability to integrate contextual cues, just when such cues are required to effectively navigate an environment. Further, the interdependencies of action, perception and cognition are highlighted. Current motor control theories are brought into question, whereby sensory attenuation is reframed as context-dependent perception instead of a result of probabilistic integration. A move toward effective training principles is attempted in this context.

For Flip

First thanks goes to my supervisors – John-Stuart Brittain and Ned Jenkinson. Thank you Ned for being open to listening to a probably slightly annoying and previously unknown-to-you undergraduate student knocking on your door and asking about a PhD in neuroscience and remembering me in the year or two that followed to let me know about the opportunity with John. Thank you John for the opportunity, for entertaining various wacky ideas while we waited for that mythical brain-stimulation device to one day arrive from a faraway land. I am grateful for you getting me in the lab so early on, especially given the absence of lab time that ensued amidst a pandemic. It is a shame we did not get more opportunities to scribble all over your whiteboard, but I am glad we had opportunities nonetheless, and I am proud of the work that has emerged.

I had a lot of help with data collection for the younger adult groups in Chapters 2 and 3 from Emily Warren, Megan Platts, Jackie Chow and Jack Richards, who were brilliant and a joy to teach and work with. Benjamin Hart helped me with the study described in Chapter 4, helping with study design by trying out different variations in piloting and then in collecting data. Chapter 5 stems from a paper written with friend and colleague Morgan Mitchell of Oxford University for a special issue of Frontiers, which at the time of writing is under review. Chapter 1 is a very slightly edited version of a paper originally published in the journal *Brain Sciences* under the name *Sensory Attenuation in Sport and Rehabilitation: Perspective from Research in Parkinson's*, where authorship is shared with John who provided thorough editing, guidance along the way and the suggestion for a review in the first place (which I learnt so much from writing – who knew there was so much out there to make sense of in neuroscience already!).

I will not pretend I know each contributing factor to the making of this thesis in an infinite and unfolding world, but I would like to thank my friends, a group of whom have been calling me doctor before even being accepted onto a doctoral programme, and whose encouragement, patience and friendship mean so much. Mum and Dad (Cathy and Jonathan Kearney) – thank you for creating a loving, nourishing environment for me to grow in and return to for replenishment and inspiration, for camaraderie, and for the editing! Joel and Benjamin Kearney, my brothers, are the life and laughter that pull me out of miserable and boring pits of contemplation. So too is my fellow adventurer Tisha Scott whose smile transforms, whose love and faith I could not do this without, and whose edits were also very helpful! Thanks also go to Jonah Bateson and Rupert Smith for editing contributions, specifically the introduction and Chapter 5.

It has often felt like there is an expectation and duty to go into isolation, finish writing up the thesis and then reemerge into society. I found myself half-way down that rabbit hole a few times, but however stoic and necessary it felt initially, each phase ended in exhaustion and loneliness. I am grateful to the communities who have welcomed me in and kept me connected, from basketball and football, to church and its surrounding activities like Lauda, STS Community Project, Action Potential and to Les, Wendy and my grandparents who provided a space to explore more deeply the meaning of all the writing that follows and some Friday afternoon training to look forward to and reflect on. Amidst it all, I am grateful to God who connects all things to all things to make each thing less thing-like.

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Contents

Introduction

Lines on the floor

In one scenario, a person shuffles forward, moving gradually towards the far end of the room. Steps are short and stuttered. The delicacy of the skill of walking is suddenly very apparent. In a second scenario, lines of tape are stuck down on the floor, arranged like a ladder along the path the person just travelled. This time, they stride confidently and smoothly across the room, feet landing precisely on each line of tape. In the first scenario, walking stutters, but in another, the many years of walking practice are gracefully revealed. The difference between the two is sticky tape.

Shuffling gait can be symptomatic of Parkinson's disease, a movement disorder affecting the basal ganglia in the brain. Cues, such as lines on the floor, can alleviate such motor impairments (Beck et al., 2015; Morris et al., 1994, 1996; Nonnekes et al., 2019; Quintyn & Cross, 1984). The lines-on-the-floor effect on gait has been a source of fascination for me, and a recurring image throughout the investigations described in the chapters that follow: how can changing the content of the environment so dramatically change the ease of movement? What does it tell us about how we all move, what does it reveal about the basal ganglia and how can it inform our understanding of approaches to Parkinson's treatment?

Ever since James Parkinson's description of a 'shaking palsy' in 1817, Parkinson's disease has primarily been considered a movement disorder. Its non-motor symptoms are becoming increasingly recognised, including emotion- and cognition-related changes (Aarsland et al., 2013; MacDonald et al., 2019), challenging the motor-only emphasis of Parkinson's categorisation (with four motor cardinal symptoms). However, as I will explore, the challenge goes beyond just the inclusion of non-motor symptoms into the diagnosis of Parkinson's. How might motor and non-motor symptoms be linked beyond just occupying the now-longer list of diagnostic criteria?

I had the exciting opportunity to help out with exercise classes for people with Parkinson's and other movement disorders at the Movement Disorder Research and Rehabilitation Centre in Waterloo, Canada. It was exciting to me because of my life-long obsession with sport, movement, how to improve movement in sport, my general joy of learning and the thrill of communal exercise in shared spaces. It was here that I got an insight into the approaches that form part of the Parkinson's disease sensory attention focused exercise (PD-SAFEx) programme. In PD-SAFEx, the lights in the gym where it takes place are sometimes turned down during exercise sessions and participants perform some exercises with their eyes closed. Participants often demonstrate improved symptom severity scores at the end of a 12-week programme, and even after a further 6-week washout period (Sage & Almeida, 2009, 2010).

The unique effects of varied sensory environments during the same movements fascinate me. One of the draws was the chance to rethink movement and imagine connections across the conceptual divide between action and perception. I was drawn to the basal ganglia, the system damaged in Parkinson's, and the possibility that it might be combining a variety of information signals from across the brain to contribute to movement. At the start of this doctorate, already with a focus on the links between sensory stimulation and motor control, Ned Jenkinson pointed out to John-Stuart Brittain (my two supervisors) and I some papers on sensory attenuation. It was the phenomenon of sensory attenuation that helped us grapple a little more deeply the symptoms of Parkinson's, whilst placing centre-stage the links between movement and sensation.

The Basal Ganglia

The basal ganglia are groups of subcortical nuclei, clusters of neurons, near the centre and the base of the brain. They are highly interconnected, hence the frequent grouping of them as "the basal ganglia", but are also connected to nearly the whole of the cortex (Miall, 2013). The dorsal striatum, made up of the caudate nucleus and putamen receives input from limbic, associative, sensory and motor areas converging from across the brain while serving as the primary input into the rest of the basal ganglia. The globus pallidus (often divided into its external and internal segments), the subthalamic nucleus, ventral striatum (nucleus accumbens and olfactory tubercle) and the substantia nigra (pars reticulata and pars compacta) make up the other main components of the basal ganglia.

A vast array of different neurotransmitters and neuromodulators adds to the complexity of the basal ganglia's intrinsic loops (Figure 1a), though these are often simplified into two parallel pathways: direct and indirect (Gale et al., 2008; Miall, 2013). As an oversimplification, the direct pathway (from striatum, straight to the globus pallidus internal and the substantia nigra pars reticulata, out to the thalamus, on to the cortex and back around to the striatum) is suggested to facilitate movements and the indirect pathway (from the striatum to the substantia nigra pars reticulata via the globus pallidus external and the subthalamic nucleus, and out to the cortex again via the thalamus) is said to suppress movements. An imbalance between the two pathways is often used to model how basal ganglia damage leads to different symptoms, or to understand the chain reaction of damage to just one region of the basal ganglia, though this and other models (e.g. the centre-surround and firing-rate model) should be held loosely as no one model adequately describes every feature of basal ganglia dysfunction in Parkinson's by itself (Gale et al., 2008).

The key attributes of Parkinson's disease's pathophysiology include the loss of dopaminergic neurons in the substantia nigra as well as the aggregation of Lewy bodies and Lewy neurites which contribute to the loss of neural function (Simon et al., 2020). The loss of dopaminergic terminals in the striatum (which receives input from the substantia nigra pars compacta, Figure 1a) is suggested to be the crucial event underlying the onset of motor symptoms in Parkinson's disease. Insufficient dopamine can be considered to reduce the capacity to enable new voluntary actions (Jenkinson & Brown, 2011). The very particular organisation of the striatum which consists of some separate regions that remain in distinct channels along corticostriatal loops, in addition to some overlapping regions thanks to dendrites that cross over, may be key to integrating disparate signals into ongoing movement, ensuring motor responses are appropriate to the creature's current motivational and behavioural state (Miall, 2013).

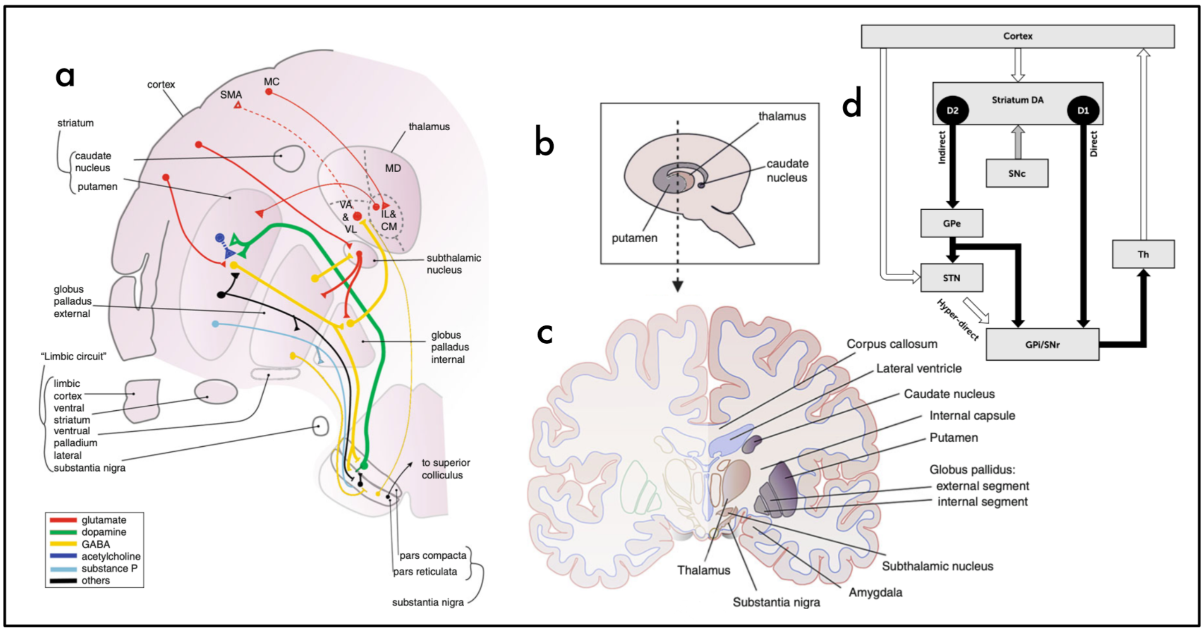


Figure 1 Diagrams of the basal ganglia from Miall (2013) – a, b and c – and Andres & Darbin (2018) – d. (a) The basal ganglia are highly connected to other parts of the brain, including the cortex and thalamus, with an array of mediating neurotransmitters. (b) Depiction of the basal ganglia along the sagittal plane. (c) depiction of the basal ganglia along the frontal plane. The basal ganglia form a complex web of structures, with many interconnections (a), contributing to the reasons why the basal ganglia is difficult to understand (Miall, 2013). (d) A schematic diagram of the direct and indirect pathways, commonly used to make sense of basal

ganglia dysfunction.

Sensory attenuation

Sensory attenuation classically describes why you cannot tickle yourself. When someone tickles my palm, it is ticklish, but when I tickle my palm, it is not (Blakemore et al., 1998, 2000). This phenomenon demonstrates how the same stimulus – the same tickling motion in the same place – leads to different sensations depending on the source of the tickling. Similarly, participants in the force-matching task (Figure 2), when attempting to match a target force, typically press harder onto their finger when they press directly with their other hand compared to when they generate the force with a slider (Kilteni et al., 2017; Parthasharathy et al., 2021; Walsh et al., 2011; Wolpe et al., 2016, 2018). The prominent explanation for these findings has been the cancellation of sensory input because of motor involvement.

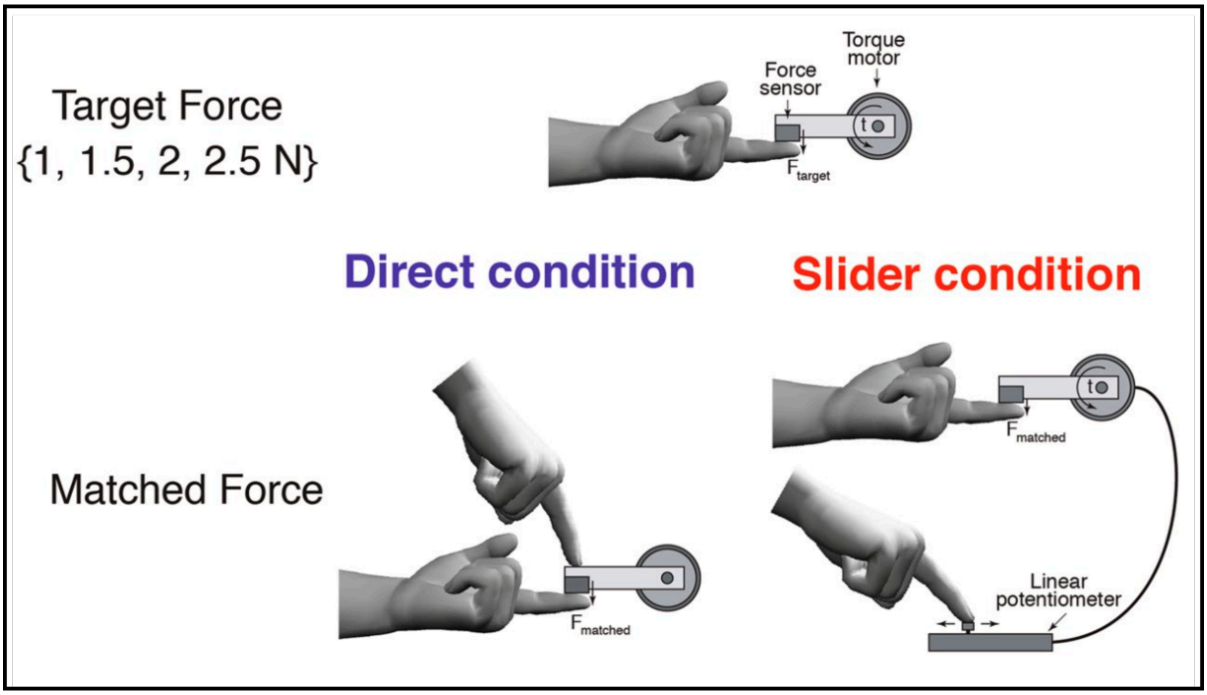


Figure 2 A typical force-matching task protocol, this one from Wolpe and colleagues (2018). Here, a motorised lever presses down onto a participant's finger with a set amount of force; this force is the target force (top). Next, the participant must match the target force in one of two matching conditions. In the direct condition (bottom left) the participant, with their free hand, presses the lever down onto the the receiving hand in an attempt to replicate the sensation felt in the target condition. In the slider condition (bottom right), the participant instead uses a slider to recreate the same sensation using the torque motor. Participants tend to press harder than they need to in the direct condition, but reproduce the force accurately in the slider condition. Pressing harder in the direct condition is believed to result

from the cancellation of sensory input because of direct motor involvement of the free hand. The mismatch between direct and slider matching conditions is thus an index of sensory attenuation.

Another way to measure sensory attenuation is with sensory evoked potentials (SEPs, sometimes referred to as event-related potentials – ERPs). An SEP is generated from electrical signals recorded at the scalp, elicited by a stimulus such as electrical stimulation of the finger. Lots of trials are performed and then averaged in search of a particular pattern that relates to the stimulus. This technique offers a way to measure how a stimulus is being processed, probably at a cortical level (Passmore et al., 2014). Thus, sensory attenuation can be measured by contrasting SEPs elicited from self-generated stimuli and externally generated stimuli. SEPs tend to be of bigger magnitude when externally generated, and smaller magnitude when self-generated, but people with Parkinson's demonstrate a reduced difference between the two conditions (Macerollo et al., 2016, 2019; Railo et al., 2020). Indeed, Parkinson's disease appears to reduce sensory attenuation, as revealed in the force-matching task too (Wolpe et al., 2018). Intriguingly, while sensory attenuation is reduced in people with Parkinson's, it appears to steadily increase with healthy ageing (Parthasharathy et al., 2021; Wolpe et al., 2016). The reason for this disparity was unclear but it demonstrated that sensory attenuation is sensitive enough to track change, and also potentially alterable. *Could it be possible to alter the sensorimotor processes revealed in the sensory attenuation paradigm and would that be of any use in Parkinson's-focused training?*

Pilot study: subthreshold and suprathreshold SEPs

To explore the usefulness of SEPs as a measure of sensory attenuation, we performed a small pilot study. The purpose was to tentatively explore the potential to track changes in the sensorimotor processing capacity of individuals that might also be affected by training. I learnt a lot from this study, but not what I expected. To keep things simple, we performed a partial replication of the Nierhaus et al. (2015) and Forschack et al. (2017) paradigm. In those studies, peripheral nerve stimulation (PNS) was delivered to the participant's finger and SEPs were measured using electroencephalography (EEG) (Figure 3). PNS was delivered either covertly or overtly, meaning the intensity of the stimulation was either slightly below a detection threshold or above a detection threshold.

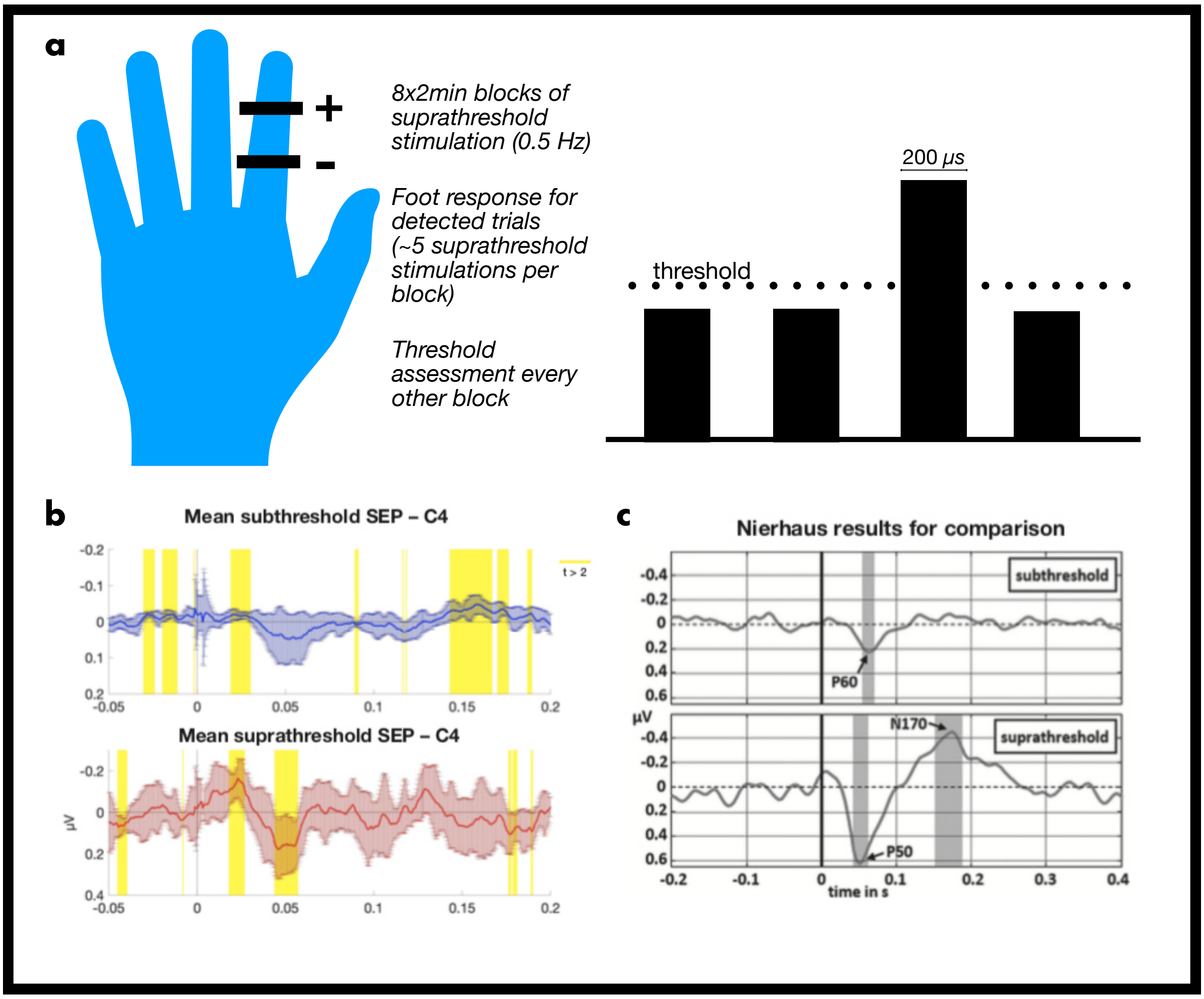


Figure 3 (a) Experiment set up. Peripheral nerve stimulation was delivered using a Digitimer DS5 current stimulation and a CED 1401 interface, operated by Spike2 software (CED). The participants stepped on a squeaky toy to indicate that they felt the suprathreshold stimulation. (b) Afterwards, we compared the responses recorded at the C4 electrode for sub- and suprathreshold stimulation. Red or blue shading around the line (the mean) indicates standard error of the mean. Timepoints where voltage is more than two t-statistics from zero. $N = 5$. (c) Figure from Nierhaus et al. (2015), one of the studies we partially replicated. We likewise found distinct patterns for sub- and suprathreshold stimulation, but the possible N20 component in our data was more akin to Macerollo et al. (2016). More curious, was the change in detection thresholds (Figure 4).

We successfully replicated the difference between subthreshold and suprathreshold PNS conditions, albeit with noisier SEPs that may have smoothed out with more participants (Figure 3). The spikes are also located earlier on in time, closer to the patterns found by Macerollo and colleagues (2016) and consistent with the N20 component which responds to tactile stimuli (Passmore et al., 2014). It was interesting to see that subthreshold stimulation – information that was not consciously detectable – still elicited a cortical response, pointing to the involvement of more than just one brain area in the processing of sensory input (Forschack et al., 2017).

However, there were two aspects of our pilot study that I found more interesting and which guided parts of the subsequent work, described in the chapters that follow. Firstly, the detection threshold – the lowest intensity in milliamps at which the PNS could be detected – changed each time it was measured (Figure 4). The detection threshold at the fifth and last time of measuring was higher than the first time of measuring, indicating a reduced sensitivity over time. Whether this was due to peripheral changes such as reduced impedance of the skin or more central factors such as attention, it highlighted either the inability of measuring without interfering, or, an effect of the task we had devised. The task was simple: lots of subthreshold stimuli were presented about two seconds apart (slightly staggered to be less uniform) with an occasional suprathreshold stimulus. Participants were required to stamp on a squeaky (dog) toy when they felt the suprathreshold stimulus, just to ensure they were engaged in the task. I could not help but wonder, were the task's set-up and instructions guiding the participants toward the suprathreshold stimulation and away from the subthreshold stimulation and thus dulling their tactile sensitivity?

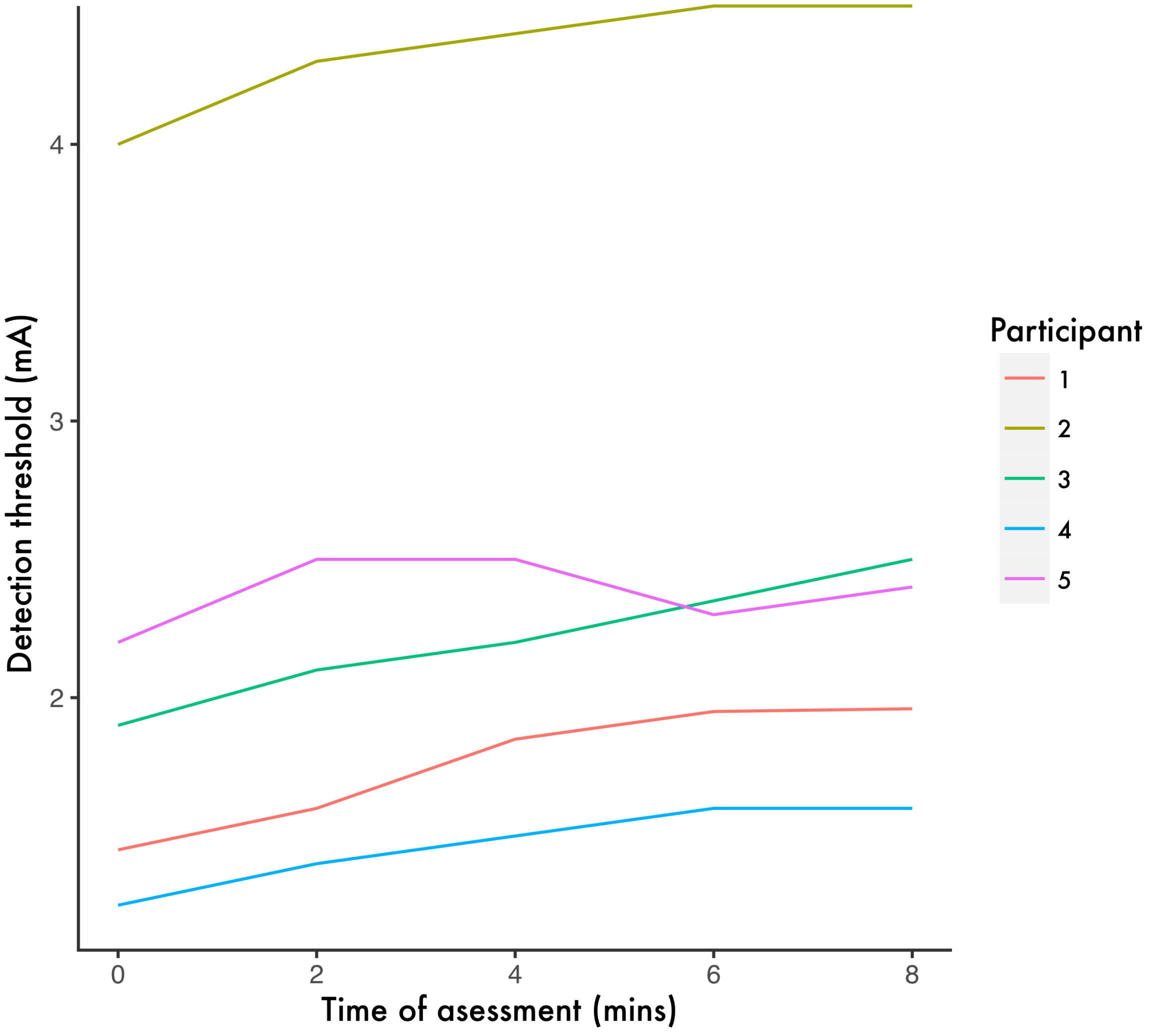


Figure 4 Detection thresholds for peripheral nerve stimulation (PNS) in an early pilot study. Thresholds indicate the lowest PNS intensity that the participant could detect, measured through a simple yes/no response protocol at five timepoints throughout the experiment. Sensitivity to the PNS pulses reduced over the course of the experiment, indicated by higher thresholds at the last timepoint compared to the first: $t(4) = -6.125$, $p = .004$.

As I discuss in Chapter 1, task set-up does indeed make a difference in how stimuli are attended. In a key study, Riley and colleagues (1999) measure the postural sway of participants on a force-plate. In one condition, participants are instructed to pinch a curtain and in another, participants are instructed to pinch the curtain but keep it as still as possible. In the latter, postural sway is significantly better, demonstrating that the sensory input from pinching a curtain does not have a uniform effect on behaviour, but depends on how and why it is being attended to. In Chapter 1, I review the sensory attenuation literature and use this principle of task-relevance in an attempt to reconcile contradictory findings in the field. Some studies demonstrate a sensory suppression effect consistent with the traditional cancellation account of sensory attenuation, whereas others find a sensory enhancement effect. I thus argue for a slight reframing of sensory attenuation, describing it as context-dependent processing, moving beyond rigid cancellation accounts. I go on to explore what sensory attenuation paradigms reveal about the roles of the basal ganglia and the cerebellum in movement and draw on a strand of research (Kaji, 2001; Robbe, 2018; Schneider, 1984) that postulates a sensory-filtering role for the basal ganglia that best explains its contribution to motor control. In the interests of informing approaches to Parkinson's-focused rehabilitation training, I bring together my conclusions on sensory attenuation and the basal ganglia for a holistic account of the symptoms of Parkinson's disease and suggest principles for effective rehabilitation approaches.

The task-relevance principle, highlighted by Riley et al. (1999), is important when considering the lines-on-the-floor effect during gait. The lines help to simplify the environment being navigated but are they being used in a way to aid the learning of the ability to navigate complex environments? To further explore principles of effective rehabilitation, I present findings of an experiment in Chapter 3 that point to how sensory cues are used and how adaptation effects emerge through repeated use. The experiments in Chapter 3 – that suggest the use of bold, salient cues can have a negative effect on cue sensitivity – utilise the same task described in Chapter 2. This task is a simple visual illusion task, where participants make one of two keyboard responses depending on how they perceive the onscreen stimuli. We demonstrate a clear effect of contextual information on participants' perception in a similar fashion to the force-matching task, pointing to a multi-sensory (not just somatosensory) nature of sensory attenuation and supporting the framing of sensory attenuation as a form of context-dependent sensation. We also compare illusion strength across three populations – older adults with and without Parkinson's, and younger adults – to further explore the reported increase of sensory attenuation with age and decrease in disease.

Chapter 4 is an account of a rather different experiment. Instead of pressing a keyboard in response to onscreen stimuli, participants completed a two-day pegboard task that involved placing pegs as quickly as possible under different sensory conditions. The interventions that alter sensory conditions (a blindfold and latex gloves) serve as an attempt to mimic approaches to rehabilitation that reduce a form of sensory input, such as the PD-SAFEx programme, but in a non-Parkinsonian population group. By using participants without a neurological disorder, we ask if the PD-SAFEx approach enacts a general principle of motor learning beyond participants who are overly reliant on visual sensory input to move. Further, we bring into question theories of motor control prominent in the field of neuroscience that offer an explanation for the lines-on-the-floor effect and even aspects of the PD-SAFEx approach, but do not so easily handle the more diverse array of training techniques that depend on the need to navigate complex environments.

Chapter 5 is written in a different style to the rest of the chapters. The style is reflective of the variety of sources drawn on to make the arguments, as I discuss literature beyond the neurosciences that have been important and fruitful to consider throughout the duration of my PhD. As such, the essay is somewhat unusual, and draws on quotations as much as quantitative evidence from experiments, and demonstrates the somewhat broader interdisciplinary approach I have taken to make sense of the central findings in Chapters 1 to 4, even if our experiments themselves have subscribed to a typical cognitive neuroscience framework (of course itself multi-faceted). I reflect more broadly on the brain, ultimately arguing that things do not make sense in isolation. That is, in spite of the silos inside which we have traditionally examined the brain, action, perception and cognition cannot be properly understood without reference to their dependence on each other (Cisek, 2019; Guo & Song, 2022). Just as a motor skill is dependent on characteristics of the environment, thought is not solely an act of the brain but rather arises as an act of a world the brain is a part of. This idea (of thought as an act of the world, not an act upon the world (Jennings, 2019, p.389)) is a destination of the work that takes seriously the interplay of action, perception and cognition, because the sensory characteristics of past and present environments come to be recognised as playing an active role in shaping thought. Rather than the basal ganglia containing, all by itself, motor programmes, the story is rather one where movement emerges from the connections between things and the basal ganglia grapples with the complexity of the brain's surroundings by drawing on other brain regions and snippets from the body and wider environment. Recognising the intimate interplay of agent and environment also challenges our approaches to rehabilitation, seeing movement as interaction and training as the shaping of environment to facilitate learning and the capacity to navigate complex environments that prompts even further learning.

The mind then, is not a self-sufficient unit, but rather intimately embedded and connected to the rest of the world. The utter absence of isolation is evident in the effects of task and context on action and perception. Recognising how we move and filter sensory information becomes crucial in approaches to Parkinson's-focused training. Further, the revelation of context-dependent movement in people with Parkinson's discloses the intricacy of motor skill more generally – why and where we move matters to us all.

> Every organism is like a melody that resonates and harmonises with living things around it.

M.R. O'Connor, summarising Jakob von Uexküll, *Wayfinding*, p.75

Chapter 1

Task-relevant sensory filtering by the basal ganglia in Parkinson's disease and in sensory attenuation experiments

1. Introduction

People with Parkinson's Disease face debilitating symptoms that often begin years before disease diagnosis (Gaenslen et al., 2011), worsen over time and significantly affect quality of life. Dopamine replacement therapy is used to treat Parkinson's and can be effective for long periods (Jost & Bausch, 2017), though it does not improve all cardinal symptoms of this neurodegenerative disorder (Sangarapillai et al., 2020), with high levels of wearing off over time and considerable dissatisfaction among patients (Jost & Bausch, 2017). While techniques such as deep brain stimulation can be employed with relative success (Bratsos et al., 2018), they are still associated with significant shortfalls (di Biase & Fasano, 2016), not least of which are the narrow inclusion criteria deemed necessary for high efficacy (Antonini et al., 2018), and the significant investment in time required for effective stimulator titration. This means there is a need for effective therapies that can be utilised in prodromal and early-stage Parkinson's in a preventative capacity, which may delay, or even complement later stage medical or surgical options. Various exercise therapies have been developed which have involved the manipulation of sensory feedback (Sage & Almeida, 2009, 2010), manipulation of movement amplitude (Ebersbach et al., 2010), multi-sensory cueing strategies (Chawla et al., 2020; del Olmo & Cudeiro, 2005; Morris et al., 1994, 1996; Spaulding et al., 2013), action-observation and motor imagery (Caligiore et al., 2017), resistance training (Corcos et al., 2013), forced-exercise protocols (Ridgel & Ault, 2019; Ridgel et al., 2009, 2015; Miner et al., 2020) and dance (Bek et al., 2020; Foster et al., 2013). Whilst varying degrees of success have been reported, an optimal strategy has not been identified (Spaulding et al., 2013) and underpinning mechanistic principles for effective rehabilitation remain elusive.

Parkinson's involves gross degeneration of midbrain dopaminergic nuclei which innervate the basal ganglia, leading to abnormal patterns of activity in basal ganglia pathways. However, it is not so straightforward how such abnormal patterns of activity give rise to the wide-ranging motor and non-motor symptoms of Parkinson's, and yet it is important in the development of effective treatments. Here, we first investigate the phenomenon of sensory attenuation which traditionally describes the suppression of sensory input resulting from motor intent. We re-examine the literature with an explicit consideration of Task-Relevance and reframe sensory attenuation as the distinct context-dependent perception of two identical stimuli. We propose that this novel framing reconciles a previously contradictory literature whilst still incorporating the concept of movement modulating sensory input. Such reframing presents sensory attenuation paradigms as a useful means to gain insight into how people monitor task-relevant signals and utilise contextual cues during movement, a concept not well captured by current sensory attenuation theory.

Next, we explore the neural substrates of sensory attenuation and their somewhat paradoxical conjunctions with Parkinson's, which implicate the basal ganglia. Non-motor symptoms of Parkinson's are increasingly gaining recognition as an intrinsic part of the disease (Armstrong & Okun, 2020; MacDonald et al., 2019; Van Laar & Jain, 2004). This is supported by the recognition that basal ganglia circuits contribute to a plethora of non-motor as well as motor functions in a sensory capacity (Kaji, 2001; Lidsky et al., 1985; Nakajima et al., 2019; Robbe, 2018). Indeed, the true function of the basal ganglia eludes any single abstract model (Gale et al., 2008; Utter & Basso, 2008). However, by exploring sensory attenuation through the lens of Parkinson's, we begin to see that a reduced ability to filter environmental signals based on task-relevance creates a more complex landscape for the attendance to salient signals, just as such signals might be more beneficial to enhance movement and perception.

Finally, we examine current exercise rehabilitation techniques for further support of this notion, and consider how the most effective techniques might be working within this framework to place increasing demands on the processing capacity of depleted neurons in the basal ganglia rather than by bypassing them, and hence provide only a short-term solution. Implications for rehabilitation design are considered, pointing to sensory attenuation paradigms of a particular design to help monitor changes in important sensorimotor processing throughout an exercise programme.

2. Sensory Attenuation and Task-Relevance

2.1. Recent and Relevant Findings

Sensory attenuation usually describes the phenomenon whereby sensory input elicited by self-generated actions is reduced compared to sensory input generated externally. Anecdotally, the inability to tickle oneself has captured this phenomenon well. Elsewhere a force-matching task has been used to demonstrate that we appear to experience external forces as more intense than self-generated equivalents (Shergill et al., 2003; Walsh et al., 2011; Wolpe et al., 2018). Sensory attenuation can also be demonstrated using electrophysiological and brain imaging techniques whereby self-generated versus externally provided cues result in attenuation of somatosensory, auditory or visual evoked potentials (Horváth, 2015; Macerollo et al., 2016; Mifsud et al., 2018). Sensory attenuation has proved an interesting and robust phenomenon that appears to index selective information processing within multiple modalities. In addition to being used to explain why self-tickle is ineffective (Blakemore et al., 1998; Kilteni et al., 2019), sensory attenuation has been demonstrated when simply observing actions (Heins et al., 2020; Sato, 2008).

Some researchers have distinguished between the attenuation of sensory evoked potentials (SEPs) at the cortical level and behavioural outcomes that indicate altered perception of a stimulus (Macerollo et al., 2016, 2019). There is good reason for acknowledging the neurophysiological responses and the behavioural measures as the two do not always present harmoniously. For instance, in healthy older adults, sensory attenuation appears to increase with age when measured with a force-matching task (Wolpe et al., 2016), but the picture is a little more complex when investigating the neurophysiological data (Ogata et al., 2009). Furthermore, behavioural measures indicated equally good distinction by participants of smooth and rough surfaces in two conditions: active touch, where the participant moves their finger across the surface; and dynamic passive touch, where the participant's finger remains still while the surface is moved. However, fMRI analysis revealed distinct brain activation patterns for the two touch conditions (Simões-Franklin et al., 2011). Across different measures and studies, the common pattern is that identical stimuli have the potential to elicit different, context-dependent responses.

Sensory attenuation appears to be reduced in people with Parkinson's, displaying diminished differences between the intensity of self-generated and externally generated sensations. When comparing sensory evoked potentials from electrical stimulation of the thumb during movement and rest, people with Parkinson's who were off medication displayed reduced attenuation of the movement-initiated stimuli compared to healthy controls (Macerollo et al., 2016, 2019). Furthermore, in the same studies, dopaminergic medication restored sensory attenuation in participants with Parkinson's. In a Parkinson's-ON group, Wolpe and colleagues (2018) found that the amount of sensory attenuation was negatively related to motor symptom severity, but positively related to dopamine dose in a force-matching task. Parkinson's symptoms are of course a problematic confound when making assessments in movement-based paradigms such as the force-matching task, especially in the OFF-state, but the link between higher dopamine dose equivalent and increased sensory attenuation reinforces the connection to dopamine and its alteration in Parkinson's disease. In a speech task, people with Parkinson's also demonstrate reduced attenuation of auditory evoked activity 100 ms after sound onset when the participant speaks as compared to when the sound is externally produced (Railo et al., 2020).

2.2. Reconsidering Sensory Attenuation Theory

Prominent theories of motor control emphasise the role of predicted sensory consequences in sensory attenuation. It is believed that we construct an internal model of the world around us which is built-up through experience, and which allows us to make predictions about the results of our movements (Figure 1a). In optimal control theory, an efference copy of a motor command is used to predict its sensory consequence to overcome sensory delays, cancelling out self-generated feedback to better detect sensory information in the environment (Franklin & Wolpert, 2011). In active inference, which subsumes predictive processing theory, the prediction itself acts as a motor command and descends further down the neural hierarchy. It is compared to the current position of the body, which gives rise to a prediction error. The overall goal is to reduce prediction error, and therefore this prediction error can either travel back up to inform higher centres of the lack of movement and update the internal model, or the prediction error is attenuated and fulfilled by reflex arcs bringing about the movement (Brown et al., 2013). Perhaps confusingly, whilst sensory attenuation has previously been used to describe the resultant phenomenon of perceived intensity for self-generated sensations, here it describes the halting of an ascending prediction error. This halted ascension is enabled by lowering the precision of the prediction error.

Both theories utilise a Bayesian-like framework, where weighting of prior and current evidence is altered based on precision (Figure 1b). Using prior knowledge provides a way to estimate and better navigate an environment (Körding & Wolpert, 2004). Moving in an uncertain environment, such as playing sport at dusk, increases the reliance on prior information, and the Bayesian framework specifies how we can optimally combine multiple sources of information to better estimate an uncertain event (Körding & Wolpert, 2005). Learning a new skill or navigating a new environment naturally involves novel unknown information, but useful information can be better extracted using predictive signals formed in a Bayesian manner from previous experience (Wolpert et al., 2010).

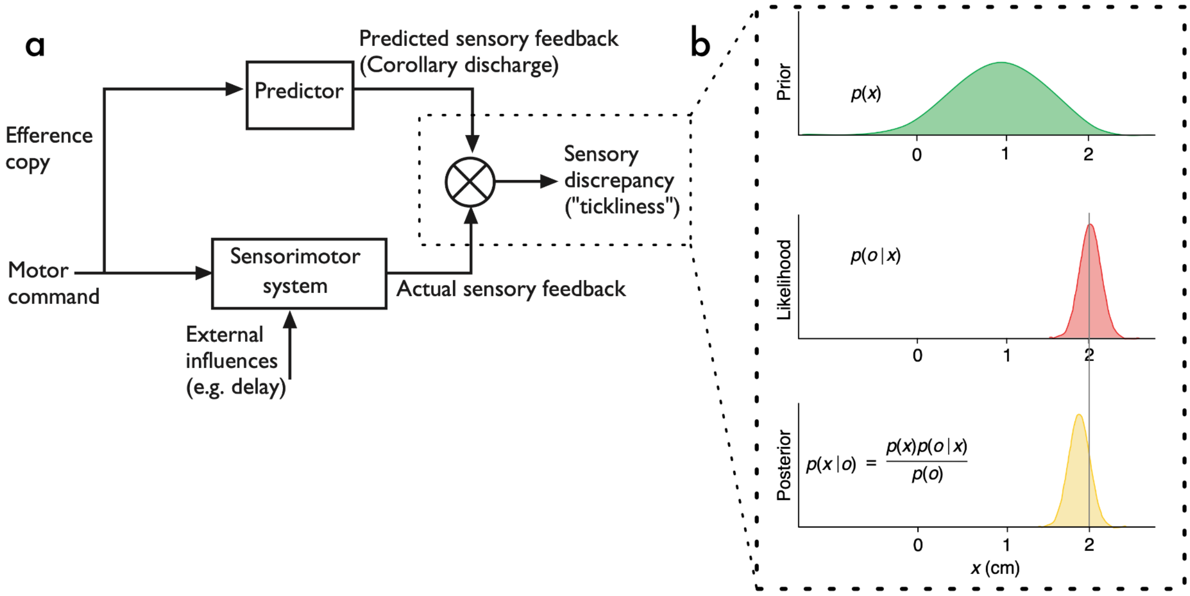


Figure 1 Schematics of the sensorimotor integration models used to explain sensory attenuation. **(a)** The diagram from Blakemore, Wolpert and Frith (2000) represents a typical internal forward model that underpins optimal control theory, proposes how a sensation, ticklishness, arises. Starting from a motor command, an efference copy is used to predict upcoming feedback to overcome noise and delay in the system, and is then compared to actual sensory feedback. The comparison of the two signals gives rise to the final sensation. **(b)** Bayesian integration is often used in optimal control and active inference accounts to model how this final sensation – ticklishness in this case – arises from the integration of predictive and sensory signals. The more certain the signal, the more influence it has on perception. The prior signal (*green curve, top,* $p(x)$) is the prediction or internal signal; the likelihood (*red curve, middle,* $p(o \mid x)$) is the new information, the sensory input. The resulting integration of the two, the posterior (*yellow curve, bottom,* $p(x \mid o)$), is informed by the noisiness of each signal, or the spread of the curves, and is determined here by Bayes' theorem ($p(x \mid o) = p(x)p(o \mid x)^{*}p(o)^{-1}$). Thus, the posterior (yellow curve) in this case more closely resembles the likelihood (red curve), though the estimate is still informed by the prior (green curve). Diagram from Körding & Wolpert (2006). To illustrate which part of the forward model Bayesian integration is used to describe, images in **(a)** and **(b)** have been connected with dashed lines added by the current author. The integration of a prior signal into sensation is a crucial concept when considering sensory attenuation: sensory input is integrated differently due to priors which can include motor involvement.

While the optimal control and active inference theories similarly predict a wide array of empirical findings, they do differ in the way that sensory attenuation during movement is described. In optimal control theory, sensory attenuation is a result of accurately predicting the sensory consequences of movement. The predictions are made with the efference copy of the motor command, providing an informative internal signal (Kilteni et al., 2020). This underpins various benefits such as overcoming noise and delays in the sensorimotor system, and heightens detection of unpredicted and potentially useful/dangerous stimuli. In active inference, sensory attenuation is not just a beneficial by-product of movement, but essential in bringing it about (Brown et al., 2013). Here sensory attenuation refers to the down-weighting of the precision of sensory signals to facilitate the fulfilment of predictions by reflex arcs. The reduced precision of a sensory signal means a reduced perception of it at higher levels during movement onset; or, put another way, reduced sensory attenuation.

Evidence from studies of people with schizophrenia suggests sensory attenuation is altered across different modalities (Shergill et al., 2014), and so measures may capture some phenomenon resulting from the fundamental way our brains engage in perception (Clark, 2015). However, the presence of non-motor contributors to sensory attenuation (Saradjian, 2015) challenges optimal control theory which ultimately only describes a perception dependent on action. It has been maintained that self-generated sensations are attenuated, making way for externally-generated sensations to be facilitated (Blakemore et al., 2000) but this neat distinction does not sufficiently explain the specificity of selective sensory modulation amongst self-generated signals based on factors such as spatial location (Chapman et al., 1987) or task-relevance (Saradjian, 2015). And active inference, which places gating of sensory afference at an inseparable level from movement does not comfortably explain why sensation can often be enhanced by movement (e.g., Simões-Franklin et al., 2011; Saradjian, 2015), though predictive processing more generally does make room for non-motor influences on perception (Clark, 2015; Hohwy, 2016).

Action, even when including imagined and observed action, is not the only factor that modifies perception. In a cleverly designed experiment, Heins and colleagues (2020) trained participants in hurdling and tap dancing—two complex movements that generate sounds as a consequence of foot contact with the floor. After an extended period of training, participants watched point-light videos of themselves during an fMRI recording, being tasked with rating the subjective quality of their performance. Scrambled video and audio were used to gauge sensitivity to errors. More sensory attenuation, as indicated by reduced activation of the auditory cortex and more reactive ratings to sounds when scrambled, occurred in the tap-dancing condition. This was argued to be due to the different relationships that sound posed to the performance of the different tasks. The authors argue the importance of sounds elicited by tap-dancing is greater to task performance and are therefore goal-related, unlike the by-product sounds of hurdling. Whilst active modulation of sensory input likely occurred in both conditions, evidence of stronger modulation for tap-dancing supports the notion that factors other than self-generation mediate sensory attenuation.

Reduced neural responses in the ventral visual stream to images based on learned regularities—that is, only the expectedness of the image was manipulated—support the view that sensory input is modulated by non-motor factors also (Dogge et al., 2019; Kaiser & Schütz-Bosbach, 2018; Richter & de Lange, 2019). There has also been criticism of efference copy models for characterising motor commands as context-independent (Gandolla et al., 2014) with studies demonstrating motor cortex excitability changes with sensory stimulation (Léonard et al., 2013; Roy & Gorassini, 2008). Furthermore, self-generation can actually heighten as well as attenuate neural responses to sensory stimuli (Reznik & Mukamel, 2019; Saradjian, 2015; Saradjian et al., 2013), which also challenges active inference as a model to explain all aspects of sensory attenuation. Whilst predictive processing accounts are flexible enough to incorporate various signals from the current context, a "generalised and multi-modal suppression of sensory input from the effector to enable movement" (Limanowski et al., 2020, p. 8) does not lend itself to the differential attenuation or augmentation of sensory gain, nor do models arguing for inflexible sharpening effects from movement (Yon et al., 2018).

2.3. Scope of the Dominant Theories

While the active inference and optimal control models are useful, and appear anatomically viable (e.g., Adams et al., 2013; Holland et al., 2020), they so-far lack a solid specification in regards to the neural substrates involved in sensory attenuation itself. Rather, the behaviour consequence of sensory attenuation has been used to explain certain Parkinson's symptoms, centred on a global decrease in sensory precision of internal predictive signals which increases reliance on external sensory signals (Brown et al., 2013; Wolpe et al., 2018). This explains how increasing the salience of external cues—such as lines on the floor to improve gait (Beck et al., 2015; Morris et al., 1994, 1996)—are needed to overcome movement deficits. However, succesful longer-term rehabilitation programmes have also taken, in some ways, the opposite approach by reducing visual input during training sessions (Sage & Almeida, 2009, 2010). And while reduced sensory attenuation in Parkinson's (Wolpe et al., 2018; Macerollo et al., 2016, 2019) indicates a deficit in successfully modulating sensory input, it is not clear, without further work at least, how this principle could inform therapeutic approaches. As we discuss in the final section, such theories do not entirely explain the rehabilitation effects of all therapies.

Such models may be limited in scope but are still useful in describing a mechanism that explains motor-related attenuation that need not be constrained to a single neural circuit. As far back as 1964, Giblin reported reduced SEPs during voluntary movement and the gating of sensory afferent signals during movement is well documented (for a review, see Saradjian, 2015). The presence of such gating does not mean worsened perception during movement though, as many tasks have since shown. The classic definition describes sensory attenuation as resulting only as a consequence of self-generation, emphasising a suppression effect, which is itself limiting. Across the literature in the sensory attenuation field though, what the tasks do is measure how sensory stimuli are being modulated by organisms.

2.4. Factors Affecting Sensory Attenuation

Sensory attenuation measures the distinct context-dependent perception of two identical stimuli and, in doing so, captures not only our internal model of prediction, but also the salience and task relevance ascribed to each sensory input. As sensory attenuation is diminished in Parkinson's, this raises the question of which aspect of this multi-faceted process is affected by basal ganglia dysfunction: from sensorimotor integration, to salience attribution, through to predicting sensory consequences. Intriguingly, while sensory attenuation is reduced in Parkinson's, it appears to steadily increase with healthy ageing (Wolpe et al., 2016). The reason for this remains unclear, but it shows that sensory attenuation is both sensitive enough to track change over time, and also potentially alterable: might it be possible to alter the sensorimotor processes captured in a sensory attenuation paradigm?

What factors do affect sensory attenuation, and what insights might they offer? The feeling of body ownership has been investigated using the rubber hand illusion where a participant is led to believe a fake hand belongs to them. Body ownership was shown to have a sensory attenuation effect, whereby somatosensory stimulation triggered by the fake hand was experienced comparably to stimulation triggered by the participant's own hand, both of which were experienced less intensely than a standard externally-generated condition (Pyasik et al., 2019). Ehrsson et al. (2004) argues body ownership arises from multi-sensory signals from the body occurring synchronously. Likewise, Kilteni and Ehrsson (2017) found that sensory attenuation was diminished in a self-generated force-match when the hands were held apart from one other, demonstrating the importance of congruence between visuospatial context and action. Sense of agency, while strongly connected to body ownership, arises from a movement feeling like it has been controlled by the self (Pyasik et al., 2019). Sensory attenuation is often assumed to give rise to sense of agency; that is, processing self-generated stimuli differently to externally-generated stimuli contributes to the sense of agency (Kilteni & Ehrsson, 2017). Indeed, sense of agency and sensory attenuation are both seen to be altered in schizophrenia (Jeannerod, 2009; Shergill et al., 2005).

Of course, movement and sensation are intrinsically linked, and the context-dependent motor symptoms in Parkinson's support this notion: freezing-of-gait can be exacerbated by changing door-frame width (Almeida & Lebold, 2010), tactile triggers can help overcome akinesia (Quintyn & Cross, 1986), and visual and auditory cues can enhance gait (del Olmo & Cudeiro, 2005). Sensory attenuation experiments tend to focus on the attenuation of sensation due to movement, but other forms of perception can also be heightened as a result of movement. For instance, the execution of actions can benefit visual perception (Miall et al., 2006), and movement training, which results in improved action fluency, enhanced subsequent visual discrimination (Guo & Song, 2019). Sherwin and Sajda (2013) found that expert musicians are better than novices at detecting anomalous sounds when listening to music; they recorded cortical activity corresponding to the playing hand giving rise to the possibility that imagined movement that mimicked the music enhanced auditory perception. Evidence for the dependence of perception on action (in addition to the descriptions of motor symptoms in Parkinson's being dependent on perception) support codependent and bidirectional links (Bosch, 2020; Guo & Song, 2019; Wykowska & Schubö, 2012).

It might be logical, given the above, to assume that a deficit in sensation such as body awareness would be a crucial factor affecting movement in Parkinson's (Quintyn & Cross, 1986). However, a deficit in proprioception is not itself enough to explain the motor symptoms of Parkinson's. Kammers and colleagues (2009) found motor control to be unaffected when using the rubber hand illusion to create false information about the hand position. Here, it is possible movements were far from complex, and accurate proprioception may have been restored the moment movement was initiated. However, perception may arise from different levels of the neuraxis, whereby a sense of agency may be experienced at a conscious level while action adjustments occur automatically (Jeannerod, 2009; Wolpe et al., 2020). This is indeed consistent with the notion of low-level attenuation of sensory precision to fulfil actions described in active inference, while other predictive processes can still influence perception in higher regions (Brown et al., 2013; Wolpe et al., 2020). In fact, predictive processing accounts might even explain both sense of ownership and sense of agency, whereby the former arises from reducing prediction error by updating the internal model (perceptual inference), and the latter arises from reducing prediction error with action (active inference) (Braun et al., 2018). So, while body awareness can interact with sensory attenuation, movement need not invariably be disrupted by disturbances occurring in parallel that involve separate regions (Humprhies et al., 2007).

Finally, Redgrave and colleagues (2010) distinguish between forms of motor control enacted by the basal ganglia that support the idea of layered control, maintaining the notion of bidirectional links between movement and sensation. It was argued that the basal ganglia loops are involved in distinct functions of goal-directed and habitual motor control, of which the latter is most affected in Parkinson's. In Redgrave and colleagues' analysis, goal-directed control describes the conscious, cognitive control of movement, which might then be more easily disrupted when one's attention is diverted. Habitual control describes the lower level, more inflexible, stimulus-response movements. This distinction is important in explaining why movement in some contexts, often more demanding ones, is worsened in Parkinson's. However, goal-directed behaviour should not be confined to describing only that performed under conscious, attentional control; movement can arise from subcortical circuits to achieve a goal, without the movement being controlled cognitively. Rather, there is surely the capacity for a goal encoded at a cortical level to have the general effect of filtering the environment for fast, responsive movements to then achieve (e.g., "walk up the stairs"), in addition to a specific cognitive control (e.g., "move my leg") (Nakajima et al., 2019; Robbe, 2018). It is the effect of this concept of sensory filtering by goal—or task—that we now examine.

2.5. Task-Relevance in Sensory Attenuation

Often overlooked in sensory attenuation studies are the effects of task demands on sensory processing. It might even seem obvious that task demands affect how we interact with our environment; the need to filter through a vastly complex and dynamic environment is crucial for an organism's survival, and it is often considered in ecological psychology that we have evolved to do this in a task-relevant manner (Cisek, 2007; Cisek & Pastor-Bernier, 2014). Proponents of the constraints-based approach in sports coaching strongly emphasise the importance of the three interacting elements of task, environment and organism (Bosch, 2020) (Figure 2). However, sensory attenuation experiments largely only consider organism and environment interactions, and explain changes in sensory processing in terms relating to organism-centred factors such as movement, expectation and attention.

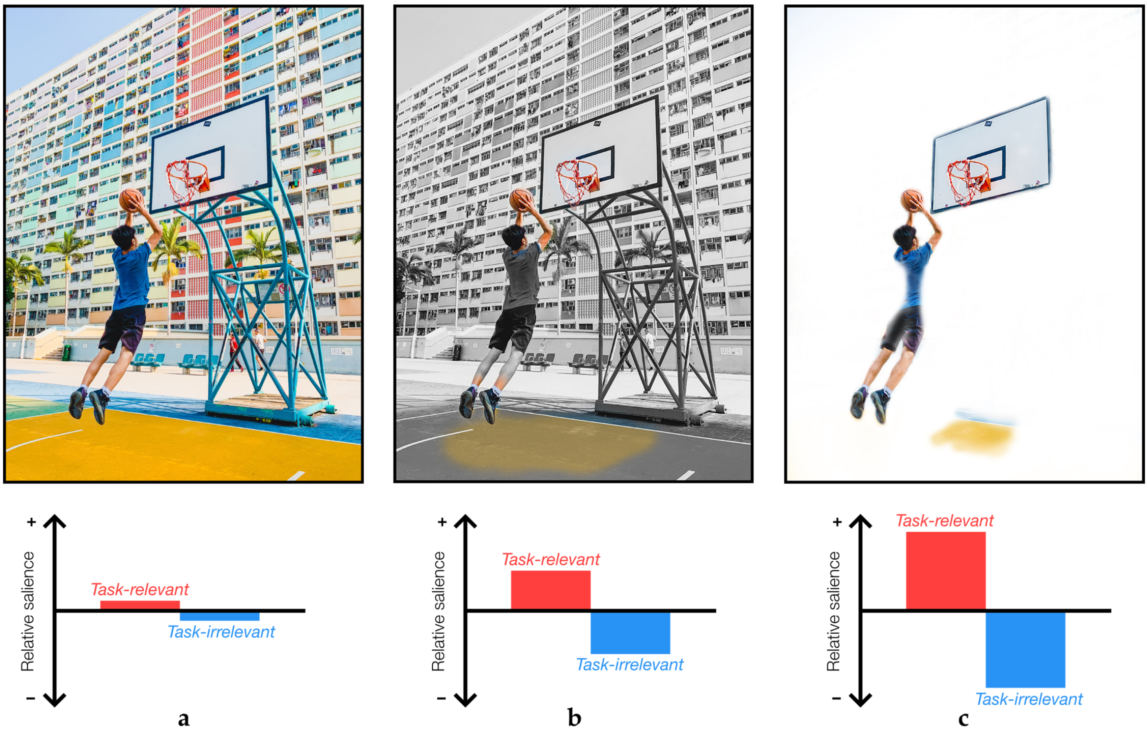


Figure 2. Visualising the effects of normal sensory attenuation when attempting to score in basketball, with schematic plots of the relative salience of task-relevant and task-irrelevant features: (**a**) the full, unfiltered scene is full of information, with little difference between relevant and irrelevant features; (**b**) but we are able to selectively filter information relevant to the task such as the ball, the basket, sense of the body in space relative to the ground and backboard; (**c**) salience of important stimuli may then be further enhanced through the use of contextual information; for example, using the proximity of the ball to the basket. The distance to the floor is not immediately as important, but will be once the ball has been released and the player lands. Original photo provided by Fahrul Azmi.

Task conditions affect our responses to stimuli. Staines and colleagues (2002) measured responses in the human brain using fMRI, finding that during simultaneous tactile stimulation to both hands, only task-relevant stimulation increased activity in contralateral primary somatosensory cortex. In a more complex task, Riley and colleagues (1999) demonstrated improved postural sway when participants were instructed to pinch and stabilise a curtain as opposed to simply making contact with it, indicating altered behavioural use of a similar tactile input when it becomes more important for the task at hand. Task complexity itself can affect the neural response to stimuli; Reiser and colleagues (2019) used a mobile EEG set-up to show that auditory evoked potentials during an oddball paradigm, as well as performance of the task, were altered when participants walked an obstacle course as compared to when they walked without obstacles. Though a small motor response was required for target sounds, it does suggest that there is competition for attentional resources in a cognitive-motor dual-task paradigm, and that more complex motor tasks may depend more on such task-relevant filtering, especially in real-world environments.

The force-matching paradigm reveals the use of distinct contextual information in perceiving and responding to an identical target stimulus. The task in both the direct matching condition and the indirect matching condition is to match a target force, so the objective remains consistent. It has been suggested that the direct condition benefits from predictive mechanisms more so than the unusual indirect condition where the hand generates the force with a joystick or slider (Shergill et al., 2003). Interestingly, people with schizophrenia have been suggested to display increased weighting of internal predictions (Teufel & Fletcher, 2020; Teufel et al., 2015), whereas internal predictive signals are of reduced precision in Parkinson's (Brown et al., 2013; Wolpe et al., 2018), yet both appear to show less force-overcompensation in the force-matching task compared to healthy controls (Wolpe et al., 2018; Shergill et al., 2005, 2014). The key pattern here then is that two stimuli in two distinct contexts are perceived less differently in a disease state—that is, they converge—and this difference results from contextual information once task has been controlled for, pointing to compounding effects on sensory processing (Figure 2 and Figure 3).

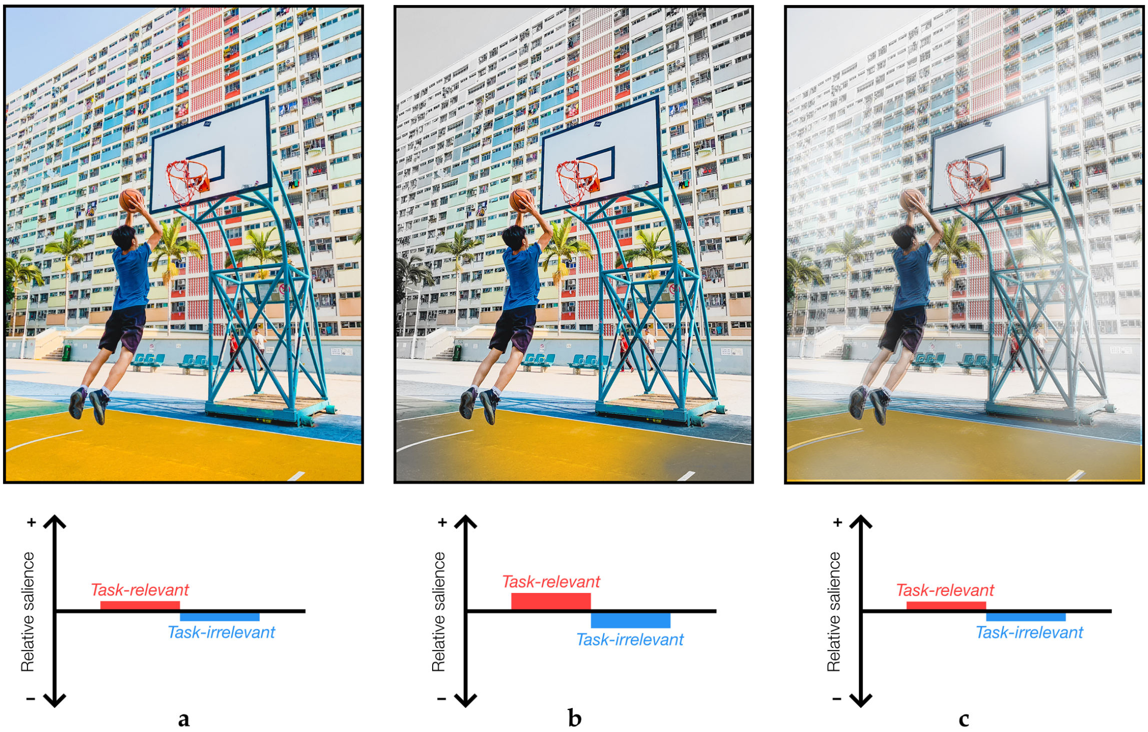


Figure 3. Visualising pathological sensory attenuation when attempting to score in basketball with deficits in task-relevant filtering and the utilisation of contextual information, with schematic plots of the relative salience of features

important for the task: (**a**) the full, unfiltered scene is full of information; (**b**) task-relevant filtering is only partially effective, failing to filter out information irrelevant to the task and leaving little difference between task-relevant and task-irrelevant information; (**c**) this makes it harder to use contextual information to further enhance sensation, and irrelevant information remains similarly salient. The illustration made might also be considered with other examples, from everyday tasks such as the oft-considered 'picking up a mug to drink' example, to dance moves and other sporting scenarios.

Further to this point, Bolton and Staines (2012) found reduced task-relevant modulation of sensory input during a tactile discrimination task in older adults compared to young adults. However, force-overcompensation—the sensory attenuation index in a force-matching task—was found to increase with age (Parthasharathy et al., 2021; Wolpe et al., 2016). This supports the notion of the force-matching task capturing the ability to utilise contextual information, such as hand position, to perceive a target stimulus and guide movement.

Perhaps this ability to utilise a contextual cue is captured by pre-pulse inhibition (PPI) and temporal discrimination tasks. In PPI paradigms, people with Parkinson's show reduced gating of auditory stimuli whereby a preceding stimulus normally attenuates the response of a subsequent stimulus when they are presented at a higher frequency (Gulberti et al., 2015). Somatosensory temporal discrimination threshold (STDT) tests have also revealed people with Parkinson's have higher thresholds when discriminating between two tactile stimuli presented in close succession (Conte et al., 2013). Researchers have pointed to a role of the basal ganglia in timekeeping operations (Bradley et al., 2012; Rao et al., 2001). Perhaps in the absence of explicit time information, the basal ganglia utilise disparate signals from across the brain to "stand-in" (Turner & Anderson, 2005), form a "consensus" (Beeler & Dreyer, 2019), and modulate a response accordingly. Indeed, the striatal networks appear to outperform the prefrontal cortex in timekeeping (Bakhurin et al., 2017). This points to the capacity to integrate useful contextual information for optimal behaviour and, in Parkinson's, could underpin performance deficits in PPI and STDT paradigms.

3. Neural Substrate

3.1. Reconciling Discrepancies in Studies Investigating the Neural Substrates of Sensory Attenuation

With the basal ganglia heavily associated with sensorimotor control, it is no surprise that sensory attenuation is affected in both Parkinson's and schizophrenia (Shergill et al., 2005, 2014), both of which are disorders of the basal ganglia. It has even been postulated that fronto-striatal circuits may help explain changes of sensory attenuation in healthy older adults (Wolpe et al., 2016, 2018). However, cortical regions such as the supplementary motor area have also been implicated (Jo et al., 2019), as has the cerebellum (Blakemore et al., 2000; Kilteni & Ehrsson, 2020), and the thalamus (Staines et al., 2002). Initially this may point to a non-specific cross-modal sensory attenuation phenomenon that describes a generalisable principle of perception and, while this may hold some truth, there is an important role for the basal ganglia in actively modulating sensory input. In fact, by examining the available literature concerning the neural basis of sensory attenuation, there appears to be a striking discrepancy that relies on the variety of tasks being used.

The findings from fMRI studies investigating sensory attenuation can broadly be split into those that show involvement of the cerebellum, those that demonstrate basal ganglia involvement, and those that show both. Pointing to cerebellar involvement, Kilteni and Ehrsson (2020) demonstrated attenuated activity of the cerebellum and secondary somatosensory cortex, and increased functional connectivity of the two structures, in healthy young adults for self-generated sensations compared to externally generated sensations, replicating some of the findings of Blakemore and colleagues (2000). Likewise, Boehme and colleagues (2020) compared people with ADHD and neurotypical controls in a self- vs. other-touch task, finding not only a difference between groups in the primary somatosensory cortex, but also an increased BOLD signal of the cerebellum and prefrontal cortex amongst other areas when the experimenter administered touch compared to self-touch.

Capturing a combination of both basal ganglia and cerebellum involvement, a comparison of people with schizophrenia and healthy controls (Shergill et al., 2014) demonstrated that the cerebellum was active in both groups during a modified force-matching task. They speculated that the cerebellum seemed to be performing a comparator function. However, they also found increased activation of the caudate for healthy controls when sensation was synchronous with movement, and increased cerebellar activation when sensation was delayed (along with other differences across condition and group). Simões-Franklin and colleagues (2011) compared active, passive and dynamic-passive touch for rough surface detection, reporting greater activation of the cerebellum and lentiform nucleus for the active condition compared to the passive conditions.

Supporting basal ganglia involvement, Leube et al. (2010) compared people with schizophrenia to healthy controls during a task comparing visual consequences of self-generated actions in conditions of delay and no delay. They found reduced activation of the putamen in patients which accompanied a reduced ability to discriminate the delayed action consequences. Nonetheless, to add to the assortment of findings, Ackerley and colleagues (2012) reported altered activations across a range of sensory areas elicited by a paint brush on the arm under self-touch and passive touch conditions, but not the basal ganglia or the cerebellum.

This somewhat mixed set of findings may best be explained by the variety of tasks used. The studies attempting to recreate the force-matching tasks have needed to heavily modify the task for use in (usually) an MRI scanner, and the constraints of such neuroimaging techniques make altered paradigms necessary. Movement may also be controlled differently in such paradigms, and is often triggered by a very simple visual cue, without the clear task goal in the behaviour-only paradigms where matching a previous force in a more complex environment demands active selective filtering using memory and task information in the absence of simple visual cues.

The self- vs. other-touch paradigms appear more consistent in design (Blakemore et al., 2000; Boehme et al., 2020; Ackerley et al., 2012) with some commonalities in findings such as modulation of primary somatosensory cortex, but also differences. Movement is still instructed with an on-screen cue which might not be so problematic in this case, but there is no clear task goal and therefore no monitoring of performance or control of attention which may affect perception as well as the way movement is being initiated (Ackerley et al., 2012).

Perhaps the most informative designs are those which embrace the reality of a different set up and use videos of participants' movements in the scanner, and/or manipulate visual or auditory information to alter its predictability (Heins et al., 2020; Leube et al., 2010). This builds on the assumption that there is an attenuation effect from observing action as well as performing it (Sato, 2008).

Heins and colleagues (2020) only compared conditions where a strong sensory attenuation effect was expected, but Leube et al. (2010) compared healthy controls and people with schizophrenia. Participants opened and closed their hands which was filmed and played back for them to see in the scanner with no delay or with small delays to create congruent and incongruent action consequences. Not dissimilar to Heins et al. (2020) where participants rated movement quality which worsened with scrambled videos, participants were tasked with detecting the synchrony of the video with their movements (Leube et al., 2010). Those with schizophrenia were more likely to incorrectly perceive movements as asynchronous, and sometimes also incorrectly perceived asynchronous movements as synchronous. Such error detection paradigms used in these two studies index the ability to distinguish self from externally generated stimuli captured in sensory attenuation measures, with better detection thresholds during related movement (Chapman et al., 1987; Eliades & Wang, 2008; Synofzik et al., 2010). Activation of putamen and thalamus was reduced in patients compared to controls during this error detection task during distinct delay and no-delay conditions (Leube et al., 2010).

There are of course challenges in collecting this type of data in those with movement disorders, but considerations should be made for the different types of motor control that are likely being invoked in these designs. Externally triggered movements, such as when a finger-tap is elicited by an on-screen stimulus (Kilteni & Ehrsson, 2020), have been strongly associated with cerebellar circuits, whereas internally generated movement—that is, movement elicited and guided more so by memory signals—are associated with basal ganglia circuits (Turner & Anderson, 2005; Martinu & Monchi, 2013; van Donkelaar et al., 2000). If the basal ganglia are predominantly involved in memory-guided movement, and filter information for action in a task-relevant manner (Robbe, 2018), then investigation of sensory attenuation in basal ganglia disorders should consider task design, including sensory cues, carefully. Cerebellar circuits are also altered in Parkinson's though, which is thought to be pathophysiological rather than compensatory (Martinu & Monchi, 2013). Perhaps these systems might work in a complementary fashion whereby global task-dependent filtering decomposes a complex environment into smaller and simple components that can be responded to with other more appropriate systems such as the cerebellum (Yamazaki & Lennon, 2019). A future direction for research in sensory attenuation might be to compare attenuation during different forms of motor control for further insight into its neural underpinnings.

3.2. The basal ganglia through a Sensory Lens: Task-Relevant Signalling

Movement can vary across environments, perhaps radically demonstrated by athletes in the phenomenon of choking in sport (Bosch, 2015) and even sports-related dystonia with its variety of quirky alleviating manoeuvres (Sadnicka et al., 2018; Lenka & Jankovic, 2021). Motor symptoms in Parkinson's are also responsive to sensory environment and task demand, which are exacerbated in more challenging environments (Almeida & Lebold, 2010; Ehgoetz Martens et al., 2014, 2015; Klockgether & Dichgans, 1994; Quintyn & Cross, 1986) but alleviated when aided by sensory cues that help navigate an environment (Beck et al., 2015; Chawla et al., 2020; Morris et al., 1994, 1996; Spaulding et al., 2013). This leaves a narrow set of often impractical environments where free-flowing movement is possible. Importantly though, this demonstrates that Parkinson's is not purely a kinetic disorder, and rather that the basal ganglia has a sensory processing function that heavily impacts movement (Kaji, 2001; Lidsky et al., 1985; Robbe, 2018; Schneider, 1984).

Before movement is even considered, the basal ganglia appear influential in task-relevant sensory filtering to achieve behavioural goals. Nakajima and colleagues (Nakajima et al., 2019) describe a need for animals to filter relevant stimuli through sensory noise. It has been shown that the need to engage sensory filtering can depend on the amount of sensory noise and also behavioural goals (Gilbert & Li, 2013). Goal-related movement has often been functionally linked to the basal ganglia (Gale et al., 2008), but such behaviourally-relevant sensory filtering has also been demonstrated in non-motor aspects of behaviour. McNab and Klingberg (2008) demonstrated basal ganglia involvement in filtering visual stimuli, and suggested that working memory capacity may be related to how well (ir)relevant information is filtered, finding that increased globus pallidus activity correlated with increased working memory capacity. It has also been demonstrated that memory for deep-encoded words is impaired in Parkinson's compared to shallow-encoded words, with higher beta oscillations (an indicator of reduced novel processing) during deep-semantic processing, suggesting a difference in the initial encoding phase (MacDonald et al., 2019). In a recent study, evidence was found for a pathway between the prefrontal cortex and the basal ganglia which mediates top-down filtering of irrelevant stimuli based on task demand and not movement (Nakajima et al., 2019).

Considering a task-dependent sensory processing role appears fruitful in motor control studies too. Neuronal recordings have shown that the basal ganglia respond to sensory stimulation more prominently when they are relevant for upcoming motor control (Kaji, 2001). This may provide a mechanism to explain how basal ganglia lesions mostly affect automatic movements that require sensory guidance (Kaji, 2001). Schneider (1987) meanwhile argues for a transient and adaptable system which respond differently to stimulation during different tasks. Schneider found that in cats, neurons in the entopeduncular nucleus (homologous to the internal segment of the globus pallidus in humans) and the caudate nucleus do not respond to facial stimulation or jaw movement, but those cells do become responsive if they are stimulated during ingestion-related jaw movements. These findings suggest a more complex and dynamic relationship to movement, and the basal ganglia system is well placed to monitor internal signals relevant to task demands with input from across the cortex (Andres & Darbin, 2018).

Understanding the role of the basal ganglia in a sensory capacity begins to make sense of some of the context-specific motor symptoms in Parkinson's, and lays a foundation for the existence of a common mechanism to underlie the vast array of motor and non-motor symptoms. Basal ganglia disorders are themselves diverse, expressing a range of motor, cognitive and emotional symptoms (Andres & Darbin, 2018; Schneider, 1984; Utter & Basso, 2008). It is worth considering then, that damage to the basal ganglia in Parkinson's affects processes that underpin environment-specific motor symptoms, in addition to non-motor symptoms. A viable alternative might be that non-motor symptoms arise from the overload of more cognitive pathways in Parkinson's which may be required to control movement due to degeneration of circuits involved in habitual (lower-level, stimulus-response) control of movement (Redgrave et al., 2010). There is evidence however of both reduced storage capacity and an impaired ability to filter out irrelevant information that underlies such non-motor functions as visual working-memory (Lee et al., 2010), which hints at a more general sensory filtering function of the basal ganglia that could underpin some motor and non-motor Parkinsonian symptoms.

3.3. Sensation to Action

How might impaired sensory filtering be important not just in enhancing movement more generally, but the initiation of actions? A possible mechanism has been demonstrated in early animal experiments. Researchers showed that electrically stimulating the lateral hypothalamus of a cat would sensitise the perioral area, so that touching the area around the mouth would cause the animal to orient toward the stimulus and open its mouth. This reflex would only work when the hypothalamus was stimulated (Flynn et al., 1971), so by modulating sensory processing, movement was initiated. In an excellent review, Robbe (2018) argues against the basal ganglia as an action selector. Instead, the basal ganglia continuously track sensorimotor signals, which can contribute to action production. Such a sensorimotor transformation is demonstrated in membrane potential recordings of medium spiny neurons (MSNs) in mice trained to lick a reward spout following a whisker deflection (Sippy et al., 2015). The MSNs depolarised during whisker deflection after training, and optogenetic stimulation of those neurons was able to substitute for the whisker deflection and elicit the licking action. During whisker deflection though, the MSNs were more active for successful trials compared to unsuccessful, indicating that a motor response could be elicited with a predictive sensory stimuli (Robbe, 2018). Interestingly, it was the MSNs in the direct pathway—the pathway that is underactive in Parkinson's—that depolarised with the whiskers and predicted a licking response (Sippy et al., 2015).

3.4. Sensorimotor Integration

The basal ganglia are strongly positioned to monitor internal and external signals, contributing to motor responses. The generation of actions appropriate to task and environment requires integration of signals from multiple sources (Robbe, 2018; Haber & Calzavara, 2009). Motor symptoms in Parkinson's reveal deficits in sensorimotor integration. Consider the finding that people with Parkinson's display difficulty tracking a visual target on screen by using jaw movements to control another onscreen signal (Connor & Abbs, 1991). There are multiple sources of information that require monitoring and integration to successfully perform the task, both internal and external, across modalities. However visually guiding movement is often helpful or even necessary in Parkinson's, and motor deficits can be overcome with visual cues (Beck et al., 2015; Morris et al., 1994, 1996). One explanation might be that reducing the demands on integration processes of the basal ganglia, achieved by using only vision to guide the foot to a line on the floor for example, restore functionality (Vitório et al., 2014). In support, bilateral integration from whisker stimulation by MSN was found to be diminished in dopamine-depleted mice (Ketzef et al., 2017). Alternatively, visual cueing strategies might make use of alternative and more intact pathways (Martinu & Monchi, 2013; Sage & Almeida, 2010), but it is intriguing that using visual information during movement in different ways can have opposing effects on movement quality.

With a wide range of inputs to the basal ganglia and a role integrating multimodal information for action, studying oscillatory activity across neural systems can prove useful to track complex processing dynamics. Oscillatory changes in Parkinson's have been well established, notably in the basal ganglia (Brittain et al., 2014; Jenkinson & Brown, 2011; Brown, 2006) but also in cortex (Pollok et al., 2012; Marsden et al., 2001). Of particular interest, there has been a focus on the modulation of activity within the alpha/mu (8–12 Hz) and beta (13–30 Hz) frequency bands (Brittain et al., 2014). Focussing on Parkinson's, the time-course of beta has been shown to index movement kinematics (Little et al., 2012), the severity of motor impairment (Chen et al., 2010), and cortico-muscular coupling at beta frequencies is reduced in both early and late stages of Parkinson's (Pollok et al., 2012; Roeder et al., 2020). These observations reinforce arguments we have made about the role of the basal ganglia, as well as offering insight into changes in sensorimotor processing in Parkinson's. Changes in neural synchrony, by means of phase-resetting or neural entrainment, offer potential mechanisms for instigating differential responses to sensory stimuli (Bauer et al., 2020). Beta synchrony in the basal ganglia is reduced during movement, but also in response to cues that are predictive of movement (Brittain & Brown, 2014). Whilst it has been argued that beta synchrony indexes the likelihood for a need for a new action (Jenkinson & Brown, 2011), it might more fundamentally signify the capacity for processing new information (Brittain et al., 2014) which resultantly may facilitate action. Excessive beta synchrony impedes response to novel demands, creating a neural landscape unable to match the complexity of surrounding environments (Andres & Darbin, 2018; Brittain et al., 2014), harming vital task-dependent sensory filtering and sensorimotor integration processes necessary for appropriate behavioural responses (Figure 3).

4. Establishing Principles for Rehabilitation

How do we enhance such vital task-dependent sensory filtering and sensorimotor integration processes? Returning to the motor control theories which point to an imbalance between predictive and sensory signals, we can see how altering information in the sensory environment can affect movement. Sensory cues such as lines on the floor or sounds can alleviate symptoms during walking (Beck et al., 2015; Quintyn & Cross, 1986). Rudimentary sensory cues often simplify and contextualise the perceived environment and can be a useful tactic to improve motor performance, possibly by improving the precision of the sensory input and reducing the demand on "priors" (Figure 1). Such rudimentary cues which simplify the environment, however, do not necessarily train the ability of the nervous system to filter and extract useful information in more complex surroundings. Some attempts at cueing have been promising as a form of rehabilitation (Badarny et al., 2014; de Oliveira et al., 2021; Morris et al., 1994, 1996) but the long term benefits are not clear (Nieuwboer et al., 2007; Spaulding et al., 2013). I have thus far argued that the basal ganglia play a role in task-relevant filtering and then also in utilising useful signals for ongoing behaviour: how then, might we exercise this system and how else can we consider rehabilitation approaches, beyond cueing strategies that more obviously and immediately alleviate symptoms?

In one approach, Sage and Almeida (2009, 2010) utilised a form of exercise called PD-SAFEx where limb movements and gait exercises were performed in low-light conditions, increasing attention to proprioceptive input for guiding movement, forcibly shifting it away from visual input. The researchers found the programme improved symptom severity scores at the end of the programme and after a non-exercise washout period of 6 weeks. Another example of a promising rehabilitation method is forced-exercise cycling (Ridgel & Ault, 2019). An early example of this illustrates the concept well; Ridgel and colleagues (2009) had participants perform tandem cycling where they had to maintain the same high cadence dictated by the other cyclist. Participants with Parkinson's improved their symptom severity scores after an 8-week training programme.

There is a deficit in Parkinson's first of using task-relevance to filter complex environments which is mediated by the basal ganglia (Cisek, 2007; Nakajima et al., 2019; Robbe, 2018; Brown et al., 1997) and then to use this information as useful contextual cues for behaviour (MacDonald et al., 2019; Turner & Anderson, 2005; Beeler & Dreyer, 2019; Schneider, 1984). The two rehabilitation approaches described here – low-light proprioceptive and walking training (Sage & Almeida, 2009, 2010) and forced-exercise cycling (Ridgel & Ault, 2019; Ridgel et al., 2009) – may be training task-relevant filtering and contextual cue integration reliant on basal ganglia function. PD-SAFEx participants have reasonably clear task-goals to make use of during sessions such as gait training involving one high knee each step and opposite hand touching ear. Participants complete these movements in low-light conditions where vision can be excessively relied upon (Abbruzzese & Berardelli, 2003).

Similarly, participants in Ridgel and colleagues' forced-exercise protocol have a very clear task goal to match the cadence of the paired cyclist, which cultivates skilled sensorimotor integration of one's own and another's movement in a dynamic situation. Other approaches to exercise rehabilitation may be more naturally training sensory filtering capacities, such as rock-climbing (Langer et al., 2021) and dance (Bek et al., 2020). Crucially, a route to effective recovery (or slowing disease progression) that involves movement in complex sensory conditions can at least be fruitful. A variety of routes are worth considering, especially when strategies do not have the same effect for every person and cueing tricks can lose effectiveness over time (Nonnekes et al., 2019).

Nonnekes and colleagues (2019) emphasised the inventiveness of people with Parkinson's in developing effective compensatory strategies to overcome gait deficits. Such strategies might be considered more effective because they are developed within the specific environment that the person navigates. As the context of an event affects our response to it, rehabilitation in daily-life settings might be appealing. However, this could highlight the importance of the compatibility of a strategy, and not necessarily the concept of transfer specificity. When considering specificity, it is important to recognise not just that we are better at recalling something in the same physical space it was encoded (Godden & Baddeley, 1975), but also that internal factors such as attentional context can affect motor learning (Song & Bédard, 2015). In sport, specificity considerations underline factors such as muscle fatigue, force landscapes and speed of movement, all of which form a context that may affect transfer from practice to competition (Bosch, 2020). Furthermore, the evidence actually points to a reduced ability of people with Parkinson's to make use of such contextual factors during recall (MacDonald et al., 2019). This poses a challenge, but as no two contexts of a movement are ever the same, perhaps it is better to train the underlying ability to identify and utilise contextual cues and to do so in a range of interesting environments that invite exploration and the use of task-relevant filtering to draw out cues to enhance movement.

With the short-term success of simple sensory cues, there might be a temptation to bombard a patient with cues to overcome motor deficits. However, in the absence of simple cues the basal ganglia are required to incorporate other internal signals relating to task and context to make sense of a complex environment (Beeler & Dreyer, 2019; Turner & Anderson, 2005) and this can be a useful tool in training. Finally, task will alter what signals are relevant and irrelevant, meaning a movement may look the same but still affect the brain's response to that movement (Bek et al., 2021; Staines et al., 2002), which is ultimately the principle underpinning sensory attenuation—active modulation of sensory input. In an exercise programme, determining sensory input in terms of which artificial cues are provided is not sufficient, as controlling sensory experience is not possible. A coach or facilitator can provide a stimulus, but that will only be part of the experience, as task and environment critically alter our response to each sensory event, and therefore inform our unpredictable experiences and capacities to engage with the world as a whole.

5. Conclusions

We have reviewed sensory attenuation through the lens of Parkinson's research with a particular interest in sport and rehabilitation. Studies investigating sensory attenuation measure the distinct responses that can emerge from two identical stimuli presented under different contexts. Differences in these responses indicate that contextual information has been utilised in active modulation of the sensory input, captured by a facilitation or suppression of the response to a stimulus. Diseased states appear to cause a convergence of responses that are more differentiable in healthy populations, indicating a reduced ability to integrate relevant sensory signals for perception or to enact appropriate movements. However, a crucial step precedes the utilisation of contextual cues, and we have considered the importance of task-relevance in both reconciling seemingly conflicting findings in sensory attenuation research and simultaneously informing on the symptoms of Parkinson's disease. There is a dual effect of basal ganglia dysfunction in Parkinson's where a reduced ability to filter relevant signals from a complex environment overwhelms a basal ganglia system already at reduced capacity, just when contextual cues might be used to enhance movement and perception (Figure 2 and Figure 3). Sensory attenuation paradigms may capture this process and offer a useful tool to track changes elicited by effective interventions and may even form the foundations of effective rehabilitation strategies themselves. Regardless, examining the sensorimotor processes that underpin sensory attenuation through the lens of Parkinson's research paves the way for establishing key principles that may be useful in guiding the design of effective rehabilitation.

Context

context is a powerful thing.
not because of what it is, but because of the
relations it represents.

it reveals an inseparability,
a connectedness of all things
a dynamism because for something to have context

it must relate,

it moves us between things
to consider the relations

Chapter 2

Sensory attenuation as context-dependent processing

1. Introduction

We argued in Chapter 1 that sensory attenuation paradigms, beyond just assessing the involvement of movement and sometimes expectation, measure context-dependent sensation. For instance, the oft-used force-matching task (Kilteni et al., 2020; Walsh et al., 2011; Wolpe et al., 2016, 2018) requires participants to replicate an experienced target force on one finger delivered by a computer-controlled lever. When they attempt to replicate this force using a removed dial or slider, they are quite accurate. However, when attempting to replicate the target force by pressing down on top of the lever with a finger from the other hand, participants significantly overcompensate. The differences seen between matching conditions requiring different motor output is compatible with the view that motor involvement attenuates sensory input, but it is also consistent with the notion that the presence of a finger from the other hand creates a unique context in which to perceive the force. As such, creating a 25 cm gap between the force-exerting finger and the force-receiving finger was enough to reduce the overcompensation effect (Kilteni & Ehrsson, 2017, 2020). Additionally, a context-dependent perception explanation of sensory attenuation measures also helps make sense of findings where sensation of a stimulus is heightened because of motor involvement (Guo & Song, 2019; Miall et al., 2006; Sherwin & Sajda, 2013). This alternative perspective thus helped to make sense of some contradictory findings in the literature, whereby some studies report a motor-induced sensory suppression and others report an enhancement of sensory input.

Sensory attenuation then, is not simply a uniform dampening of sensory input during movement. Rather, it is crucial to consider what exactly is the sensory input being measured, how it is needed to perform the set task, and what factors create a unique context to perceive the target stimulus. Even classic sensory gating studies (Chapman et al., 1987; Flynn et al., 1971) can be interpreted in this way, where concurrent stimuli and other more global factors such as attention alter the characteristics of sensory evoked potentials. We cannot therefore assume that the gating effects of movement are uniform and absolute. Additionally, as Riley and colleagues (1999) demonstrated, as discussed in the previous chapter, simple physical alterations to the task set up can change how sensory information is being used.

Framing sensory attenuation as a form of context-dependent perception, that may involve self-generation of the stimuli, is compatible with the task-relevant sensory processing role the basal ganglia play in movement (Kaji, 2001; Robbe, 2018; Schneider, 1984). As such, information, or signals, continually flow in and out of the brain (not solely when, say, an electrical stimulus is delivered), and influence how a target stimulus is perceived. Support for the involvement of the basal ganglia is seen in the fact that this ability appears harmed in Parkinson's, in both experiments using sensory attenuation paradigms such as the force-matching task (Wolpe et al., 2018) and in the way heightened sensory cues that simplify a complex environment such as lines on the floor can instantaneously alleviate some motor symptoms (Morris et al., 1996; Beck et al., 2015). Even in word recall tasks, people with Parkinson's have demonstrated a reduced ability to utilise the usual memory benefits of deep-semantic encoding compared to shallow-non-semantic encoding (MacDonald et al., 2019); similarly, Parkinson's may impair integration in the basal ganglia of sensory and motor activity to help process action-verbs while object-noun processing is spared (Cousins & Grossman, 2017). Thus we can argue that people with Parkinson's exhibit a a reduced capacity to utilise contextual information to guide action and perception.

The Craik-O'Brien-Cornsweet effect is a visual illusion where we perceive one of two panels to be lighter in colour than the other despite them being identical. This "error" is made because of the shading lines, also known as Mach bands (after Ernst Mach, see Lotto et al., 1999), which give the impression of a particular lighting context (Figure 1). The effect of Mach bands in this Cornsweet illusion is akin to how we see light illuminate and shadows darken colours in our environment which we know are actually the same base colour (e.g. a wall painted with the same pot of paint being lit by sunlight in parts and shaded elsewhere). The illusory effect can be eliminated by covering the Mach bands revealing the panels to be identical in colour. The mistake we make is thus evidence of context-dependent perception: we do not perceive the panel colours in isolation but as part of a whole, integrating other signals.

In the experiment I describe in this chapter, we used the Cornsweet illusion as a way of assessing context-dependent perception. We first confirmed a significant illusion effect does take place by varying the contrast of the panels over multiple trials to quantify illusion strength. We then compared illusion strength – as an index of context-dependent processing – across three groups: adults with Parkinson's, and younger and older adults without Parkinson's. Sensory attenuation, as demonstrated with the force-matching task, has been shown to increase with age (Parthasharathy et al., 2021; Wolpe et al., 2016). We therefore expected older adults to experience greater illusion strength than younger adults. In the group with Parkinson's, similar to Wolpe and colleagues (2018), we sought to demonstrate a positive correlation between Levodopa Equivalent Dose and illusion strength. Participants were not required to refrain from taking their usual dopaminergic medication for this study and thus the effect of Parkinson's disease on context-dependent perception was expected to be detected in this relationships of illusion strength with dopamine level estimate and also disease severity.

2. Methods

2.1 Participants

Three hundred and fifty-six adults participated in this study approved by The University of Birmingham Ethics Committee after giving informed consent. Two hundred and twelve younger adults without Parkinson's (95.9% of original sample; 18-35 years), eighty-five healthy older adults without Parkinson's (91.4%; 64-86 years) and forty-one adults diagnosed with Parkinson's (97.6%; 47-76 years) met the task-performance inclusion criteria outlined below and were included in our analysis. The younger adults group were recruited through the University of Birmingham Research Participation Scheme, the older adults group were recruited through Prolific (an online recruitment platform), and the Parkinson's group via a lab database of volunteers with Parkinson's disease. Table 1 shows a breakdown of group characteristics for participants included in the analysis.

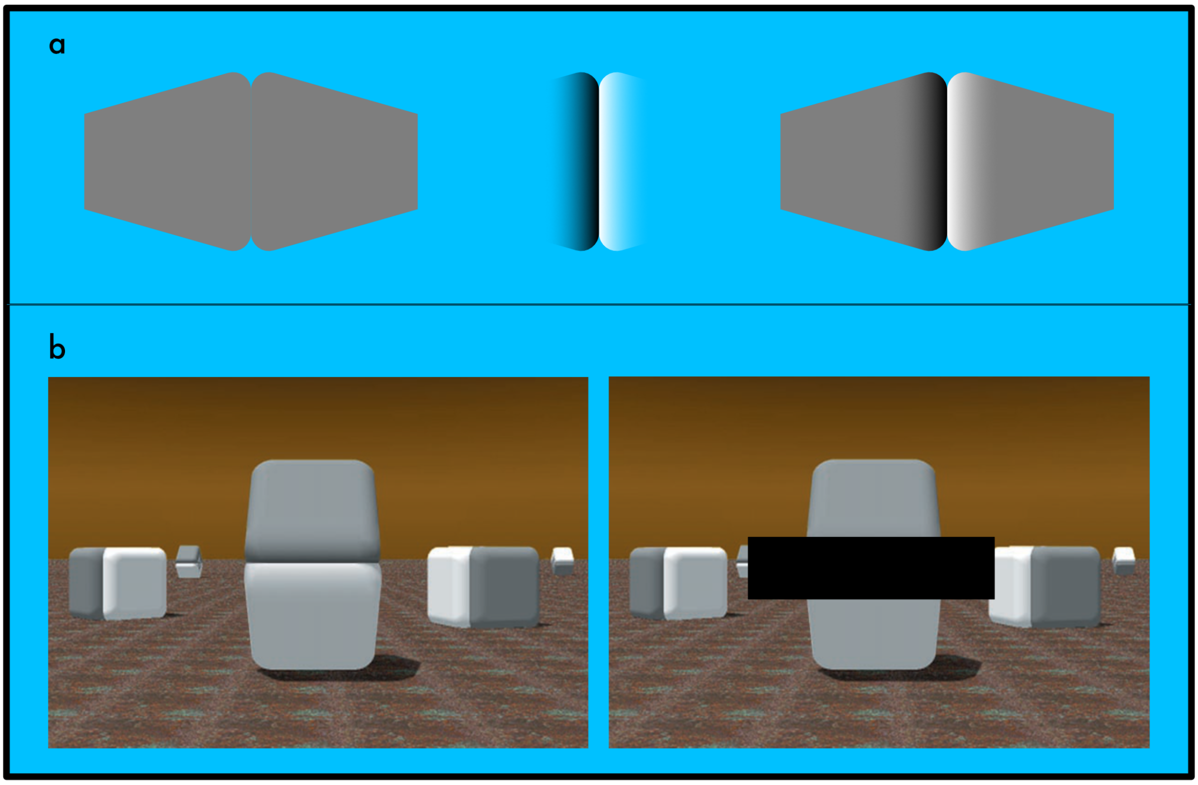


Figure 1 (a) Composition of the Cornsweet illusion stimulus used in the

present study, shown here on a blue background to make the Mach bands visible. Even in this simple arrangement, the Cornsweet effect should still occur where the same panels (left), appear to be different colours (right) when combined with the Mach bands (middle). (b) A more complex arrangement of the Cornsweet illusion from Purves et al., (1999, p. 8549). Purves and colleagues found the extra elements in this arrangement (such as vertical arrangement of panels, 3D effects and additional object) contributed to a stronger illusion effect. The key to the illusion is the presence of Mach bands in the middle of the panels (see image on left versus image on right), which provide contextual information to suggest a particular lighting arrangement shaping how we perceive the base colour.

2.2 Task and stimulus design

All experiments featured the main Cornsweet illusion task (Figure 2). In this task, a Cornsweet illusion stimulus was presented, which consists of two panels connected at the middle as if part of the same, somewhat unusual object (Figure 1a). Vertically arranging the panels in a complex 3D-looking environment creates a stronger illusion effect (Purves et al., 1999) but we used a simpler arrangement of what we considered the essential elements for an illusion to occur. In this case, an illusion is defined as incorrectly judging the right panel to be lighter despite it being the same (as in Figure 1) or darker. The reader may want to test this themselves by looking at the right-hand image in Figure 1 and deciding which panel appears lighter. Then, covering the central Mach bands with a finger, pen or piece of paper, notice that the panels—just as in the left-hand image in Figure 1—are the same lightness.

The task required participants to simply select which panel they thought was lighter. To assess the strength of the illusion, 29 combinations of panel colours (Figure 3) with 15 different contrast levels in total were presented to explore how often the illusion occurred when the right panel was darker than the left. Larger contrasts—that is, one panel is much lighter than the other—should be less susceptible to the illusion effect, and smaller contrasts should be more susceptible. Through repeated presentations of different contrasts in a random order, we were able to see how strong the illusion effect was based on participant responses.

The stimuli were designed using Affinity Designer, and the contrasts were formed by changing the colours of the panels using a HSL (hue, saturation, lightness) colour wheel where hue and saturation were set at 0, and lightness was varied on a scale of 0 (white) to 100 (black). Contrast between panels ranged from -35 (where the left panel was 35 points lighter than the right) to 35 (where the left panel was 35 points darker), and included 0 where panels were identical in colour.

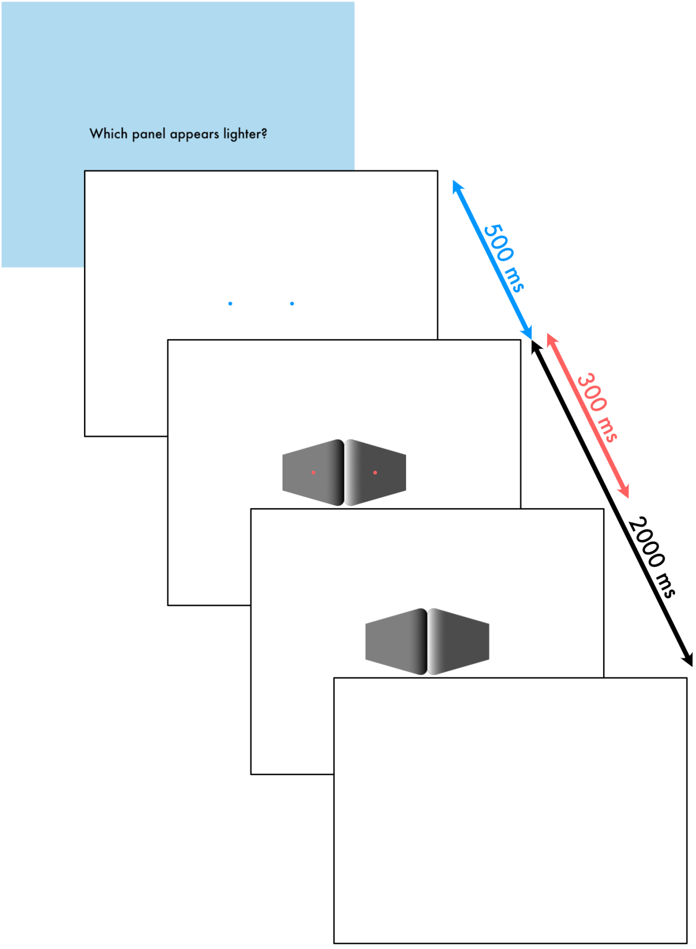


Figure 2 After being asked which panel appears lighter, blue fixation dots cued the appearance of the Cornsweet stimulus, which was accompanied by red dots for 300 ms. The Cornsweet stimulus appeared on screen for a total of 2 seconds, but a response was possible after this.

The Mach bands were black on the left and white on the right, and faded from a solid colour on the inside edge of the panels to complete transparency (Figure 1). This composition gave the impression of shading and luminance, as if a light source was positioned to the right of the shape, with the panels contoured at the middle. For consistency, we kept the Mach bands arranged this way throughout, so as to reinforce a sense of permanence for the source of light. Continually randomising the location of the light source across trials risked having an effect on averaged illusion effect for each participant, as a more vacillating light source might weaken the priors underpinning the illusion (e.g. the light-from-above Cornsweet effect is stronger than a horizontal light source because we are so used to light coming from above in the form of sunlight). We preferred here the option of a fixed light source to maintain an illusion effect dependent on our experience of light and colour. Furthermore, variations in the direction of light have already been explored by Purves and colleagues (1999), and the focus here rested on assessing illusion strength between different populations (and within individual participants in Chapter 3), negating a need to control for any hemispatial bias that could be created from not randomising the location of the light source.

In each trial, red fixation dots indicated the area of the panel participants were to judge (Figure 2), responding with a left or right key press depending on which panel they thought looked lighter. The stimulus appeared at the centre of the screen for 2 seconds before disappearing, and participants could make their response during this or for an unlimited time after, maximising participant engagement by linking their response to the progression of trials. Response time was stored and used to exclude responses that took longer than 10 seconds in the analysis of reaction time (99.9% of trials kept). A long time window (10 seconds) simply meant extreme outliers were removed, allowing for participants to respond how they wished and using reaction time to characterise the nature of the illusion effect (Figure 5). Participants were still only exposed to the stimuli for 2 seconds, preventing excessive studying of the image and it prevailed that mean responses for all participants across every contrast were shorter than 2 seconds (Figure 5a). For the remaining analyses, we deemed the participant level inclusion criteria sufficient to ensure high quality response data.

It is important to note the difference between control trials and illusion trials in our experiment. As we are defining an illusion in this stimulus arrangement as incorrectly judging the right panel to be lighter when it is in fact the same or darker, this means illusions are only possible when the right panel is the same or darker than the left. What about stimuli where the left is darker than the right? Here, the Mach bands simply exacerbates the lightness of an already lighter panel and thus no illusion effect can be measured. A right arrow response to indicate the participant thinks the right panel is lighter is simply the correct response, and a left response would be incorrect, but not because of an illusion effect. These trials are control trials, and will be made up predominantly of correct responses. Hence, control trials were useful for assessing task performance, and participants' datasets were excluded from analysis if they fell below 95% accuracy in control trials. In illusion trials, we expected a mix of correct and incorrect responses, and the percentage of incorrect responses indexed illusion strength (Figure 4). Overall, we expected the illusion effect to make right responses more likely than left responses, as shown in Figure 5.

For the Cornsweet illusion task, participants completed 87 trials in total, across three bins, each comprising the 29 panel combinations and the 15 unique contrasts. The task was assembled in PsychoPy (Peirce et al., 2019) and made available to participants online via Pavlovia (https://pavlovia.org).

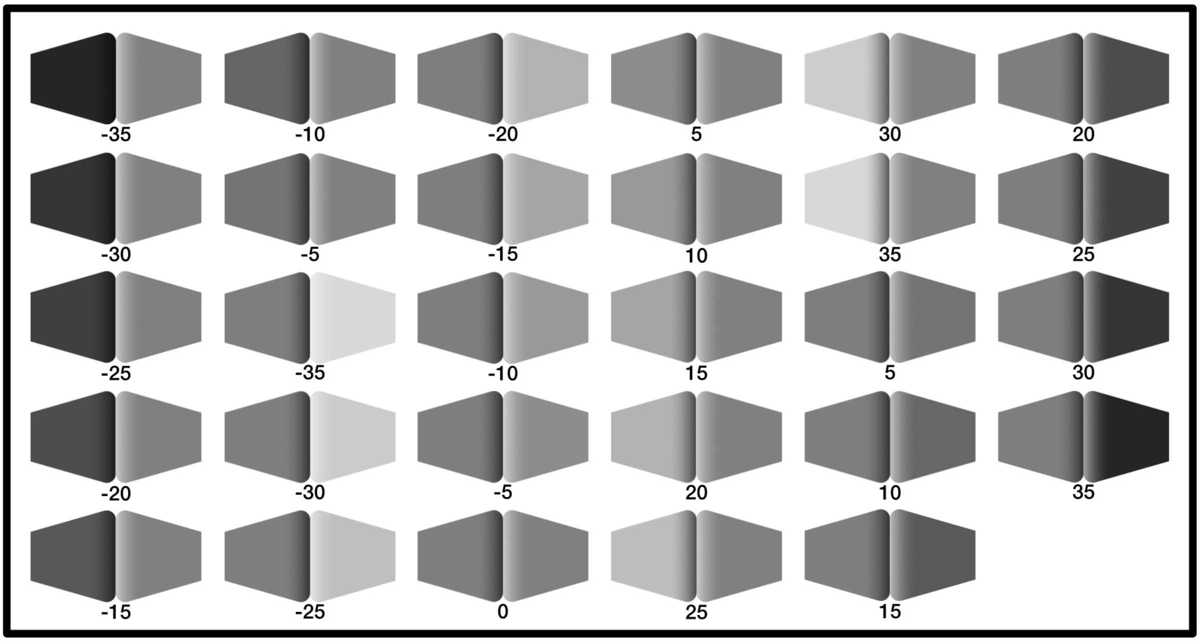


Figure 3 All the stimuli presented during one of three bins to assess illusion strength. The Mach bands were set at 60% opacity. There are 15 different contrasts, including the stimulus with panel contrast of 0.

2.3 Levodopa equivalent dose

A levodopa equivalent dosage (LED) calculator designed and openly provided by John Turner on the brilliant parkinsonsmeasurement.org was used to generate an LED (a well-accepted standard of measurement of dopamine intake) given the variety of medications used by participants with Parkinson's, aiding comparison. I referred to Tomlinson et al. (2010) and Schade et al. (2020) to check calculations and fill in gaps such as (COMT and MAO-B inhibitors), complying with the more recent publication at points of contradiction. Importantly, rather than calculating a daily dose, participants reported the dosage and time of medications taken in the last 6 hours, or the last taken medication, for a rough estimate of activity of the medication at the time of the study. We thus used Turner's programme to calculate a "Current LED" which takes into account LED, time taken for drug to reach max effectiveness, and the time taken for the drug to lose half its effectiveness. Turner's programme assumes multiple drugs do not interact and have additive effects when taken together, but helps in reaching a closer estimate of circulating dopamine levels for our attempt to assess its role in context-dependent action and perception in this study. Some participants also provided information on additional medications being taken for non-Parkinsonian co-morbidities. For consistency within, only medications being taken for Parkinson's were analysed in this study, which does of course highlight the heterogeneity of attempting to tease apart the effect of dopamine alongside other medications.

2.4 Activities of Daily Living and Key Tapping Score

Owing to the links established between sensory attenuation measures and movement competence, we anticipated the possibility that variability in motor skill and lifestyle might confound our investigation of age and dopamine related changes in context-dependent perception. All older adults were accordingly asked to complete a short Activities of Daily Living (ADL) Questionnaire as an indicator of activity levels, functional capacity and engagement with wider communities (Dias et al., 2019; Lawton & Brody, 1969; Reuben et al., 1990; Slachevsky et al., 2019). The version we used comprised 13 questions asking the participant if they have either: (a) never done, (b) stopped doing, or (c) still do the named activity, with each answer corresponding to 0, 1 or 2 points respectively. The maximum score was 26, indicating the highest possible level of activity. We complemented the ADL score with a Key Tapping Score, calculated as the number of times the space bar was pressed in a 30 second period where the participant was instructed to tap the key as fast possible. A 5 second practice was provided beforehand, and only the 30 second Key Tapping Score was included in our analysis as a second, more acute, indicator of motor ability. Both ADL score and Key Tapping Score were included in a model comparison as part of a Bayesian linear regression analysis with our main outcome measure illusion strength as the dependent variable.

2.5 Data analysis

The main outcome measure in this study was illusion effect, which we measured as the proportion of incorrect responses made during illusion trials. We thus split illusion trials from control trials, using the latter as inclusion criteria as outlined above, and calculated the percentage of incorrect responses from the remaining 45 trials for each participant. We compared illusion trials and control trials using a t-test to confirm the presence of an illusion effect. Illusion effect was then compared across groups in an ANOVA, and was also used in two Bayesian linear regression analyses (allowing for many model comparisons) to explore possible effects of LED in the group with Parkinson's, as well as motor ability and lifestyle activity indicators (ADL and Key Tapping Scores) in both older groups. Additionally, to visualise the illusion effect in greater detail in what is a novel task, we calculated reaction time for each contrast level and plotted each group separately. Finally, we fit a logistic regression curve using a binomial distribution to the binary response data of individual participants, displaying one example in Figure 5 to further elucidate the illusion effect and the ambiguity of perception at particular contrast levels. The majority of data processing and analysis was performed using MATLAB, with contributions in places from RStudio (reaction time plots) and JASP (linear and logistic regression analyses).

Table 1 Group characteristics for participants included in the analysis.

Group	Young adults	Older adults	Adults with Parkinson's
N	212	85	41
Mean age (SD)	19.7 (1.7) years	69.2 (4.6) years	63.6 (7.9) years
Key Tapping Score (SD)	n/a	153.6 (24.7)	156.2 (26.9
Activities of Daily Living Score (SD)	n/a	16.5 (4.0)	18.9 (3.2)
Levodopa Equivalent Dose current estimate (SD)	n/a	n/a	75.3 (67.1) mg
Years since Parkinson's diagnosis	n/a	n/a	9.4 (6.9) years

3. Results

3.1 Illusion effect

The mean percentage of incorrect responses during illusion trials was 39.8% (SD = 11.9%), whereas the mean proportion of incorrect responses during control trials was 0.3% (SD = 1.0%). An independent samples t-test unsurprisingly revealed this difference between incorrect responses for illusion and control trials to be significant ($t(337) = 60.949$, $p < .001$, $d = 3.315$), also shown in Figure 4. Thus, we replicated the Cornsweet effect with our task, demonstrating the influence of Mach bands as contextual cues on perception.

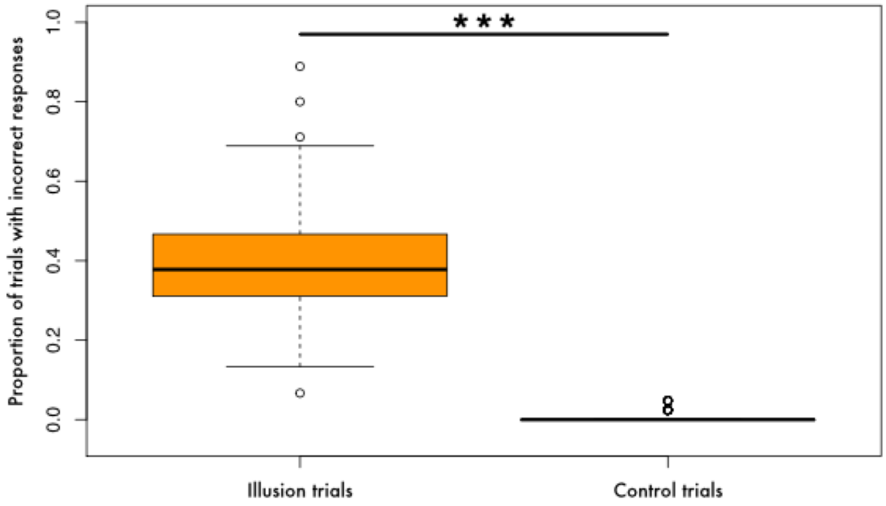


Figure 4 Boxplot of the proportion of incorrect responses during illusion trials vs control trials for all 356 participants. The bold horizontal line represents the

median, the upper and lower edges of the box represent the upper and lower quartiles, the horizontal lines at the ends of the whiskers the upper and lower extremes, with outliers marked by circles. ***$p < .001$.

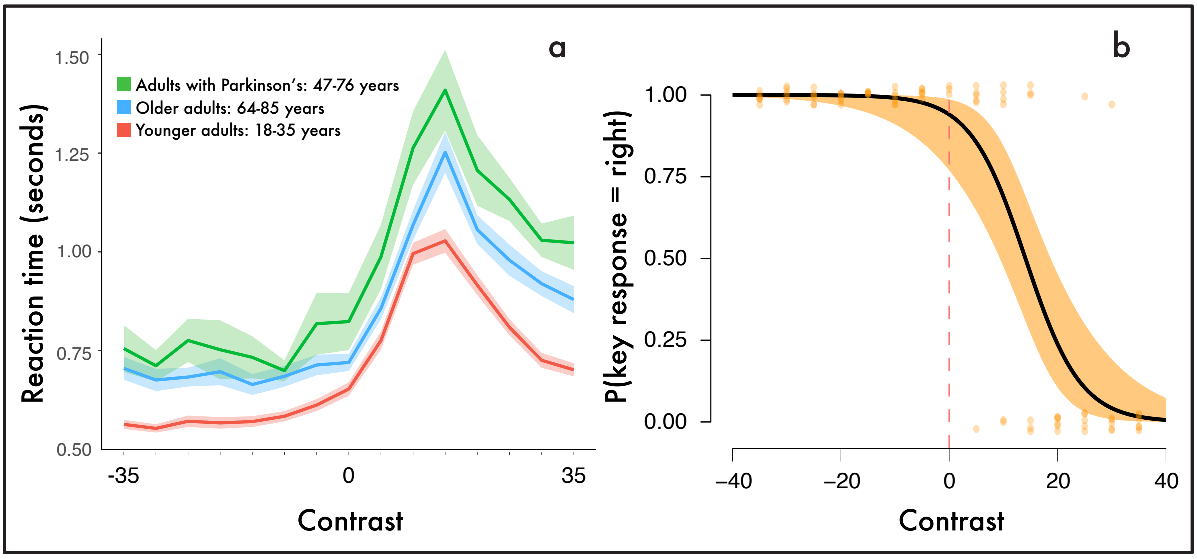


Figure 5 Participants' key responses are affected by the contrast of the panels. The contrast is calculated as the difference (on a grayscale of 0 to 100) the left and right panel. A positive value indicates the left panel is lighter, a negative value indicates that the right panel is lighter, and 0 that they are equal. (a) Mean reaction times across participants for each contrast level, with a line for each group and standard error of the means represented by the shading around each line. Younger participants were generally quicker responding, but all participants slow for positive contrasts where ambiguity created by the illusion effect increases. (b) Response data from a single participant, modelled with logistic regression using a binomial distribution (df = 85, BIC = 47.044, McFadden $R^2 = 0.651$, $p < .001$). The Y-axis represents the probability from 0 to 1 that the participant responds with the right arrow key. The curve is asymmetrical as the illusion effect creates more right key responses.

3.2 Illusion effect group comparison

To ensure no differences between groups in attention, a comparison of incorrect rates across control trials ANOVA revealed no effect of group ($F(2,335) = 1.007$, $p = .366$). An ANOVA revealed a significant main effect of group for illusion effect ($F(2,335) = 6.659$, $p = .001$, $\eta^2 = .038$), where older adults without Parkinson's demonstrated the strongest illusion effect with 43.5% (SD = 12.1%) of the responses to illusion trials being incorrect. Adults with Parkinson's were incorrect in 41.1% (SD = 12.1%) of illusion trials, and younger adults were incorrect 38.1% (SD = 11.4%) of illusion trials. Post-hoc tests with Bonferroni correction revealed only the difference between healthy older adults and younger adults to be significant ($p = .001$, $d = .461$;

older adults vs adults with Parkinson's: p = .844; adults with Parkinson's vs younger adults: p = .413), comparisons also shown in Figure 6 with 95% confidence intervals. We therefore demonstrated that illusion effect increases in healthy old age.

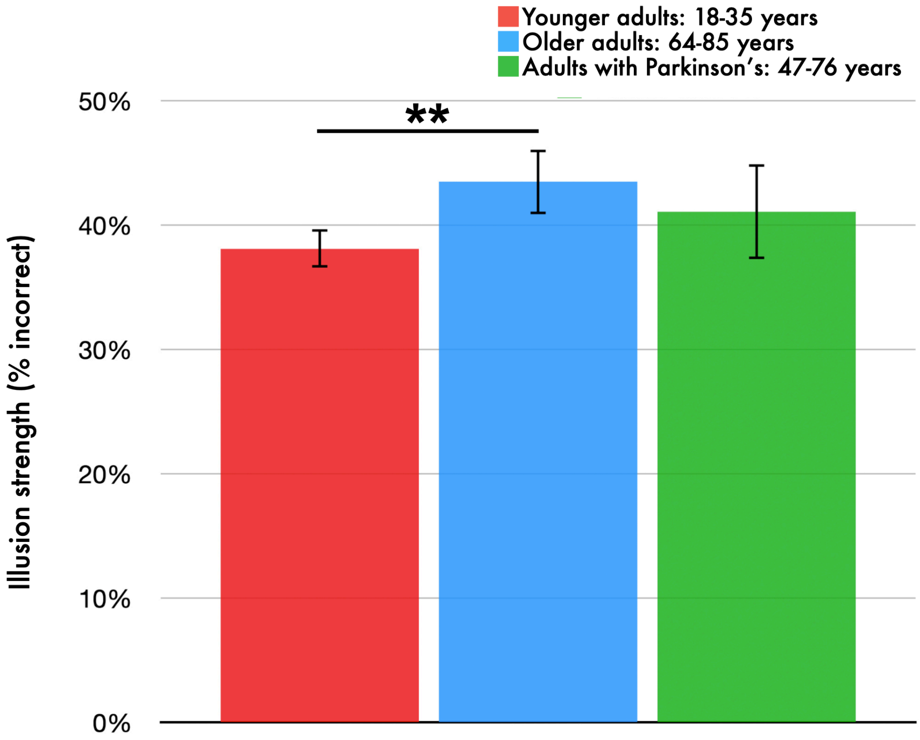


Figure 6 Illusion strength, as a measure of context-dependent processing (Mach bands as context inform the perception of panel contrast), is greater in older adults compared to younger adults. People with Parkinson's demonstrated an illusion strength in between that of the other two groups, but the difference was not significant. Error bars represent 95% confidence intervals. **p = .001.

3.3 Regression analysis

To assess the effect of dopamine levels on illusion strength, which has been linked to sensory attenuation in people with Parkinson's (Wolpe et al., 2018), we used a Bayesian Linear Regression to model the relationship between estimated Current LED at time of testing. The first model (Table 2) consisted of data only from participants with Parkinson's (*N* = 41). Table 2 shows the best eight models, out of 32. We included LED Current, Time Since Diagnosis, ADL Score, Key Tapping Score and Age as covariates, where illusion strength was the dependent variable. We found no evidence to reject the null model in favour of any of the possible model permutations, with no apparent relationship between LED Current and illusion strength (BF(10) = 0.357, R^2= 0.010), also shown in Figure 7.

In a second model (Table 3), we included only older adults without Parkinson's (*N* = 85) in another Bayesian Linear Regression. We included ADL Score, Key Tapping Score and Age as covariates. Table 3 shows all eight model permutations. We again found no evidence of a better model than the null model. Taken together, there was no observable correlation between estimated dopamine levels and illusion strength, nor generic motor ability and lifestyle variables.

Table 2 Model comparisons from a Bayesian Linear Regression with data from adults with Parkinson's (*N* = 41). Only the best 8 models are shown. Unexpectedly, LED Current was not predictive of illusion strength, at least insofar as the data are not explained by a linear relationship. Five covariates were included, with illusion strength as the dependent variable: ADL Score, Age, Key Tapping Score, LED Current and Time Since Diagnosis.

Models	P(M)	P(M | data)	BF_M	BF_{10}	R^2
Null model	0.167	0.505	5.108	1.000	0.000
Key Tapping Score	0.033	0.055	1.686	0.544	0.036
Age	0.033	0.050	1.539	0.499	0.031
Time Since Diagnosis + Key Tapping Score + Age + ADL Score + LED Current	0.167	0.038	0.195	0.074	0.095
LED Current	0.033	0.036	1.086	0.357	0.010
ADL Score	0.033	0.033	0.999	0.329	0.005
Time Since Diagnosis	0.033	0.033	0.982	0.324	0.004
Age + Key Tapping Score	0.017	0.023	1.417	0.464	0.082

Table 3 Model comparisons from a Bayesian Linear Regression with data from older adults without Parkinson's (*N* = 85). Only the best 8 models are shown. There is no evidence of a linear relationship between illusion strength and any of the three covariates: ADL score, Age, Key Tapping Score.

Models	P(M)	P(M | data)	BF_M	BF_{10}	R^2
Null model	0.250	0.674	6.190	1.000	0.000
Age	0.083	0.093	1.124	0.413	0.016
ADL	0.083	0.060	0.706	0.269	0.005
Key Tapping Score	0.083	0.052	0.602	0.231	0.001
Age + ADL Score + Key Tapping Score	0.250	0.038	0.120	0.057	0.019

Age + ADL Score	0.083	0.032	0.368	0.144	0.019
Age + Key Tapping Score	0.083	0.030	0.343	0.135	0.017
ADL Score + Key Tapping Score	0.083	0.021	0.231	0.091	0.006

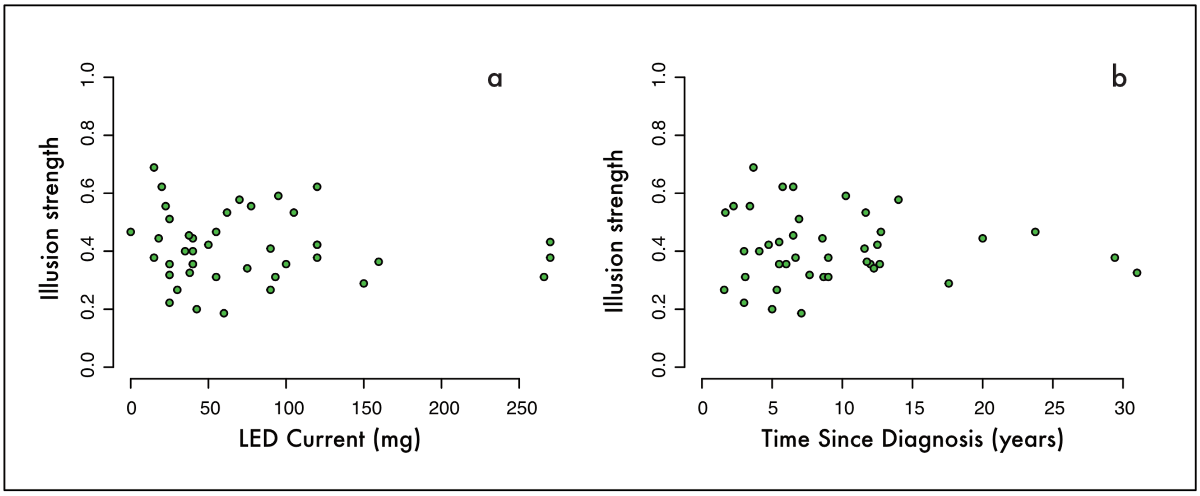


Figure 7 Scatter plots of illusion strength (proportion incorrect responses during illusion trials) and LED Current (a) and Time Since Diagnosis of Parkinson's (b), illustrating a lack of correlation between variables (Illusion Strength ~ LED Current: $R^2 = 0.010$; Illusion Strength ~ Time Since Diagnosis: $R^2 = 0.004$).

4. Discussion

4.1 Key findings

In this study, we demonstrate that context affects perception. In the illusion trials, the Mach bands have the effect of causing the participants to choose the darker panel when asked which one was lighter. Participants selected the incorrect panel in nearly forty percent of the trials, while selecting the correct panel near perfectly in control trials. The Cornsweet illusion task is thus a useful measure of context-dependent perception.

We demonstrated, in line with Wolpe and colleagues' (2016) findings from a force-matching task, that healthy older adults demonstrate greater levels of context-dependent perception than younger adults. Wolpe and colleagues (2016) suggest the increased force-overcompensation they found by older adults in the force-matching task is the result of worsened tactile sensitivity with age which thus requires greater weighting of prediction signals to guide behaviour consistent with Bayesian perception frameworks (Körding & Wolpert, 2004, 2006), thereby resulting in more sensory suppression and greater force-overcompensation. While plausible, this explanation has been disputed (Parthasharathy et al., 2021); alternatively, sensory attenuation could develop through experience (Idei et al., 2021, 2022) whereby infants may display an absence of sensory attenuation (Meyer & Hunnius, 2021) and responses become more context-specific through learning, indicative of a more complex nervous system, at least in places (Wolpe et al., 2016) and subject, of course, to experience (Konishi & Bohbot, 2013).

We did not find a difference in illusion strength in the Parkinson's group compared to the other groups. In the absence of any on/off medication requirements, we opted instead to explore the correlational relationship between estimated dopamine levels and illusion strength amongst the Parkinson's participants. Expecting to replicate Wolpe and colleagues' (2018) finding of a positive correlation between LED and force-overcompensation, we were surprised to find no relationship between LED and illusion strength in the present study (Figure 7), even when including additional factors such as Time Since Diagnosis, ADL Score and Key Tapping Score (Table 2). We opted for a slightly different LED measure, estimating current dopamine levels at the time of study rather than a daily dose, owing to the transient nature of many dopamine medications. We considered LED Current to be a sophisticated estimate of dopamine levels comparable to Wolpe and colleagues' (2018) approach to recording a daily LED (LEDD) and requiring participants to complete the study in a specified 2 hour window related to levodopa self-administration timing.

However, in the absence of a correlation between LED Current and illusion strength in the present study, four possibilities arise. Firstly, the combination of LEDD and a time-controlled approach to testing could more accurately gauge dopamine dose and its links to context-dependent processing. Secondly, illusion strength could be linked to LEDD and not LED Current, though this seems unlikely unless the first possibility is also true. Third, the positive correlation between dopamine dose and sensory attenuation found by Wolpe et al. (2018) could instead be reflective of disease severity, which was found to be negatively correlated with sensory attenuation (though many links elsewhere have been made to dopamine and sensory integration, cf. Beeler & Dreyer, 2019; Jenkinson & Brown, 2011; Ketzef et al., 2017; Petzinger et al., 2015). Fourth, it is possible that LED Current did gauge dopamine levels effectively but that illusion strength was unaffected. It is this final possibility I will discuss in more detail.

4.2 Context-dependent perception and task complexity

Jenkinson & Brown (2011) argue that sufficient dopamine levels uphold the capacity for effective movement, playing a role in coordinating oscillatory activity in preparation for action (see also Beeler & Dreyer, 2019; Brittain et al., 2014; Brittain & Brown, 2014). Crucially, dopamine levels are themselves modulated by salient input from internal or external cues. Thus, in the absence of salient cues, dopamine levels remain low (too low in Parkinson's), and there is a reduced ability to perform new movements. As argued in Chapter 1, in the absence of clear, salient cues, the basal ganglia are involved in searching for and integrating useful cues from elsewhere, and it is this ability that is harmed in Parkinson's. The lines-on-the-floor phenomenon illustrates that when clear, salient cues are available, movement becomes fluid, but breaks down stuttered in their absence, implicating the basal ganglia in navigating a complex environment. The force-matching task usefully lacks the clear, salient cues to inform perception that are part of this current Cornsweet illusion task. The Cornsweet illusion task, in this current form, despite being a measure of context-dependent perception where Mach bands and prior experience are integrated in the perception of panel colour, also comprises very simple, salient contextual cues that likely bypass any need for complex searching and integrative behaviours that depend on capable and dopamine-bountiful brain regions.

Complexity of the task and environment is important to consider, just as word memory in Parkinson's is only impaired when more complex integration is involved (MacDonald et al., 2019; Cousins & Grossman, 2017), and just as visual feedback can aid movement when it shortcuts the need to navigate a more complex environment (Beck et al., 2015; Morris et al., 1994, 1996) but can harm movement when the visual feedback itself is an additional source of information to integrate (Connor & Abbs, 1991). We provide further evidence here that while context-dependent action and perception is a useful concept to reframe sensory attenuation to make better sense of Parkinson's symptoms, contextual cue integration–when sufficiently salient and simple–is not impaired. As argued in Chapter 1, the basal ganglia affected by Parkinson's exhibits a reduced capacity to both filter complex environments in a complex environment and then integrate the resulting variety of contextual cues into ongoing movement. Therefore, context-dependent movement is a more useful concept than motor-induced sensory suppression for understanding Parkinson's, but it is still not, by itself, a complete explanation for Parkinsonian symptoms.

4.3 Future directions and implications

There are other ways of presenting the Cornsweet illusion, and Purves and colleagues (1999) found greater illusion strength with a more complex, visual scene (Figure 1). Some evidence, albeit inconsistent, in studies of people with Schizophrenia suggest visual illusions can be impaired in people with dopaminergic disorders affecting the basal ganglia (Grzeczkowski et al., 2018; Notredame et al., 2014). It would therefore be interesting to see if a more complex Cornsweet illusion scene similarly elicits a stronger illusion effect amongst people with Parkinson's, or if the image on screen is still too simple. Alternatively, the use of distractors could be used to require participants to filter out task-irrelevant information in conjunction with the Cornsweet illusion task to place greater demand on the basal ganglia (Lee et al., 2010; McNab & Klingberg, 2008).

For Parkinson's training approaches, it remains important to challenge and grow the ability to navigate complex environments. Many approaches to training, in Parkinson's rehabilitation and in sports, can involve a simple cue facilitated by the coach to help the participant or athlete initiate a particular action (O'Connor et al., 2017). While there may be benefits in terms of achieving action quickly, it also may not be demanding much from the nervous system to promote plastic growth and the skilful improvisation of movement in the absence of that simple cue.

4.4 Conclusion

In a novel Cornsweet illusion task, we demonstrated context-dependent perception in all participants, where Mach bands likely elicited the integration of prior knowledge with the perception of panel colours to dramatically shape the response profile. We further demonstrated a shift of illusion strength in healthy old age, possibly reflecting experience-related change over a lifespan. In the absence of a link between dopamine dose and illusion strength in the Parkinson's group, we argue for the usefulness of recognising context-dependent perception when coupled with a careful appreciation of task and environment complexity.

Chapter 3

Altered use of contextual cues with training

1. Introduction

Having observed observed no gross shift in task performance between the two older adult groups in the previous chapter – rather demonstrating a change in perception related to age – we now seek to perturb this sensory attenuation index through training. Can illusion strength be "trained" through exposure to different cue characteristics (e.g. the Mach bands) and, if so, how is this capacity altered in healthy ageing and Parkinson's disease? These questions are important because exercise-based approaches to neurological rehabilitation use cues in a variety of ways, but an understanding of the underlying mechanisms mediating their benefits is lacking (Nonnekes et al., 2019).

The symptoms of Parkinson's disease are remarkably context dependent. In many environments, patients may exhibit short, shuffling steps when walking. Cluttered (Tan, 2009) and precarious (Ehgoetz Martens et al., 2014) environments can exacerbate such symptoms. Even reducing the size of a door frame can elicit more episodes of freezing – a sudden inability to initiate or continue walking (Almeida & Lebold, 2010). However, such symptoms can be alleviated with simple cues: drawing lines on the floor enables much improved walking with bigger steps (Beck et al., 2015), and sounds and tactile cues (Nonnekes et al., 2019; Quintyn & Cross, 1986) can similarly be useful to enhance movement while the cues are present and even with some lasting effects (Morris et al., 1996). Such cues can be considered contextual cues: that is, sources of information that guide movement or perception of a target stimulus but, according to a particular task set-up, are not the target of perception themselves.

Far from negating the usefulness of augmented contextual cues in everyday life, it is unclear if such strategies restore function to damaged regions of the basal ganglia, or if they serve as a compensation mechanism (Nonnekes et al., 2019; Spaulding et al., 2013) with declining effectiveness over time when implemented in a long term programme (Nieuwboer et al., 2007). Morris and colleagues (1996) used lines on the floor to visually cue steps to help participants with Parkinson's walk with greater speed and bigger stride length. They found after-effects lasting the maximum period of two hours where stride length and velocity were improved after the removal of the visual cues. However, other approaches in weeks-long programmes have demonstrated promising effects on Parkinson's symptom severity while avoiding augmented contextual cues to guide movement (Ridgel et al., 2009, 2015; Ridgel & Ault, 2019; Sage & Almeida, 2009, 2010). PD-SAFEx for instance (Sage & Almeida, 2009, 2010) requires participants perform movement drills in low-light conditions, purposefully reducing visual input, with lasting improvements in symptom severity. How are salient cues being used during training and what effects might a lines-on-the-floor set up have – not just on gait kinematics, but on perceptual abilities important for moving in complex environments?

To find out how the perception of contextual cues change with training, we devised a simple task called the Cornsweet illusion task, using the Craik-O'Brien-Cornsweet effect (Kingdom & Moulden, 1988; Purves et al., 1999). The Cornsweet effect (for short) is a visual illusion that reveals that perception of target stimuli is dependent on its situated context. The effect is achieved when two panels of identical colour are judged to be different because the shading at the meeting point of the panels creates unique lighting contexts (see Figure 1, Chapter 2). The shading used here are Mach bands – gradients of black and white from 100% to 0% opacity.

Morris and colleagues (1996) measured walking characteristics in response to the introduction of visual cues. Here, with this task, rather than measuring any improvement in movement, we measure how cues are being perceived, indicated with a simple keyboard response, where the illusion effect results directly from the influence of Mach bands on perception. In the absence of salient cues, the basal ganglia play a role in finding and piecing together other sources of information to inform ongoing action and perception (Kearney & Brittain, 2021). Therefore we interpret the residual gait improvements in Morris et al. (1996) to result from a new compensatory stepping behaviour, rather than a renewed ability to search and use cues in a complex environment.

In the Cornsweet illusion task, we asked participants to pick which panel they thought was lighter while varying the panel contrast to establish how strong the illusion effect was at different time points. A stronger illusion effect indicated greater influence of the contextual cues (Mach bands) on perception. We sought to change the strength of the illusion effect through "training". As perception is tightly intertwined with action, as evidenced in the sensitivity to context of Parkinson's symptoms, and movement ability can be improved through training that manipulates the availability of sensory information (e.g. PD-SAFEx, Sage & Almeida, 2010), we expect such training to alter illusion strength. The training here involved repeated trials either with more prominent or more subdued Mach bands.

We expected participants repeatedly exposed to more prominent Mach bands in "Strong Mach Training" to both experience a stronger illusion effect and also to adapt to this level of cue salience. The result of this adaptation to prominent Mach bands would be a subsequent reduction in illusion strength indicative of a waning effect where relevant contextual information becomes integrated into perception with less vigour and relative influence. We similarly expected participants to adapt to subdued Mach bands in "Weak Mach Training", instead experiencing a weaker illusion effect in the training block but demonstrating a stronger subsequent illusion effect when returning to baseline conditions. We tested two variations of Strong Mach Training and Weak Mach training in Experiments 1 and 2 amongst younger adults to determine which aspects of the task induced adaptation. Experiment 1 involved a direct manipulation of Mach band opacity, whereas Experiment 2 involved a noise overlay to indirectly alter Mach band salience. We then extended this work by taking the most effective variant and repeating the experiments on groups on otherwise healthy older adults in Experiment 3, and adults with a Parkinson's disease diagnosis in Experiment 4.

2. Methods

2.1 Participants

A total of three-hundred and fifty participants took part in one of four experiments. Experiment 1 included young adults and comprised three different training conditions, where Mach band opacity was increased, decreased or left unchanged during the training block. Experiment 2 also involved young adults, but comprised four training conditions aiming at achieving a similar effect as Experiment 1 by layering the images with noise to obscure the Mach bands and panels rather than directly changing Mach band opacity and relative salience. Experiments 3 and 4 were the same as Experiment 1 but included adults without Parkinson's and with Parkinson's, respectively. The task-performance inclusion criteria required participants to respond correctly in at least 95% of the control trials, as in the previous chapter. Across Experiments 1 and 2, two-hundred and four adults met the task-performance inclusion criteria (92.3% of original sample; 18-35 years). In Experiment 3, eighty-eight participants met the inclusion criteria (94.6%; 64-86), and in Experiment 4, thirty-five participants did so (97.2%; 47-76 years). Participants were randomly assigned to the experimental conditions. The study was approved by the The University of Birmingham Ethics Committee and participants provided informed consent at the start of the study after reading the information sheet.

Table 1 Group characteristics across the four experiments of participants included in the analysis based on task-performance inclusion criteria requiring at least a 95% accuracy rates in control trials.

Experiment	**1: Young adults**	**2: Young adults, noise manipulation**	**3: Older adults**	**4: Adults with Parkinson's**
N	92	112	88	35

Mean age (SD)	19.5 (1.1) years	20.0 (2.1) years	69.1 (4.5) years	63.4 (8.0) years
Key Tapping Score (SD)	n/a	n/a	153.8 (24.5)	156.9 (26.8)
Activities of Daily Living Score (SD)	n/a	n/a	16.6 (3.9)	18.8 (3.2)
Levodopa Equivalent Dose current estimate (SD)	n/a	n/a	n/a	74.7 (62.5) mg
Years since Parkinson's diagnosis	n/a	n/a	n/a	8.3 (5.3) years

2.2 Task and stimulus design

This task used the stimuli as described in Chapter 2, with the addition of varied Mach band opacity during the training block, and partial and complete noise overlays shown in Figure 1 (i and j). The tasks were implemented in PsychoPy (version 2022.1.3) and participants took part in the study online using Pavlovia. The majority of the analysis was performed using Matlab (2021a) with some support from JASP (2020, version 0.14.1). As described in Chapter 2 (Sections 2.3 and 2.4), Key Tapping Score, Activities of Daily Living (ADL) Score and Current Levodopa Equivalent Dose (LED) were established for each participant at the start of the experiment.

2.3 Training

A novel aspect of this study is the attempt to "train" an index of sensory attenuation (distinct responses to identical stimuli in distinct contexts). In this case, we examined how changing the salience of the contextual cue altered illusion strength. To do this, we assessed illusion strength in a baseline block consisting of three bins of 29 trials each (87 trials total). Each bin consisted of two stimuli from each of the 15 contrast combinations, apart from contrast 0, which was only presented once due to being less informative than the other contrast levels. In every condition across each experiment, the baseline block remained the same. A longer "training" block followed, where the sensory information in the scene was altered. As displayed in Figure 2, the training block consisted of 12 bins (348 trials). The task —choosing the lighter-appearing side—remained the same throughout.

In Experiments 1, 3 and 4, we manipulated Mach band opacity in the training block across three conditions (Figure 3). In the Weak Mach condition, Mach band were reduced in opacity to 0.2; in the Medium Mach condition, Mach bands remained at the same 0.6 opacity, as in the baseline condition; in the Strong Mach condition, Mach bands were increased to 1.0 opacity. A test block and two washout blocks followed the training block which were identical to the baseline block.

In Experiment 2, we manipulated Mach band salience indirectly using noise overlays that targeted different parts of the scene across four conditions. In the

Gradation Noise condition, a noise overlay obscured only the Mach band. In the No Noise condition, the stimulus remained unchanged from baseline. In the Surround Noise condition, a noise overlay obscured everything in the scene except for the Mach bands. In the Solid noise condition, a noise overlay covered the whole scene. Each noise overlay was made from the same speckled white, black and grey image and was set at 0.5 opacity.

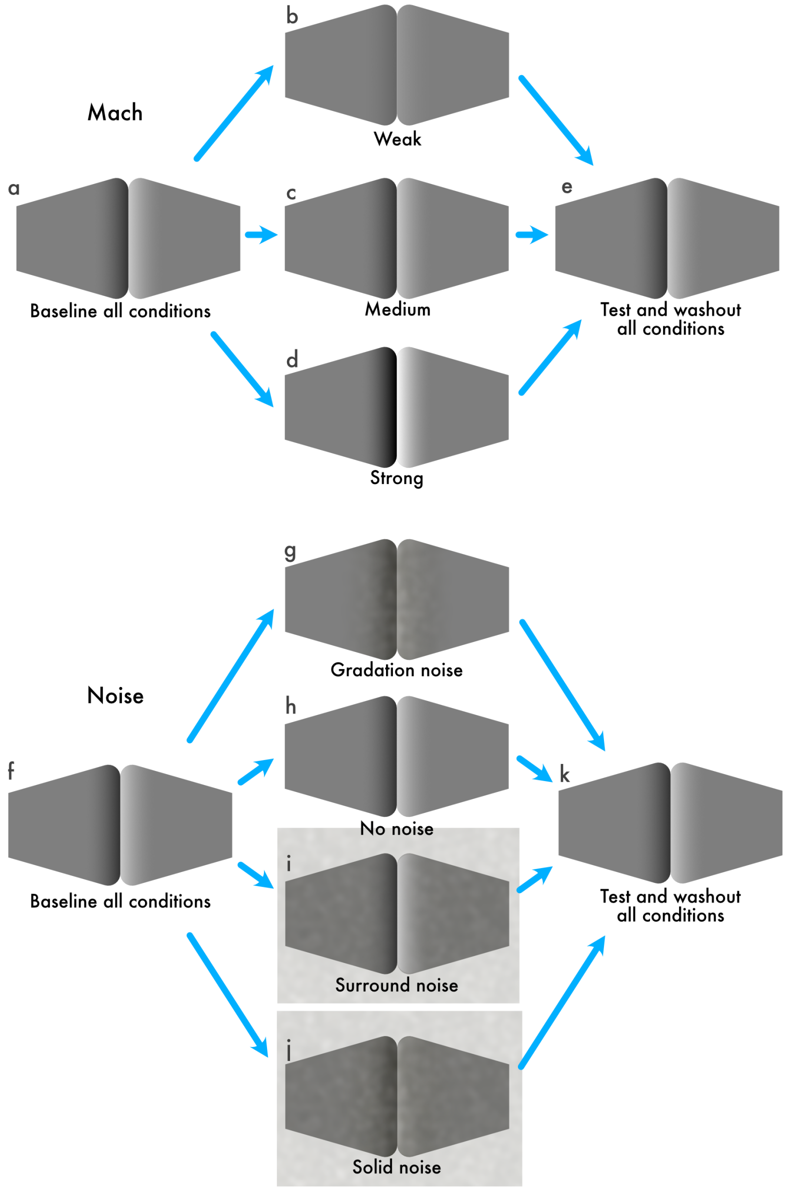


Figure 1 Examples of stimuli used from baseline to training to test and washout blocks, here demonstrated using panels of contrast 0 (where the panels are of identical lightness). Note how the Medium Mach condition (c) and No Noise condition (h) remained unchanged from the baseline and test stimuli that were used in all conditions (a,e,f,k). Descriptions of contextual cue changes: (a,e,f,k) baseline and test stimuli for all conditions used Mach bands of 0.6 opacity; (b) Mach band opacity reduced to 0.2; (c) Mach band opacity remained at 0.6; (d) Mach band

opacity increased to 1.0; (g) noise overlay of opacity 0.5 covering only the Mach bands; (h) no noise overlay, unchanged from baseline; (i) noise overlay of 0.5 opacity covering everywhere except the Mach bands; (j) solid noise overlay of 0.5 opacity covering everything.

With each bin providing a measure of illusion strength (based on proportion of incorrect responses in the 15 illusion trials per bin), we measured illusion strength throughout the baseline block, across the training block, and then again in a test block at the end. The test block was identical to the baseline block, where no noise overlays were present and Mach bands were set at 0.6 opacity. The test block was there to assess if there was any lasting change in how the stimulus was perceived when baseline conditions returned (0.6 opacity Mach bands, no noise). We included two additional washout blocks of just two bins each to see how long any potential training effects lasted.

Figure 2 Experiment structure. Inaccuracy measures were calculated for each participant for each bin of 29 trials, where a range of panel combinations were presented (29 stimuli, 15 different contrasts). Thin lines separate each bin and thick separating lines indicate where a pause occurred

There were opportunities for the participant to take a break or just pause briefly after every block or every three bins, whichever was shorter. The participant pressed the space bar to resume at a time of their choosing. Written instructions were provided on screen before the task begun, which the participant could progress through at their own pace. Two practice trials were also provided at the start. The Cornsweet stimulus in the first practice trial remained on screen until the participant performed a key response. In the second practice trial, as with the rest of the experiment, the Cornsweet stimulus remained on screen for two seconds. In the two practice trials only, progression was only achieved with a correct key press. Otherwise, no form of feedback was provided at any point during the task.

2.4 Data analysis

In all our analysis, we focused on the proportion of incorrect responses in illusion trials as our measure of illusion strength, which arises from the combining of old and new information to guide perception. To explore the unique training effects of each condition and for a deeper look at possible differences in adaptation processes between populations, we modelled the response data with a generalised linear mixed effects model (GLMM), that focused on the block-by-block changes in response inaccuracy (5 levels: baseline, training, test, washout 1, washout 2) and the conditions in each experiment which weakened or strengthened contextual cue salience (3 levels in Experiments 1, 3 and 4: MachWeak, MachMedium, MachStrong; 4 levels in Experiment 2: NoiseGradation, NoiseNone, NoiseSurround, NoiseSolid). Mixed effects models include random effects as well as fixed effects and facilitate statistical inference of uneven sample sizes, and are useful for examining repeated measurements in multi-level structured data (Yu et al., 2021). Specifically, it was useful for us to make statistical inferences about the difference between younger adults, older adults and adults with Parkinson's despite different sample sizes, and examine block-group interactions where blocks were formed of variable bin numbers.

To understand how illusion strength changed over time as a result of the experimental conditions, we devised a GLMM with group and block as fixed effects, and participant-level intercept term (ID) as a random effect to prevent inappropriate pooling of data. The data structure was a table with 22 rows per participant, with each row corresponding to one bin. For each group of participants, we added parameters to this core element (group + block + (1 | ID)) and compared models by plotting residuals, comparing AIC and BIC values, likelihood ratios, comparing adjusted R^2 values and noting the confidence intervals of the covariance parameters (Harrison et al., 2018). Using Matlab, we applied a base model using the *fitglme* function with notation:

$$\text{incorrect} \sim \text{group} + \text{block} + (\text{group:block}) + (1 \mid \text{ID})$$

The variable *incorrect* contained an inaccuracy value between 0 and 1 for the 15 illusion trials in that bin; *group* is the table column indicating the condition that trial was a part of (MachWeak, MachMedium or MachStrong) and *block* indicates which block the trial belongs to (baseline, training, test, washout 1, washout 2). *group:block* was included to assess the interaction between the two we expected, with baseline blocks being identical across groups before training block conditions diverged. Participant identifier (*ID*) was included as a random intercept to indicate the nesting of unique participants in each group with no crossover and prevented inappropriate clustering as participant IDs appeared in multiple rows (Harrison et al., 2018). This base model was applied to each experiment and compared to reduced and alternative models to assess the significance of factors of interest. Finally, all GLMMs used the maximum pseudo likelihood fit method and an identity link function.

We used this same model structure for each experiment, changing it only to examine population differences by grouping data from Experiments 1, 3 and 4 and adding one term, *population*, to reflect which experiment the participant were part of, including it as a fixed effect by itself and as part of a three-way *group* x *block* x *population* interaction. We examined main effects of group, block and group x block interactions by comparing the full model with reduced models using the likelihood ratio test (LRT). We then explored the effects of training (both during training and after) by subtracting mean baseline inaccuracy for each participant from the rest of the blocks and using 95% confidence intervals to indicate whether or not the illusion strength was significantly different from baseline.

3. Results

3.1 Experiment 1

The GLMM for younger adults in Experiment 1 incorporated *block*, *group* and a *block* x *group* interaction with Bayesian information criteria (BIC) = -3321.5, likelihood ratio = 1729.3 and R^2 = 0.671 (Table 1), which was significantly better than the null model (LRstat = 1990.8, ΔDF = 16, $p < .001$). For full model comparisons, see Supplementary Table 1.

$$\text{incorrect} \sim 1 + \text{block*group} + (1 + \text{ID}) + (1 + \text{bl})$$

In line with the principle of marginality which implies interaction effects should not be tested in the absence of their inclusion as main effects (Wagenmakers et al., 2018), to assess the significance of main effects, we instead compared a reduced version of this model without the *block* x *group* interaction (*incorrect ~ 1 + block + group + (1 ∣ ID) + (1 ∣ bl)*) to reduced models without either *block* or *group* with LRTs (Supplementary Table 1). Resultantly, we demonstrated a significant main effect of *block* (LRstat = 41.82, ΔDF = 4, $p < .001$), and for *group* (LRstat = 51.48, ΔDF = 2, $p < .001$). As we expected, there was a significant interaction between block and group (LRstat = 948.25, ΔDF = 8, $p < .0001$), revealed by comparing the full model above to a reduced model without the interaction. Training interventions thus uniquely affected illusion strength, while baseline illusion strength, included as a random effect, may explain some of the variance in overall illusion effect across all blocks.

Being exposed to stronger Mach bands during training increased illusion strength during that block in comparison to baseline (N = 30, mean inaccuracy change = 10.1%, 95% CL [5.58 14.61]). Afterwards however, as shown in Figure 3, illusion strength decreased relative to baseline in the test block (N = 30, mean inaccuracy change= -7.85%, 95% CL [-11.53 -4.17]) and did not return to baseline even by the second washout block (N = 30, mean inaccuracy change = -5.28%, 95% CL [-9.76 -0.80]). The effect was significantly different within-subject compared to baseline, but was not significantly different across-subjects compared to unchanged Mach bands. Strong Mach Training therefore increased illusion strength acutely but weakened the illusion effect experienced by participants when returning to baseline conditions.

Being exposed to weaker Mach bands during training decreased illusion strength during that block in comparison to baseline (N = 33, mean inaccuracy change = -19.1%, 95% CL [-22.08 -16.04]), but afterwards, illusion strength increased relative to baseline in the test block (N = 33, mean inaccuracy change = 3.6%, 95% CL [0.42 6.81]) before returning to baseline levels in the first washout block (N = 33, mean inaccuracy change = 3.24%, 95% CL [-0.22 6.7]). In the within-subjects comparisons, participants demonstrated a weaker illusion effect during Weak Mach Training, which resulted in a stronger subsequent illusion effect.

Perhaps surprisingly, participants exposed to unchanged Mach bands during training experienced a decrease in illusion strength in that block in comparison to baseline (N = 29, mean inaccuracy change = -3.66%, 95% CL [-6.6 -0.73]). Afterwards, illusion strength returned to baseline in the test block (N = 29, mean inaccuracy change = -1.17%, 95% CL [-4.99 2.65]) and remained for washout blocks (N = 29, mean washout 1 change = -2.8%, 95% CL [-7.10 1.34] and mean washout 2 change = -1.18%, 95% CL [-6.07 3.7]). Being exposed to the same conditions throughout saw participants experience a dip in illusion effect which levelled out and remained unchanged in test and washout blocks.

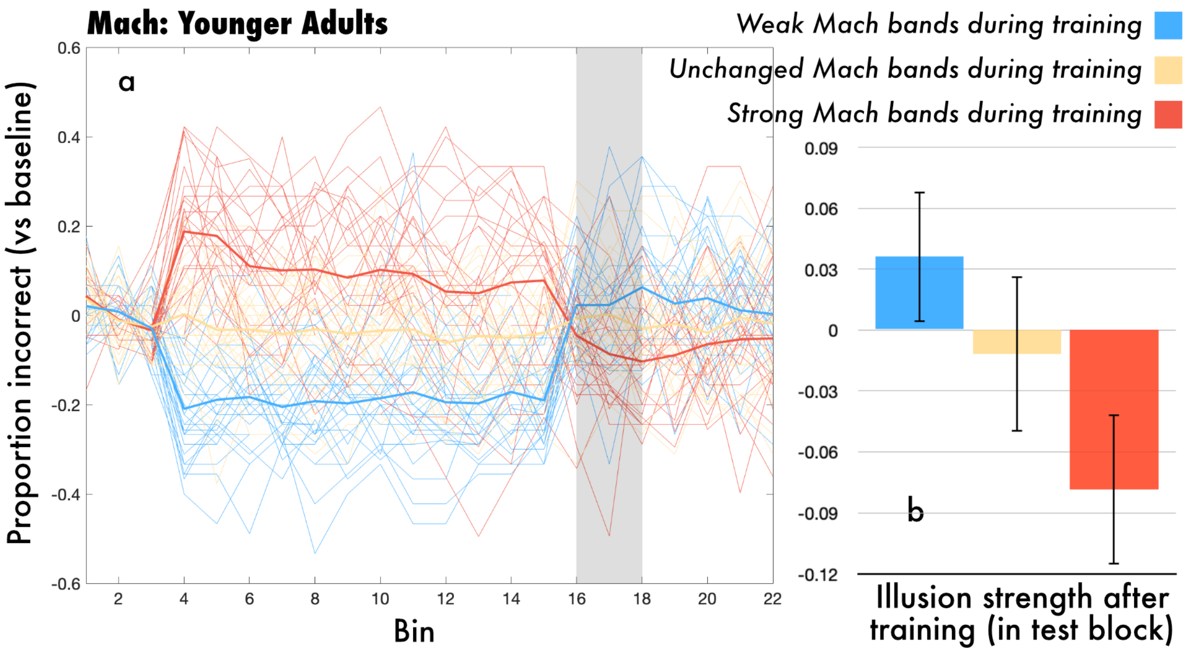


Figure 3 Illusion strength changes from baseline in Experiment 1. (a) Proportion of incorrect responses for each bin for the three conditions. Thick lines show group means, while thin lines represent individual participants. All values have had the individual mean baseline score subtracted to demonstrate illusion strength relative to baseline. (b) Bar chart showing the mean test block response inaccuracy compared to baseline (grey zone in (a)) with error bars displaying 95% confidence intervals. Strong Mach bands (100% opacity) during the training block caused more incorrect responses (greater illusion strength) during that training block, but illusion strength dropped below baseline in the test block. Conversely, illusion strength was weakened during training for participants exposed to weak Mach bands (20% opacity), but actually increased in the test block when the original 60% opacity Mach bands returned.

3.2 Experiment 2

The GLMM for younger adults in Experiment 2 incorporated *block*, *group* and a *block* x *group* interaction with Bayesian information criteria (BIC) = -3705.3, likelihood ratio = 1942.5 and R^2 = 0.622 (Supplementary Table 2), which was significantly better than the null model (LRstat = 2068.8, ΔDF = 22, p < .001). For full model comparisons, see Supplementary Table 2.

incorrect ~ group + block + (group:block) + (1 | ID) + (1 | bl:group:block)

Through comparison of one reduced model (*incorrect ~ 1 + block + group + (1 | ID)*) to reduced models without either *block* or *group* with LRTs (Supplementary Table 1), we demonstrated a significant main effect of *group* (LRstat = 23.486, ΔDF = 3, p <.001), but not for *block* (LRstat = 5.901, ΔDF = 4, p = .207). A comparison of our starting model including *block*, *group* and a *block* x *group* interaction (*incorrect ~ 1 + block*group + (1 | ID)*) with a reduced model without the interaction (*incorrect ~ 1 + group + block + (1 | ID)*) revealed a significant interaction between *block* and *group* (LRstat = 695.44, ΔDF = 12, p < .001). Training interventions uniquely affected illusion strength, while baseline illusion strength interacted with group and block in a three-way interaction as a random effect.

As shown in Figure 4, being exposed to relatively stronger Mach bands via a surround noise condition during training increased illusion strength during that block in comparison to baseline (N = 28, mean inaccuracy change = 14.1%, 95% CL [10.05 18.23]). Afterwards, illusion strength decreased relative to baseline in the test block (N = 28, mean inaccuracy change= -4.78%, 95% CL [-8.36 -1.20]) , returned towards baseline levels in the first washout block (N = 28, mean inaccuracy change = -3.61%, 95% CL [-7.69% 0.47%) and dipping back below baseline in the second washout block (N = 28, mean inaccuracy change = -3.95%, 95% CL [-7.80 -0.10]). Within this group, Strong Mach Training via a surround noise overlay therefore increased illusion strength acutely but weakened the illusion effect experienced by participants when returning to baseline conditions.

Being exposed to weaker Mach bands during training via a noise overlay targeting only the Mach bands decreased illusion strength during that block in a within-subjects comparison to baseline performance (N = 30, mean inaccuracy change = -14.6%, 95% CL [-17.69 -11.51]). Afterwards, illusion strength returned to baseline in the test block (N = 30, mean inaccuracy change = 2.84%, 95% CL [-1.02 6.71]), remaining there until the last washout block (N = 30, mean inaccuracy change = 0.77%, 95% CL [-2.93 3.44]). Participants demonstrated a weaker illusion effect during Weak Mach Training, which resulted in a stronger subsequent illusion effect.

Participants exposed to unchanged stimuli and participants exposed to solid noise overlay followed a similar pattern of illusion effect changes. Illusion strength remained unchanged in the unchanged stimuli group (N = 27, mean inaccuracy change = -1.42%, 95% CL [-4.93 2.09]) and in the solid noise group (N = 27, mean inaccuracy change = -2.75%, 95% CL [-6.22 -0.73]). Illusion strength remained unchanged through the test block (Figure 4) until the last washout block in both groups (unchanged stimuli in washout block 2: N = 27, mean inaccuracy change = 0.85%, 95% CL [-4.44 6.14]; solid noise group in washout block 2: N = 27; mean inaccuracy change = 0.0%, 95% CL [-4.68 4.65]). Being repeatedly exposed to both unchanged stimuli and stimuli with an overlay that equally affected the target and contextual elements saw no changes in illusion strength over time.

A similar pattern of results was evident in Experiment 2 compared to Experiment 1, but with a weaker and non-significant post-training effect of the manipulation that reduced Mach band salience in Experiment 2 (see blue elements of Figures 3 and 4). Further, a solid noise overlay left illusion strength unchanged in that particular group, as with the unchanged stimuli. Owing to the significant effects of Weak Mach Training and Strong Mach Training in Experiment 1, and the apparent redundancy of a solid noise overlay condition, we took forward the task from Experiment 1 forward into the subsequent experiments with older adults with and without Parkinson’s disease.

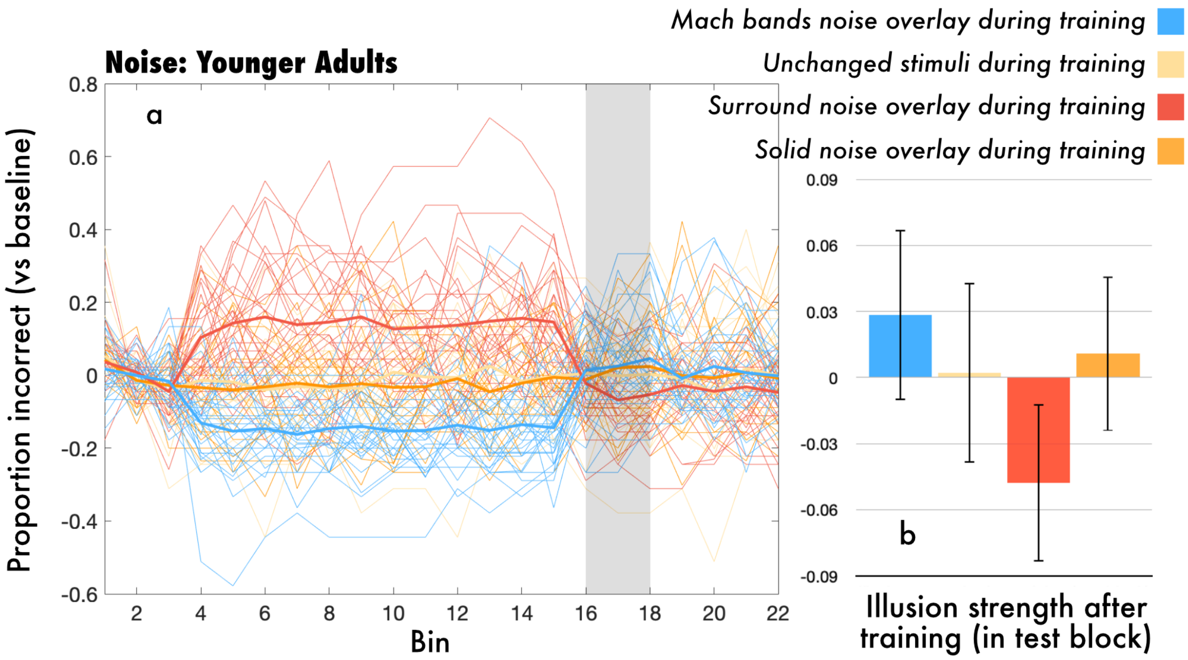


Figure 4 Illusion strength changes from baseline in Experiment 2. (a) Proportion of incorrect responses for each bin for the four conditions. Thick lines show group means, while thin lines represent individual participants. All values have had the individual mean baseline score subtracted to demonstrate illusion strength relative to baseline. (b) Bar chart showing the mean test block response inaccuracy compared to baseline (grey zone in (a)) with error bars displaying 95% confidence intervals. A noise overlay targeting Mach bands (blue) weakened illusion strength during training, and a noise overlay targeting elements surrounding but not including the Mach bands (red) increased illusion strength during training. Only the surround noise condition in this experiment saw a change in illusion strength in the test block where illusion effect was weakened, suggestive of a waning effect after repeated exposure to salient cues.

3.3 Experiment 3

The GLMM for older adults without Parkinson's in Experiment 3 incorporated *block*, *group* and a *block* x *group* interaction with Bayesian information criteria (BIC) = -3088.7, likelihood ratio = 1623.8 and R^2 = 0.804 (Supplementary Table 3) also with a three-way *baseline* x *group* x *block* interaction term as a random effect, which was significantly better than the null model (LRstat = 2457.1, ΔDF = 19, p < .001). For full model comparisons, see Supplementary Table 3.

incorrect ~ group + block + (group:block) + (1 | ID) + (1 | bl:group:block) + (1 | bl) + (1 | group) + (1 | block)

Through comparison of one reduced model (*incorrect ~ 1 + block + group + (1 | ID)*) to reduced models without either *block* or *group* with LRTs (Supplementary

Table 3), we demonstrated a significant main effect of *group* (LRstat = 61.111, ΔDF = 2, p <.001), and for *block* (LRstat = 67.866, ΔDF = 4, p < .001). A comparison of our starting model including *block*, *group* and a *block* x *group* interaction (*incorrect ~ 1 + block*group + (1 | ID)*) with a reduced model without the interaction (*incorrect ~ 1 + group + block + (1 | ID)*) revealed a significant interaction effect between *block* and *group* (LRstat = 1069.3, ΔDF = 8, p < .001). Block and group altered illusion strength changes with significant interaction as a main effect, and individual variation in baseline illusion strength also impacted group and block related responses to training. Secondary outcomes indicative of motor ability and daily life activities (Key Tapping Score and ADL Score) had no effect.

Strong Mach Training increased illusion strength within-subjects in the training block (N = 29, mean inaccuracy change = 11.37%, 95% CL [5.07 17.66]) but weakened illusion effect in the subsequent test block (N = 29, mean inaccuracy change = -9.63%, 95% CL [-17.45 -1.81]) which remained below baseline until the last washout block (N = 29, mean inaccuracy change = -11.22%, 95% CL [-18.66 -3.78]), shown in Figure 5. Strong Mach Training saw participants experience increased illusion strength during training but with a subsequent reduction in illusion strength.

Weak Mach Training decreased illusion strength during training (N = 30, mean inaccuracy change = -27.38%, 95% CL [-30.45 24.30]), which returned to baseline levels in the test block (N = 30, mean inaccuracy change = -3.4%, 95% CL [-7.63 0.80]) and stayed there till the last washout block (N = 30, mean inaccuracy change = -3.76%, 95% CL [-8.02 0.50]). Participants experienced a large decrease in illusion strength during Weak Mach Training, and returned to baseline levels afterwards (and were the only group to do so in this experiment).

In this experiment, participants experienced a weakened illusion effect during a training block with unchanged stimuli also (N = 29, mean inaccuracy change = -6.4%, 95% CL [-12.02 -7.8]), which remained below baseline levels for the test block (N = 29, mean inaccuracy change = -9.97%, 95% CL [-16.42 -3.53]) until the second washout block (N = 29, mean inaccuracy change = -8.80%, 95% CL [-15.52 -4.77]). It therefore appears that in the older adults of this experiment, there was a general decline in illusion strength over time, even without manipulating the Mach bands.

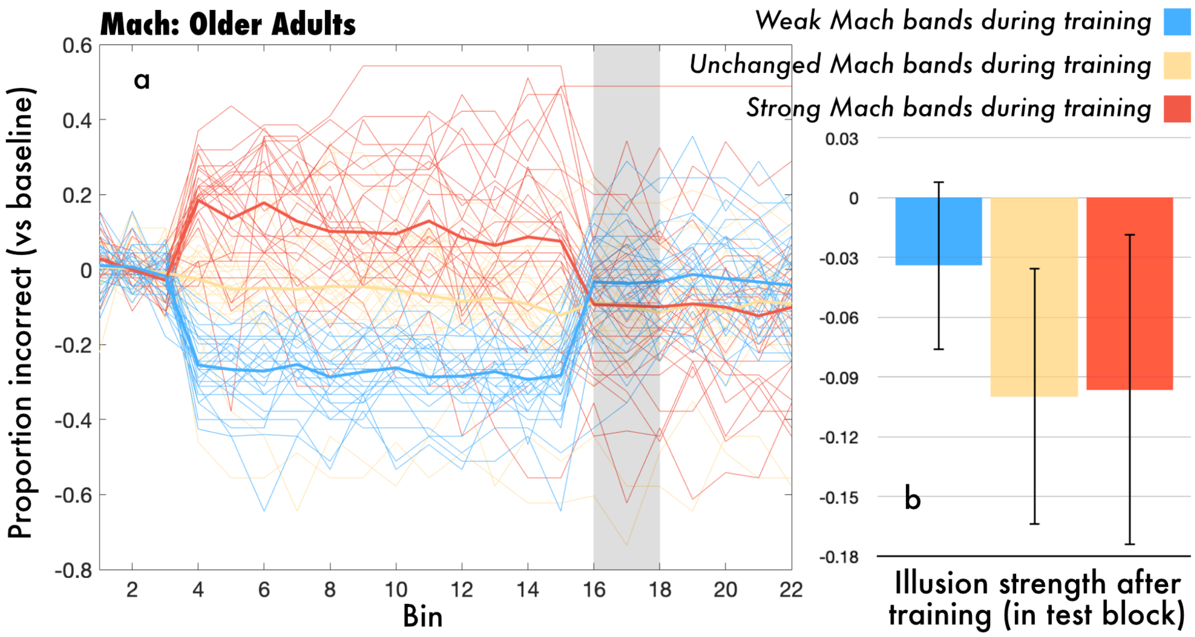


Figure 5 Illusion strength changes from baseline in Experiment 3. (a) Proportion of incorrect responses for each bin for the three conditions. Thick lines show group means, while thin lines represent individual participants. All values have had the individual mean baseline score subtracted to demonstrate illusion strength relative to baseline. (b) The bar chart shows the mean test block response inaccuracy compared to baseline (grey zone in (a)) with error bars displaying 95% confidence intervals. The test block is the first point at which participants in Weak or Strong Mach Training return to baseline conditions. Strong Mach Training sees participants experience a weaker illusion after training, but as training with unchanged stimuli achieves this too, it is likely a decline in illusion strength happens in this group anyway. In the context of a general illusion strength decline, Weak Mach Training was able to return participants to baseline levels of illusion strength, an index of contextual cue perception.

3.4 Experiment 4

The GLMM for older adults with Parkinson's in Experiment 4 incorporated *block*, *group* and a *block* x *group* interaction with Bayesian information criteria (BIC) = -1123.1, likelihood ratio = 631.32 and R^2 = 0.807 (Supplementary Table 4) also with a three-way *baseline* x *group* x *block* interaction term as a random effect, which was significantly better than the null model (LRstat = 1006.4, ΔDF = 19, p < .001). For full model comparisons, see Supplementary Table 4.

incorrect ~ group + block + (group:block) + (1 | ID) + (1 | bl:group:block) + (1 | bl) + (1 | group) + (1 | block)

Through comparison of one reduced model (*incorrect ~ 1 + block + group + (1 | ID)*) to reduced models without either *block* or *group* with LRTs (Supplementary

Table 4), we demonstrated a significant main effect of *group* (LRstat = 15.332, ΔDF = 2, p <.001), and for *block* (LRstat = 29.406, ΔDF = 4, p < .001). A comparison of our starting model including *block*, *group* and a *block* x *group* interaction (*incorrect ~ 1 + block*group + (1 | ID)*) with a reduced model without the interaction (*incorrect ~ 1 + group + block + (1 | ID)*) revealed a significant interaction effect between *block* and *group* (LRstat = 448.78, ΔDF = 8, p < .001). Various secondary characteristics such as LED Current, Time Since Diagnosis Key Tap Score, ADL and age, included as random effects, made no improvement to the model.

In Experiment 4, adults with Parkinson's similarly experienced an increase in illusion strength during Strong Mach Training (see Figure 6, N = 14, mean inaccuracy change = 14.22%, 95% CL [6.00 22.44]). Returning to baseline conditions in the test block saw illusion strength drop 11.48% (95% CL[-18.13 -4.84]) below earlier baseline levels which remained below baseline levels until the end (mean inaccuracy change in washout block 2 = -10.37%, 95% CL[-17.46 -3.29]). Strong Mach Training thus increased illusion strength during training within-subjects, but as in every experiment now, led to a decreased illusion effect in the test block.

Weak Mach Training weakened the illusion effect during training (N = 10, mean inaccuracy change = -24.25%, 95% CL[-31.02 -17.48]), and participants experienced a return to baseline illusion strength in the test block (N = 10, mean inaccuracy change = -4.23%, 95% CL[-9.34 0.87]). Illusion strength remained at baseline levels until washout block 2 (N = 10, mean inaccuracy change = -3.18, 95% CL [-9.45 3.09]). Similarly to Experiment 3, Weak Mach Training was the only training type that restored illusion strength to baseline levels.

Participants who trained with unchanged stimuli experienced a slightly lower but comparable illusion effect during training (N = 11, mean inaccuracy change = -2.39%, 95% CL[-6.65 1.87]). Reaching the test block however, illusion strength dropped significantly below baseline levels (N = 11, mean inaccuracy change = -6.57%, 95% CL[-10.23 -2.92]). Hovering just under baseline levels, illusion effect was up again slightly for washout block 1 (N=11, mean inaccuracy change = -4.68%, 95% CL[-10.39 1.04]) and washout block 2 (N = 11, mean inaccuracy change = -4.71%, 95% CL[-11.47 2.04]). Training with unchanged stimuli again suggests illusion strength declines slightly over time with repeated presentations.

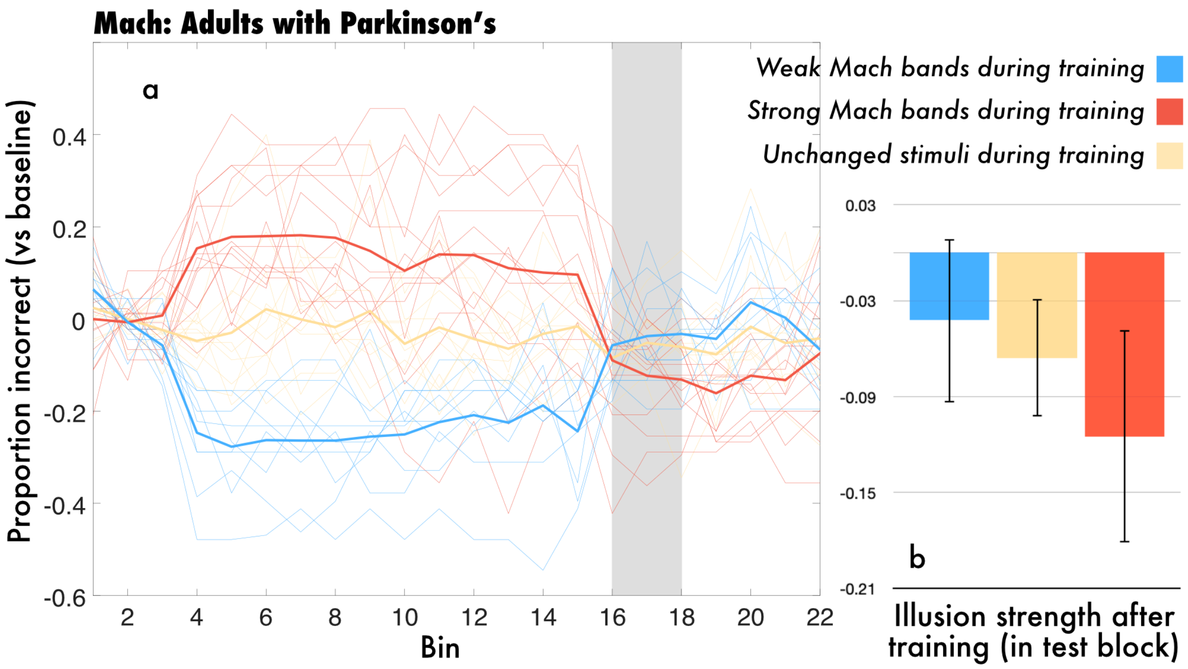


Figure 6 Illusion strength changes from baseline in Experiment 3. (a) Proportion of incorrect responses for each bin for the three conditions. Thick lines show group means, while thin lines represent individual participants. All values have had the individual mean baseline score subtracted to demonstrate illusion strength relative to baseline. (b) The bar chart shows the mean test block response inaccuracy compared to baseline (grey zone in (a)) with error bars displaying 95% confidence intervals. Strong Mach Training led to a subsequent decrease in illusion strength which lasted to the end, training with unchanged stimuli saw a slight decrease over time, significantly below baseline at test but not in the other blocks, and Weak Mach Training saw participants return to initial illusion effect levels.

3.5 Pooled analysis from Experiments 1, 3 and 4

The GLMM for all of the experiments which featured a direct Mach band manipulation were pooled together for comparison across the three population groups: younger adults, older adults with Parkinson's and older adults without Parkinson's. Baseline illusion strength (1 | *bl*) was included in all models owing to its beneficial effect on model strength in all four experiments. The best performing model for this pooled data was the GLMM *without* a population variable, neither as a main effect or when included as an interaction:

$$\text{incorrect} \sim \text{group*block} + (1 \mid \text{ID}) + (1 \mid \text{bl})$$

Population is a notable absence, where it made no significant difference to the model as main effect, revealed by comparing a base model (*incorrect* ~ 1 + *group* + *block* + *population* + (1 | *ID*) + (1 | *bl*)) to a reduced model (*incorrect* ~ 1 + *group* + *block* + (1 | *ID*) + (1 | *bl*)) with no significant effect of *population* (LRstat = 0.618, ΔDF

= 2, p = .734). To explore *population* as an interaction term, a second base model (*incorrect* ~ 1 + *group***block***population* + (1 | *ID*) + (1 | *bl*)) was compared to a model with *population* still included as a main effect (owing to the principle of marginality, Wagenmakers et al., 2018), but with a two-way interaction between group and block (*incorrect* ~ 1 + *group* + *block* + *population* + *group*:*block* + (1 | *ID*) + (1 | *bl*)). This comparison revealed the model to be best when population was not included as an interaction term (LRstat = 947.43, ΔDF = -8). For all comparisons, see Supplementary Table 5. Together, these results suggest population, while having a significant effect when looking at baseline strength only (Chapter 2), had no meaningful effect on the overall pattern of results.

4. Discussion

4.1 Training alters cue perception

Aware that a skill such as walking can be enhanced in the presence of visual cues, even with positive after-effects (Morris et al., 1996), we sought to explore changes in how contextual cues inform perception, knowing that task-relevant sensory-filtering and ongoing integration of contextual information in complex environments are harmed when basal ganglia capacity is compromised (Kearney & Brittain, 2021). Increased contextual cue salience consistently resulted in an after-effect of reduced illusion strength. Conversely, repeated exposure to Mach bands with reduced opacity did have a positive rebound effect in Experiment 1 whereby participants experienced a stronger illusion effect in the test block. This significant finding was not replicated in the following experiments. By itself, reducing salience of contextual cues is not supported here as a robust intervention to modify perceptual abilities revealed by the Cornsweet effect. However, the Weak Mach Training condition was the only condition that saw older adults (with and without Parkinson's) return to their original illusion strength in the test block; in contrast, the other conditions saw reduced illusion strength in the test block, symptomatic of a general waning of illusion strength over the course of the experiment.

In this study, we examined how participants' perception of the Cornsweet illusion adapted to increased or decreased levels of cue salience and the subsequent effects of the adapted state on the baseline level of illusion. The Cornsweet illusion task provided a simple way to continually assess the influence of context on perception, indexing how cues are being attending to. We found that the use of cues, as reflected in illusion strength, changes over time. Moreover, stronger cues increased illusion strength during the training block but reliably reduced illusion strength in the subsequent test block. No significant effect was found for population in the pooled analysis, suggesting that all participants did not vary in response to the training. This is apparent in the way that younger adults and older adults with and without Parkinson's, on average, all exhibited increased illusion strength with stronger contextual cues, weakened illusion strength with weaker contextual cues, and some degree of a rebound effect in the opposite direction.

As shown in Chapter 2, the Cornsweet illusion task involves simple visual stimuli (even if it relies on complex top-down/integration processes, see Purves et al., 1999 & Gilbert & Li, 2013). The absence of onscreen distractors may mean the task-relevant sensory filtering capacity we attribute to basal ganglia pathways is not sufficiently challenged, and thus adults with and without Parkinson's display the same pattern of illusion strength changes (Figures 5 and 6) and estimated dopamine levels had no explanatory power in our model for Experiment 4. However, we demonstrate in all experiments that participants adapt to a particular level of cue salience that impacts how cues are attended to in later conditions. The presence of such adaptation has implications for cue provision during training and forms of exercise rehabilitation, where cues can be useful to initiate an action. The adaptation effects we demonstrate suggest that excessive cue salience may prompt a reliance on artificial cues which is not necessarily helpful to improve the capacity of the nervous system to make use of often subtle or obscured information in the environment.

4.2 How can cues guide behaviour and alleviate symptoms?

According to Nonnekes and colleagues (2019), in their review of the compensatory techniques that people with Parkinson's devise to overcome motor impairments, the mechanisms by which such compensatory "tricks" work is not well understood. It has been demonstrated that a variety of sensory cues (Chawla et al., 2020; Spaulding et al., 2013), including lines on the floor (Beck et al., 2015, Morris et al., 1994, 1996), can alleviate symptoms of Parkinson's disease. What we demonstrate here is that increasing the salience of contextual cues dramatically alters perception of panel brightness, as measured in the increase in illusion strength in each of the four experiments. Thus, augmented cues may be acting to shortcut the need for complex perceptual processes (such as task-relevant filtering and contextual cue integration described in Chapter 1).

Salience is a way to consider the obviousness of a stimulus, how much it grabs the attention without looking for it, or how much it stands out compared to the rest of the environment. Jenkinson & Brown (2011) argue that salient internal and external signals can increase dopamine levels in basal ganglia pathways, introducing another angle to the explanation of why particularly salient cues can aid the movement of people with Parkinson's where base dopamine levels can be depleted. Typically, cognition, perception and action are all considered separately via isolated approaches in psychology and neuroscience (Cisek, 2019; Song et al., 2019).

However, attentional focus is an important aspect of movement: directing athletes' foci toward movement consequences in the surroundings can enhance movement and motor skill learning (Wulf et al., 2001, 2009, 2010), but directing focus toward limb movements can worsen skill performance (Bosch, 2015; Sadnicka & Kornysheva, et al., 2018).

Borrowing Marc Jeannerod's definition of intentional movement as the "means by which the organism and environment reciprocally interact" (in Malabou, 2008, p.75), it is no surprise that changing the environment affects movement and perception, shown very simply here in how contextual cue salience alters panel brightness perception. Of interest, is not just creating an environment full of salient cues that instantaneously improve skill performance. However useful it might be to tape bright orange lines on the floor en route to all one's favourite locations (or more realistically: Badarny et al., 2014; de Oliveira et al., 2021), highly salient cues may, less usefully, reduce cue sensitivity. A particular aim here was to explore how perceptual ability is altered through the modification of contextual cues.

4.3 Implications for training and rehabilitation

In the context of a general decline in illusion strength, evidenced in the groups presented with unchanged cue salience, Weak Mach Training effects are encouraging. However, this rather reinforces the findings that we adapt to the sensory conditions present, rather than proposing that subdued sensory input comprise a new approach to training and rehabilitation. If highly salient contextual cues do indeed harm the perceptual ability measured by Cornsweet illusion task, then how can lines on the floor sometimes display a lasting improvement in walking performance (Morris et al., 1996) and when might this approach be useful as opposed to those which increase processing demand (Ridgel et al., 2009, 2015; Ridgel & Ault, 2019) and intentionally decrease reliance on visual information (Sage & Almeida, 2009, 2010)?

James T. Enns describes, in *The Thinking Eye, The Seeing Brain* (2004, p.257-263), anti-gravity hills. Such hills are particular locations where it appears that something like a ball or car can roll *up* hill. The key to these locations, Enns argues, is the true horizon being hidden from view, multiple surface planes being *in* view, and a local story about the location to inform the experience. The point here, is that context is continually informing perception; there is a flowing river of signals shared between organism and environment, and so in the absence of an obvious give-away about which way is up (the horizon), other sources of information take its place. Sometimes, though, it is hard to attend to any useful sources of information. When meaningful engagement with the environment is not possible, such as for patients with near-total degeneration of the inner-ear causing a perpetual sense of falling and inability to balance, signals delivered to the tongue from a head-mounted accelerometer help the person to both meaningfully interact with the environment while wearing it, but then also for a short period after the device is removed (Bach-y-Rita, 2005; Doidge, 2008, p.1-26; Tyler et al., 2003). This sensory substitution approach was so successful that the duration of the after-effects after each session of use got longer and longer until the device was no longer needed (Doidge, 2008).

In Badarny and colleagues' (2014) study, perhaps something similar occurs: training in a virtual-reality, tiled-floor environment elicited residual as well as acute improvements in some people with Parkinson's (though with long term assessment of its effects still necessary). Some participants in that study described thinking about the virtual tiled floor after the headset was removed, providing a new attentional focus, but the intervention also could have enhanced walking enough to begin to pick up on new and useful feedback sources elsewhere. The risk of course, is that excessive use of highly salient contextual cues reduces the demand on the nervous system, on the participant, to be challenged and stretched (Lewis et al., 2000; O'Connor et al., 2017). Analogously, M.R. O'Connor in her book *Wayfinding* describes how navigation technology may help find a way quicker, but shifts the responsibility onto the technology. As such, recent tools like GPS bypass much of the needs for skilful navigation and connection with place nurtured over time, and resultantly harms spatial memory (Dahmani & Bohbot, 2020).

4.4. Conclusion

In this chapter I have shown that the influence of contextual cues on perception changes through repeated presentation, whereby Strong Mach Training led to negative residual effects in illusion strength, and Weak Mach Training led to either a stronger illusion in the test block or a return to baseline levels. Thus, while others have shown highly salient cues in training can be useful tools to improve kinematic measures (Beck et al., 2014; Morris et al., 1994, 1996), perceptual ability is not necessarily being trained in the way we might hope. Here, acute changes in the Cornsweet illusion effect – that indexes sensory integration processes – are generally followed by rebound effects in the opposite direction. Using this novel Cornsweet illusion task, we demonstrated that illusion strength can indeed be "trained", revealing the effect of cue salience on the perceptual processes that are elsewhere important in movement.

Melt

The language to communicate is not
needed beforehand. Only a willingness to
engage, to be present. Wholly present.

Our boundaries melt away, the reality
of our radical openness recognised, a
wholeness tasted. The language to communicate
is not needed beforehand. It emerges here.

We want to possess the map first.
It is called allocentric knowledge.
Like following a blue arrow on Google Maps,
we know where to go before we go, seated
on a lofty throne.

Far richer is egocentric knowledge.
It is when we only know the route
at the journey's end. Part of a whole.
Wholly present, we submit to the adventure
without seeing from above. A map not needed,
except to tell stories of where we have been.

> Fragments in this first sense is a reality of being creatures who can only apprehend with our senses in bites, in touches, in smells, in sounds, and in focused but shifting sight. We live in the reality of these pieces where the world is always too much for us to hold all at once. We creatures live in pieces, and we come to know our redemption in pieces.

Willie James Jennings, *After Whiteness*, p.34

Chapter 4

Sensory suppression training does not uniquely enhance performance in a pegboard task

1. Introduction

In the classic force-matching task, a popular measure of sensory attenuation, older adults respond in a more context-specific manner whereby the divergence in force-production between two types of matching conditions (direct and indirect) is larger than that of younger adults (Wolpe et al., 2016). We demonstrated this increase in the incorporation of a unique context into stimulus perception in Chapter 2 with the Cornsweet illusion task, and this ability that may well emerge with greater experience (Chambers et al., 2018; Idei et al., 2021), especially given an apparent absence of sensory attenuation in infants (Meyer & Hunnius, 2021). However, it has also been suggested that increased sensory attenuation – the distinct perception of an identical stimulus owing to its unique context – may emerge as compensation for worsened tactile sensitivity (Seidler et al., 2010; Wolpe et al., 2016; though see Parthasharathy et al., 2021).

Context-dependent processing, in a complex enough task, worsens in Parkinson's (Wolpe et al., 2018), but symptom severity can be improved with movement training in low light conditions (Sage & Almeida, 2009, 2010). Such exercise during low light conditions was intended to focus attention toward proprioceptive control and away from visual guidance, but could also be explained as a response to increased sensory uncertainty, much like the compensation explanation in older adults. This uncertainty explanation has already been used to explain symptoms in Parkinson's: weak predictive signals are thought to impair movement by failing to attenuate sensory input and thereby giving the person with Parkinson's an overwhelming sense of not moving (Brown et al., 2013). In such a framework, the rehabilitation possibility offered is one where sensory uncertainty could also be used to shift demand onto prior signals to enhance neural capacity (or just predictive weighting) for improved navigation of uncertain environments, not just ones filled with highly salient, certain sensory signals. In the two differing populations who are thought to display lowered sensory sensitivity in different ways, it appears that altering environment properties (reduction in peripheral tactile sensitivity and low-light conditions) alters a sensorimotor processing ability that could be important for moving through complex environments (Kearney & Brittain, 2021).

With this background, we sought to see how reducing both tactile and visual input during a pegboard task, performed across two sessions on separate days, would affect movement and retention in young healthy adults. The compensation explanation in the elderly and the uncertainty explanation in Parkinson's stem from the concept of increased reliance on memory (or priors) to navigate conditions of uncertainty as predicted by Bayesian-informed models of action and perception (Knill & Pouget, 2004; Körding & Wolpert, 2004). If these compensation and uncertainty explanations are true, and if they generalise beyond these populations, then we can hypothesise that better pegboard performance will emerge towards the end of Day 1 and on Day 2 in participants performing the pegboard tasks gloved and blindfolded, owing to the uncertain conditions demanding more from the participant's predictive capacity, which supposedly underpins optimal motor control. Further, training under uncertain conditions in training (blindfolded and gloved), should benefit performance under uncertain conditions in testing (blindfolded) and Day 2 training (blindfolded). Testing participants with and without vision offered a way to assess training effects specific to sensory context (absence or presence of vision), and we briefly discuss different perspectives by which alterations in the sensory environment might evoke neural adaptation.

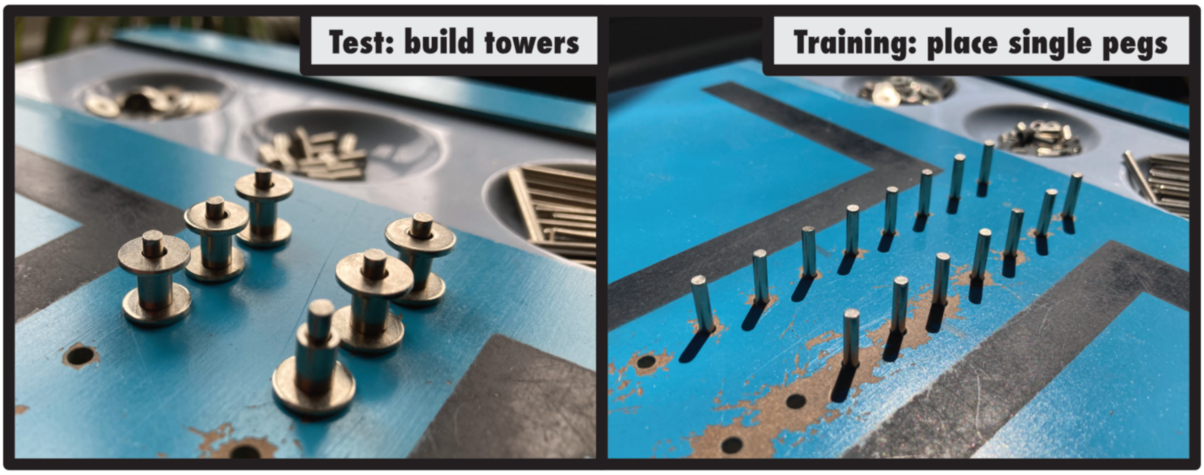


Figure 1 In test trials, participants built "towers" that consisted of 4 components: a peg, two washers and a collar. Participants built as many as they could in 30 seconds, with the number of accurately placed parts counted at the end. This task was performed at the start, middle and end of the session each day in both groups and in standard vision and blindfolded conditions. In training, participants placed single pegs, aiming for as many as they could, also in 30 second trials.

2. Methods

Twenty participants took part in this study, split evenly between and assigned randomly to one of two group. The Jamar Pegboard tasks require fine motor skill and complex movements to pick small metal pieces from bowls and reorient them onto the pegboard. The researcher demonstrated the two pegboard tasks to the participant. In the tower task, the participant built towers (Figure 1) with four components. In the peg task, participants filled the holes on the board solely with pegs. The tower task used for testing was performed blindfolded first and then with vision available, while the peg task was completed under training conditions specific to each group (Figure 2). Both groups completed tests in the same conditions, and additionally, both groups completed Day 2 under the same experimental conditions. For Day 1 training however, if the participant was in the uncertainty group, they trained on Day 1 with latex gloves on both hands and a blindfold covering both eyes. In the full-senses group for Day 1 training, no attempt was made to suppress sensory input.

Every trial that formed the training and test blocks lasted 30 seconds, and the participant tried to assemble as many towers or place as many pegs as possible. Performance was measured by the number of pieces accurately placed on the board at the end of the 30 seconds. For the towers task used for testing, this included the peg, a washer, a collar and another washer, in that order, and pieces of incomplete towers were still counted providing (1) they were accurately placed and in the right order, and (2) that there were no more than two incomplete towers at the end of the trial. We analysed performance in the vision and non-vision towers task in two separate 2(training group) x 6(time of towers task) repeated measures analyses of variance (ANOVA). Another ANOVA, 2(training group) x 6(test-difference at each time point), was used to assess the convergence of test scores in vision and non-vision conditions with the expectation that performance in blindfolded conditions (non-vision tests) could improve more in the uncertainty group, whereas performance in vision tests could improve more in the full-senses group leading to a convergence in the former and a divergence in the latter.

Finally, the researcher in each session recorded the strategy employed by each participant in the training blocks in their attempt to place as many pegs as possible. It quickly became apparent that peg-placing strategies fell into two categories: guided and unguided. In the guided strategy, participants would use one hand to find the target hole and the other hand to move the peg to the hole. And in the unguided strategy, participants would simultaneously have a peg in each hand moving the pegs towards the target holes without the guidance of the other hand.

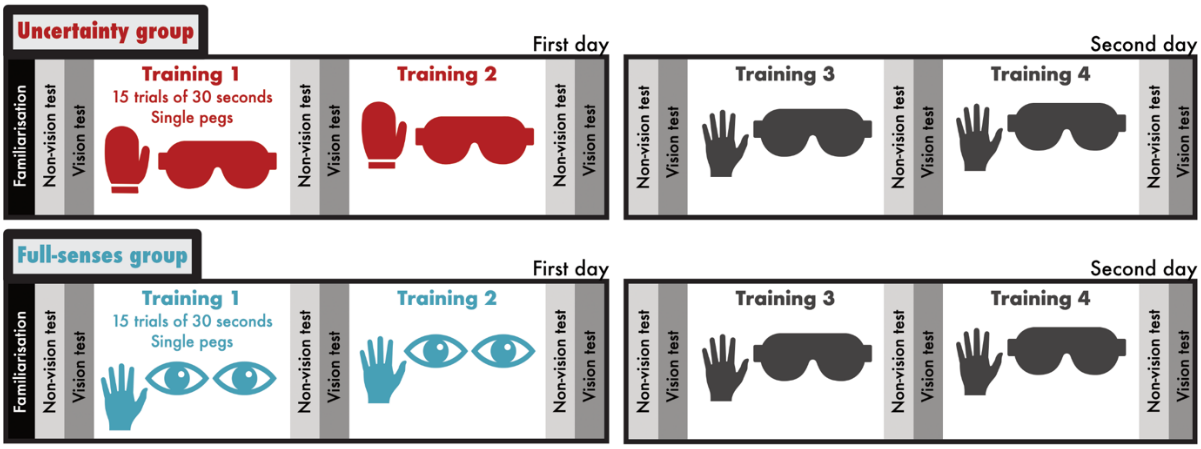


Figure 2 The experimental protocol was spread over two days, with the same towers task repeated by both groups six times interspersed throughout, but different sensory conditions for the Day 1 single peg training blocks. Day 2 was performed under the same conditions for both sets of participants.

3. Results

3.1 Analysis of training and group effects on test performance

T-tests revealed no group difference at baseline in the first vision ($t(18) = 0.534$; $p = .600$) and non-vision ($t(18) = 0.228$; $p = .822$) towers tasks. There was significant effect of time point of test in the vision tests ($F(5, 90) = 15.045$, $p < .001$, $\eta^2 = .127$) and the non-vision tests ($F(3.313, 59.635) = 17.754$, $p < .001$, with Greenhouse-Geisser sphericity correction, $\eta^2 = .202$) indicating improvement in performance, but no significant effect of group ($F(1, 18) = 0.482$, $p = .496$ for vision tests & $F(1, 18) = 0.778$, $p = .39$ for non-vision tests) nor group and time interaction ($F(5, 90) = 0.482$, $p = .496$ for vision tests & $F(3.313, 59.635) = 1.590$, $p = .197$ with Greenhouse-Geisser for non-vision tests). Further, there was no significant change in the difference between vision and non-vision tests across time ($F(5, 90) = 1.318$, $p = .263$), no main effect of group ($F(1, 18) = 0.158$, $p = .696$), and no significant interaction with group ($F(5, 90) = 1.603$, $p = .167$). In sum, the two groups performed similarly at the start of the experiment and both improved peg-placing skills across the course of the experiment evidenced in improved test performance. However, there were no between-group differences as a result of their distinct Day 1 training procedures.

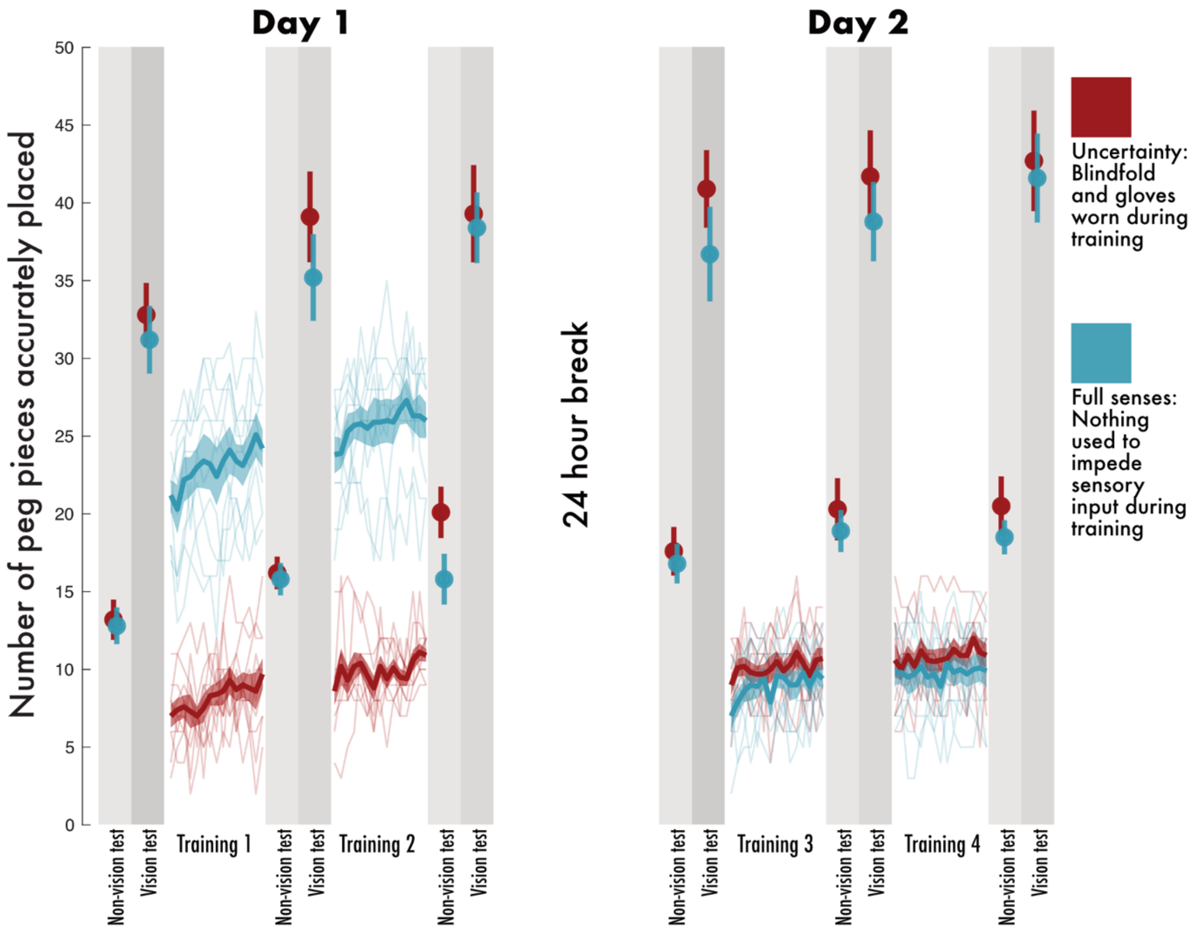


Figure 3 Number of peg pieces accurately placed in test and training trials. There were three non-vision tests and three vision tests each day (grey shading) where participants built as many towers as they could. Fifteen trials of the single peg task constituted the training blocks. Training means are indicated by thick lines with individual participants represented by thin lines. The two groups performed under different conditions in training on Day 1, but the same conditions were in place for all test trials and also Day 2 training. Standard error of the mean is indicated by vertical lines for tests and the shaded area for training.

3.2 Analysis of effect of training group on strategy employment

We observed and recorded the predominant strategy used by each participant in the single peg training on each day, and calculated the percentage usage in each training group. A chi-squared test of independence showed a significantly different strategy count on Day 1 between groups ($\chi^2(1, N = 20) = 7.5$, $p = 0.006$, odds ratio = 3.05, 95% CL[0.58 5.54] for odds ratio) but not on Day 2 ($\chi^2(1, N = 20) = 0.220$, $p = 0.639$) when conditions became the same (Figure 4). Distinct Day 1 training conditions elicited unique strategy employment, but Day 2 training, where both groups trained blindfolded and without gloves, saw a similar proportion of guided and unguided strategies for each group.

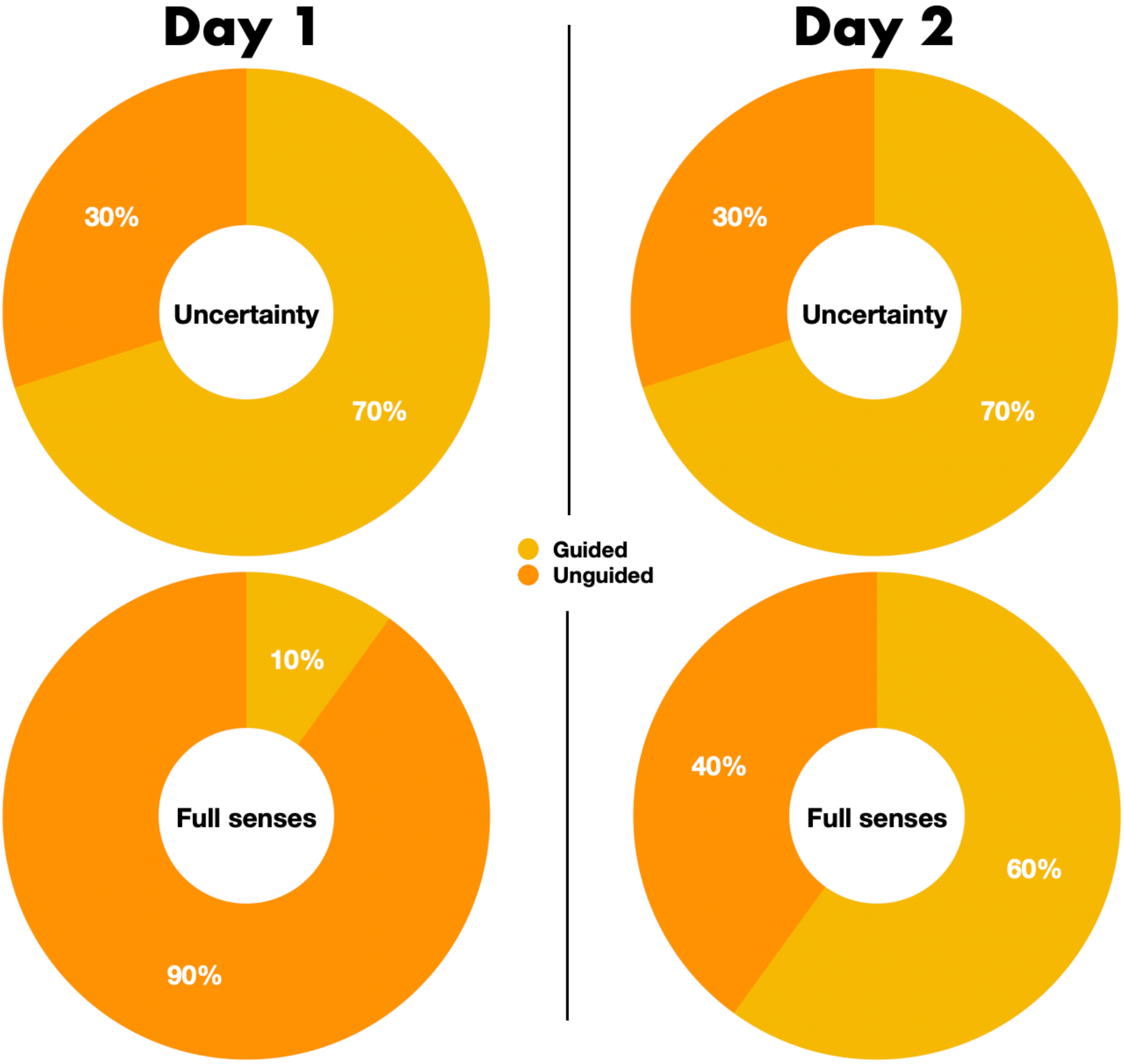


Figure 4 Two strategies emerged as participants performed the pegboard task. In what we describe as guided and unguided, participants either picked up a single peg with one hand and guided with the other hand by moving between the peg and the target location (guided), or participants picked up pegs with each hand and aimed for the target location without guidance from the other hand (unguided). Different sensory conditions appeared to drastically alter predominant strategy deployment but without lasting effect.

3.3 Post-hoc analysis: strategy and test performance

Given the significant difference in strategy based on sensory conditions, we compared pegboard test performances with strategy as the between subject factor, as part of a post-hoc analysis. Participants fit into three categories: (1) unguided strategy on both days (N = 7), (2) guided strategy on both days (N = 8) and (3) unguided then guided (N = 5); no one exhibited the other mixed strategy combination. Thus, two 3(strategy) x 6(time of towers task) ANOVAs again revealed significant main effects of time point in the vision tests ($F(5, 85) = 14.863$, $p < .001$, $\eta^2 = .123$) and non-vision tests ($F(5, 85) = 16.065$, $p < .001$, $\eta^2 = .187$), but with no evidence of main effects for strategy ($F(2, 17) = 0.930$, $p = .414$ in vision tests; $F(2, 17) = 1.771$, $p = .200$ in non-vision tests). Whilst participants approached training with unique approaches over the two days, there was no observable benefit in test performance in utilising one strategy combination over another.

3.4 Post-hoc analysis: assessing evidence for null effect of training group

Finally, in the absence of main effects for group, we performed a Bayesian repeated measures ANOVA which allows comparison to a null model, quantifying evidence for the null hypothesis (Wagenmakers et al., 2018). In the non-vision tests, the model with time of testing (tower tasks 1 to 6) as a main effect vastly outperforms the null model with a Bayes factor (BF10) of 1.773 x 109. The null model was 1.84 times more likely than the model with group as the main effect (BF10: 1.000/0.544). A two-main-effects model with both time and group (“Time + Group”) was only slightly less likely than than the “Time” model though, which outperformed the model with an added interaction (BF10: 1.043 x 108/1.358 x 107 ≈ 7.68 times more likely). In the vision tests, the null model also outperformed the “Group” model ((BF10: 1.000/0.585 ≈ 1.71 times more likely), with the “Time” model performing best (BF10 = 1.612 x 108). This analysis supports the null hypothesis stating no benefit of training under uncertain conditions on tower task performance, especially as the uncertainty group appear graphically (Figure 3) to be the slightly better performing group from the start. While the Bayes factors for the “Group” models in tower tasks with and without vision is only in the anecdotal strength range (Wagenmakers et al., 2018) with fairly small sample sizes (N = 10 in each condition), our search for a robust training principle finds little hope in this iteration of an uncertainty approach.

Table 1 Model comparisons in two Bayesian repeated measures ANOVAs for tower task performance measured at six points throughout (“Time”), with each model compared to the null model.

Model Comparison: vision tests					
Models	**P(M)**	**P(M | data)**	**BF $_M$**	**BF $_{10}$**	**error %**
Null model (incl. subject)	0.200	3.582e -9	1.433e -8	1.000	
Time	0.200	0.578	5.468	1.612e +8	0.760
Time + Group	0.200	0.374	2.388	1.043e +8	1.116

Time + Group + Time ∗ Group	0.200	0.049	0.205	1.358e +7	1.343
Group	0.200	2.095e -9	8.379e -9	0.585	0.624

Model Comparison: non-vision tests

Models	**P(M)**	**P(M∣data)**	**BF_{M}**	**BF_{10}**	**error %**
Null model (incl. subject)	0.200	2.925e -10	1.170e -9	1.000	
Time	0.200	0.519	4.309	1.773e +9	0.474
Time + Group	0.200	0.330	1.972	1.129e +9	2.243
Time + Group + Time ∗ Group	0.200	0.151	0.713	5.170e +8	1.196
Group	0.200	1.590e -10	6.361e -10	0.544	0.675

4. Discussion

4.1 Key Findings

In this experiment, we asked participants to accurately place as many pieces on the pegboard as possible in different combinations of task and sensory conditions. We were particularly interested in how masking some sensory input might change how participants move and learn. Removing vision unsurprisingly made the task harder: for both groups more pieces were accurately placed in the tower tasks when vision was available compared to when vision was not, and also in the Day 2 training performance compared to Day 1 for full-senses group (Figure 1). Additionally, in the single peg training task, the combination of blindfold and gloves in the uncertainty group served to worsen performance on Day 1. Training effects were present in all groups: participants got better overall with no benefit of training under uncertain conditions. There were small glimpses of group differences: at the end of Day 1, performance in the non-vision test was better on average in the uncertainty group, and at the start of Day 2, uncertainty group training performance was better on average in some, but not most, trials. However, there was no difference in Day 2 test performance between the two training groups. It appears then, that while sensory conditions altered immediate performance and gave rise to unique strategy employment, blindfolds and gloves did not dramatically benefit performance during tasks where sensory conditions were the same for both groups, neither in vision nor non-vision conditions.

4.2 Sensory uncertainty as a means to improve skill

Inspired by Parkinson's rehabilitation techniques that mask visual information to guide attention toward proprioceptive input, we wondered if the principle that underpinned this was in fact related to a Bayesian integration framework. Such a framework conceives motor control and perception as the balancing of outgoing predictive signals and incoming sensory signals based on their relative certainty – that is, how precise the signals are (Figure 5A). It has been suggested that Parkinson's symptoms can be explained with such a framework, where weak internal predictions in Parkinson's disease lead to less ability to overcome noisy environments (Figure 5B; Brown et al., 2013; Wolpe et al., 2018). This inability to extract signal from noise would explain why providing clear, precise sensory cues like tactile cues, auditory cues or lines on the floor can have an immediate benefit in alleviating symptoms like freezing and shuffling gait, and enabling more fluid movement (Quintyn & Cross, 1986). Such cueing approaches could increase the precision of sensory input, making the effects of weak prediction less noticeable. However, we wanted to know if the reverse could be used to improve precision of predictive signals over the long term. Could sensory uncertainty actually shift the demand onto the brain to come up with a solution itself, inducing longer term improvements in the capacity of the nervous system? Might uncertainty be the principle at work in the PD-SAFEx programme, whereby more reliable sensory input is reduced (Sage & Almeida, 2009, 2010), a programme that demonstrates lasting symptom improvement rather, not temporary symptom alleviation?

We show in Chapter 3 in Experiment 1 that reducing the salience of contextual cues can have a positive rebound effect in visual perception, while increased salience has a negative rebound effect. Elsewhere it has also been demonstrated that sensory uncertainty shifts reliance onto prior information, where in the absence of sensory feedback, participants relied on a priori knowledge to guide decision-making in a simple finger-tracing task with cursor deviations (Körding & Wolpert, 2004). However, in this study, we sought to investigate how masking sensory input affects a motor skill (Figure 5C). We found no significant evidence of positive training effects in the uncertainty group. The blindfold and gloves dramatically reduced training performance on Day 1 suggesting such conditions were at least sufficient to create uncertainty and make the task more challenging but still possible. However, the intended effect of removing visual input was to require the nervous system to source information from elsewhere, a search for task-relevant cues that the basal ganglia is implicated in (Bakhurin et al., 2017; Beeler & Dreyer, 2019; Kearney & Brittain, 2021). In the pegboard task however, it is possible this process is continually being undertaken in all sensory conditions that we implemented, as participants strived to get better.

The pegboard task is not as complex as, for example, a team sport, and the participants are able to perform the task from the start indicating some simplicity (Wulf & Shea, 2002) in contrast to, say, a juggling task with participants unable to juggle at the start of the study. However, while the pieces are uniform, it is nevertheless complex in the infinite ways pieces can be picked up, manipulated and placed by the participant, differing from a simulated computer task utilising a virtual and knowable world. As such, there is always some uncertainty, some element of the unknown, that means this search for information is always underway. Improvement was always possible and, much like how even though the best free-throw shooters in basketball still do not make all their free throws in their career, here, participant scores at the end of each pegboard trial varied despite an ever-present ability to to perform the skill of placing pegs. This fact, perhaps, poses the main issue to the notion of using sensory uncertainty to improve not just the precision of predictions, but capability of the nervous system. It is not just two signals at play, but vast fields of possible signals, where sensory input cannot so much be reduced as partly masked and therefore biased toward other input in an infinite world. Visual information was of course very useful and beneficial for placing more peg pieces in each 30 second trial, but participants simply adapted and both groups performed similarly in spite of their first day training conditions, with no advantage of training in more difficult conditions. The finding of similar pegboard skill improvement across training groups is consistent with the argument of Wulf & Shea (2002) who reconcile movement improvements from both making tasks more difficult and making tasks easier by considering them on a simple-complex spectrum.

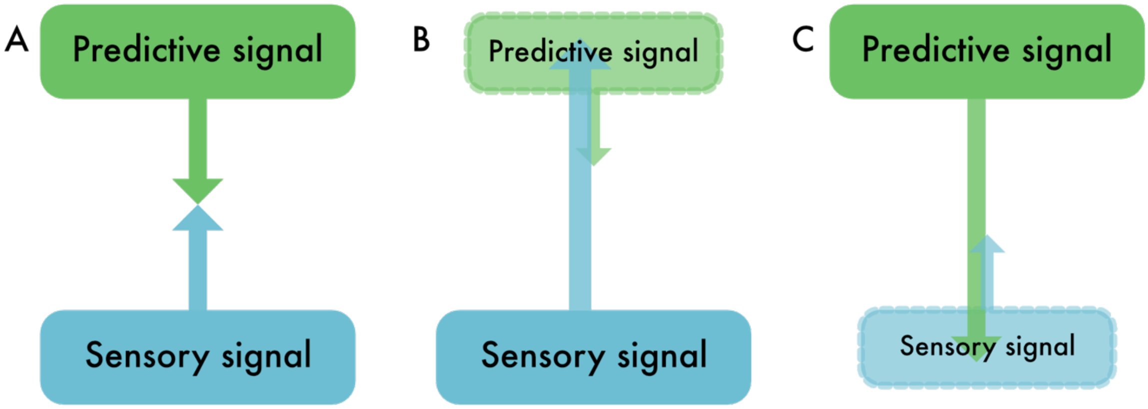


Figure 5 Schematic model of Bayesian integration approach to understanding motor control. (A) According to such a framework, signal integration is determined by relatively weighting input based on confidence, or certainty. (B) Proposed explanations of Parkinsonian symptoms using this framework suggest weak predictive signals result in an overwhelming effect of sensory input, especially of task-irrelevant signals. (C) Our approach in this experiment deliberately reduced the certainty of the sensory signals with blindfold and gloves, making the task more challenging. This could be one explanation for both motor improvements in people

with Parkinson's disease in the PD-SAFEx programme and compensatory shifts toward increased predictive weighting in healthy older age. A somewhat similar approach to sensory input reduction in Chapter 3 did show signs of a positive rebound effect, but its validity as an approach to motor improvement remained untested.

4.3 Multiple memory systems perspective

In an infinitely complex world (even inside a lab with a simple wooden pegboard), we did not so much reduce sensory input as bias it toward different sources, probably without changing the search-for-cues difficulty. The sensory masking approach could still be effective in other populations though, as the PD-SAFEx programme shows. Crucially though, the benefits of biasing sensory input may depend on there being a pre-existing over-reliance on particular sources of sensory information. People with Parkinson's tend to demonstrate a heavy reliance on vision to guide movement, which may provide clearer information in many cases, and manifests in stooping posture during walking to guide the feet visually. In the context of heavy dependence on visual guidance (Abbruzzese & Berardelli, 2003; Sacrey et al., 2009), masking visual information may be a successful approach to increasing uncertainty, where masking typically-prioritised information may then increase the demand on searching for informative cues to prompt positive training effects.

As we demonstrated in this study, sensory conditions do affect immediate performance and also the strategy employed. While strategy was not a primary outcome measure in a study where we were principally interested in movement improvement, the strategy adjustments demonstrate the flexibility of the nervous system. As Packard & Goodman (2013) point out, different environments, or contexts, elicit different memory systems, which supports the notion of altering sensory conditions to target underused or damaged systems. Similarly, the sensory substitution principles of rehabilitation outlined by Bach-y-Rita (2004, 2005) illustrate how altering sensory conditions can help participants with brain damage to meaningfully engage with their environment. It is also worth noting the success of coaching practices in sports that, rather than providing prescriptive instructions, alter qualities of the environment to coax athletes into finding their own solutions (Gray, 2020; O'Connor, 2019; Woods et al., 2020). It is not so much about making the task significantly harder, as we have done here, but perhaps about enabling deeper engagement with the sensory surround.

4.4 Sensory attenuation and the compensation explanation for increases with age

Sensory attenuation is a phenomenon whereby an identical stimulus can evoke different neural responses depending on its context and origin (Saradjian, 2015) and therefore is a useful indicator of one's ability to attend contextual cues to guide movement and perception (Kearney & Brittain, 2021). Such an ability seems important to controlling movement in complex environments, and declines of sensory attenuation measures in disease (Macerollo et al., 2015; Shergill et al., 2005, 2015; Wolpe et al., 2018) suggest higher sensory attenuation would indeed indicate a healthy central nervous system and probably better movement and perception. However, findings of increased sensory attenuation in old age (Parthasharathy et al., 2021; Wolpe et al., 2016) complicate the matter as old age is not typically associated with better motor ability (Ward & Frackowiak, 2003). Wolpe and colleagues suggest sensory attenuation increases to compensate for worsened tactile sensitivity and at least in some human populations, the selective strengthening of the basal ganglia and prefrontal pathways associated with particular sensory attenuation measures (Wolpe et al., 2016, 2018) is believed to be part of a compensatory suite of changes in response to cognitive decline. Others have suggested sensory attenuation emerges with experience (Idei et al. 2021, Chambers et al., 2018), supported by the apparent absence of sensory attenuation in infants (Meyer & Hunnius, 2021) and findings of increased sensory attenuation but unimpaired proprioception in older adults (Parthasharathy et al., 2021).

Even if advanced motor ability is not associated with older adults, increased sensory attenuation seen in older adults may indicate an advanced adaptation to noisier sensory input to maintain proficient movement in healthy ageing in spite of reported decline in tactile sensitivity. In the present study, we considered the gloves as a simulation of this noisier sensory input and thus, we expected that if the compensation explanation was true, that we might find improved performance on Day 2 induced by the uncertainty training. Accordingly, sensory attenuation has been explained by a Bayesian integration framework that highlights increased prediction signal weighting when sensory signal is noisier (Bays et al., 2006; Brown et al., 2013; Wolpe et al., 2016). We found, however, a Day 2 similarity across training groups, and therefore do not support the idea that increased sensory attenuation occurs with age as a compensation for worsened tactile sensitivity; though neither can we rule out this explanation. The compensation explanation for increased sensory attenuation requires further investigation, along with a deeper exploration of how sensory attenuation measures might accompany motor skill improvements.

The only significant difference in test performance between the two groups occurred in the third non-vision towers task at the end of Day 1 (Figure 3). The sole test-performance difference could point to practice effects of the uncertainty group training blindfolded, much like practice conditions can exhibit context-specific benefits (Godden & Baddeley 1975; Jiang et al., 2005). However, this difference subsided at the start of the next day, in spite of context-specific benefits elsewhere being reported to endure multiple days (Jiang et al., 2005). The absence of an enduring difference in this case is perhaps because of the intermittent, albeit infrequent, exposure to blindfolded training for both groups, which will have provided the full-senses group with some minimal non-vision practice.

4.5 Limitations and openings

Pilot testing in preparation for this study suggested that the wearing of latex gloves did make the task slightly more difficult; however, here, we find comparable performance between gloved and gloveless conditions demonstrated by the similarity between the first day performance of the gloved uncertainty group and the second day performance of the full-senses group. In training, we would have expected the full-senses group, as a result of both practice effects and the absence of gloves, to perform noticeably better on Day 2 compared to the uncertainty group on Day 1. We aimed to achieve a subtle difference – rejecting more difficult alternative interventions, especially as tactile change was to be compounded by absence of vision – but the intervention may well have been too subtle!

While our findings offer insight into how the absence of vision affects pegboard performance, perhaps future studies attempting to emulate minor tactile disruption might consider more difficult interventions whilst instead keeping vision available. Here, however, it was important to complete training under non-vision conditions to avoid creating an over-reliance on vision, whilst we were still able to use intermittent tower tasks to track improvements in visually guided performance. There are suggestions that gloves impede tactile sensitivity of the fingers (Novak et al., 1999; Wilson et al., 1996), contrasted with findings pointing toward no difference with or without gloves (Fry et al., 2010; Thompson & Lambert, 1995). All studies mentioned here studied surgeons who could be particularly well adapted to gloved working, and Novak et al. (1999) suggest an adaptation period of up to 120 days to get used to a new double glove ensemble. In this experiment, we hoped the gloves would subtly affect the manipulation of smaller objects and the sensitivity to a smooth, flat, wooden board.

We do, in this study, highlight limitations to the models that utilise a Bayesian framework in their ability to inform means of movement improvement in a moderately complex task. Models such as optimal control theory have been crucial in bringing sensory consequences into the equation of movement generation which have previously been absent (Versteeg & Miller, 2022). Unsurprisingly, the simple yet powerful framework does not explain the full complexity of the central nervous system. The imbalance of prediction and sensory signals offers an appealingly simple way to explain dysfunctional movement, and even to explain temporary movement improvement induced by precise sensory cues, but without, by itself, offering a way to evoke adaptation and enhancement of the brain and thus how changes in uncertainty might translate to motor skill improvement.

Package it and sell it

"Ah, it's the sugar making the fruit sweet"
So we separate it, package it, sell it.

"Ah, it's the long thighs that make this athlete so fast"
So we separate look-a-likes from the crowd,
and find a way to profit.

"Ah, today was productive"
So I pick out one element I believe made it successful,
package it up, and try to repeat it.

As if I am a machine.

As if there was a single cause.

It's not what we do, but how and why it's done.
And the how and why take life-long journeys
to unpack.

Chapter 5

Conclusion: Context-dependent movement, task-relevant sensory filtering and approaches to Parkinson's training

Context-dependent movement

A recurring conclusion throughout this thesis has been the importance of context in movement. The lines-on-the-floor effect, highlighted in the Introduction, reveal the role the environment can play in action. It also points to the inseparability of action and perception: neither exist without the other.

Linking research in Parkinson's disease to findings in sensory attenuation experiments, offered a way to reframe what was happening in these paradigms. The force-matching task can be made sense of in this way: the location of the hands provide context that contributes to the perception of force and guides the ongoing action of pressing. Chapter 2 reinforced this notion by using a visual illusion task where impact of contextual cues (Mach bands) were assessed via perception of panel contrast. Chapter 3 revealed a training effect through repeated exposure to a particular level of cue salience, showing the use of cues in training matters.

One unexpected finding was the lack of change in visual illusion strength in Parkinson's disease. As outlined in Chapter 1, basal ganglia dysfunction, which characterises Parkinson's, reduces the capacity to utilise useful cues to guide movement and perception. Even though the participants with Parkinson's did not change their medication to take part in the study, illusion strength was expected to correlate with estimated dopamine levels. As this was not the case, I suggested that the simplicity of the Cornsweet scene, and the obviousness of the contextual cues (Mach bands) was still comfortably within the capabilities of a depleted basal ganglia system. Thus, the dual functions of the basal ganglia highlighted in Chapter 1 – task-relevant filtering and then contextual cue integration – point to the importance of considering task set-up.

Figure 1 in Chapter 1 represents the prominent way researchers have considered motor control for the past two decades. One of the key aspects of this model is that the interaction begins with a motor command, moving outward into the world. From the motor command, an efference copy is used to predict upcoming feedback to overcome noise and delay in the system, and is then compared to actual sensory feedback. The comparison of the two signals gives rise to the final sensation. Bayesian integration is often used in optimal control and active inference accounts to model how this final sensation arises from the integration of predictive and sensory signals. The key here is that the integration of the two signals is probabilistic – the precision, certainty or clarity of the signal decides how influential it will be in the resulting conflation of these two signals, the posterior. Models usefully exclude certain complexities to present an understandable and useable image and this model of motor control has been useful. However, two of its key characteristics – a motor command as the starting point, and signal integration based on signal quality – relegates the insightful roles of context-dependence and task-relevance in movement.

Task-relevant sensory filtering

Where cognition, action and perception have traditionally been siloed, sensory attenuation research usefully points to a link between action and perception. However, the link that has been made is limited and restricted in scope. As highlighted in Chapter 1, many researchers have argued that motor activity uniformly suppresses input, while others have argued motor activity facilitates input. To reconcile these findings, I referred to the idea of task-relevance. Formulated during the pilot study described in the Introduction, 'task-relevance' differentiates between sensory inputs depending on their importance to task completion. Thus, even though motor involvement may appear similar, two tasks can elicit unique sensations from the same stimulus. This adds a layer of complexity to the sensorimotor integration explanations offered to explain sensory attenuation measures such as the force-matching task. The importance of task-relevance in sensorimotor processing is one conclusion of this thesis.

Another conclusion is that current theories of motor control do not fully account for this single extra layer of complexity. Optimal control theory (OCT) and active inference (AI) posit that signals are integrated probabilistically. This means the signals will be weighted based on the quality of the signal themselves, based on a pre-existing formula that establishes relative weighting based on signal quality (or certainty or precision). However, the notion of task-relevant sensory filtering highlights the potential for other influences on how signals might be weighted.

Rather than precision being a sensory evaluation (i.e. signal weighting based on signal quality), precision comes to depend on its relation to factors external to that signal. Here, the signal's relation to the task affects its integration (and perception), not just its quality.

So, we can imagine signals relating to the task arriving from the prefrontal cortex, signals relating to limb position coming from the limb and the parietal cortex, and signals from a stimulus triggered by that limb. These signals congregate in the basal ganglia, as the area of interest here. The weighting of each signal is not just determined by how loud each signal is shouting, but by its relevance to the other congregating signals.

This suggestion is a key departure from the OCT and AI frameworks and is a key implication of this thesis. Task-relevance is surely a simplification of what is going on in the brain, but it works here by adding a layer of complexity to rethink sensorimotor processing. Furthermore, it has been invaluable to better understand the basal ganglia and neurological rehabilitation techniques.

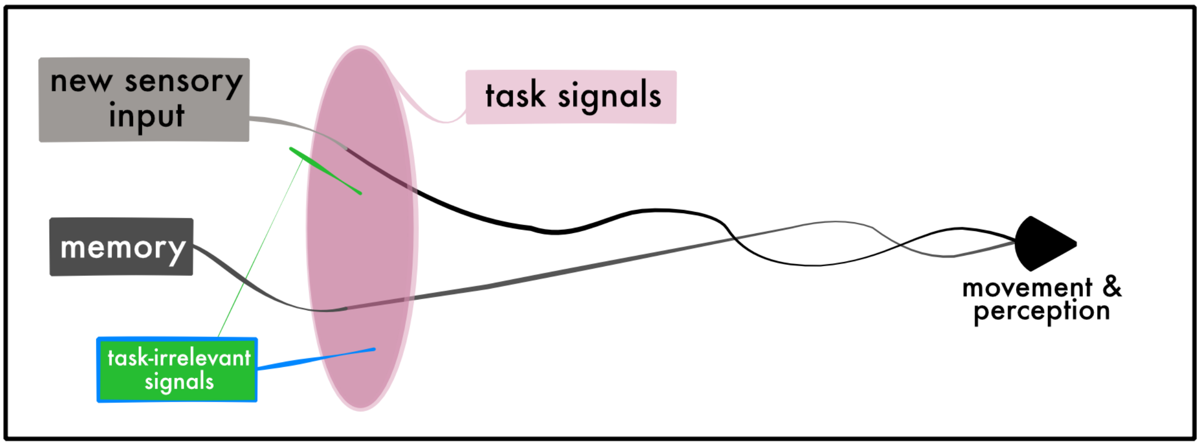


Figure 2 An alternative view of sensorimotor integration. Typically, a sensory and a motor signal, a prediction and sensory input, a prior and likelihood, are thought to be integrated based on the precision of the signal itself, its content. What I suggest here is that the influence of a signal in movement and perception is based on a signal's relation to something else. Task-relevance is one way to consider this: many signals will be shared between an organism and its environment, but the task-relevant signals will be perceived more intensely and the task-irrelevant less so, an important ability for effective movement and navigation (Kearney & Brittain, 2021). The signals that pass through this filter – based on their relation to the task and not necessarily its content – combine and can be integrated into ongoing movement and perception. This framework crucially makes sense of the disparate sensory attenuation literature pointed to in Chapter 1 and opens towards a rich discussion on approaches to effective rehabilitation.

Approaches to Parkinson's training

Approaches to training in the context of Parkinson's disease take a variety of forms. This thesis has sought to make sense of these. Chapter 1 reviewed literature relating to sensory attenuation, a phenomenon revealing aspects of sensorimotor integration processes. Using psychophysics experiments, Chapters 2 and 3 demonstrated both the influence of context in perception, and the trainability of perception through manipulating context. Then, Chapter 4 described a training protocol implemented in a more complex pegboard task. Manipulating the availability of different sensory information guided participants' strategy uptake (a form of improvisation), but skill levels remained comparable across groups. Finally, Chapter 5 linked work across different disciplines to reflect on the field of neuroscience. Drawing attention to often unnamed influences can help to avoid pitfalls in our work.

One such pitfall in rehabilitation is selecting one thing that seems to work and attempting to replicate it on a mass scale, irrespective of context. What I hope to have achieved here – for myself and the reader – is an attentiveness to the overlooked, and often ordinary, contributors to effective movement. The PD-SAFEx programme, in which participants exercise in low-light conditions, may work by demanding a shift away from sources of information that have become overly relied upon. The forced-exercise cycling protocols implemented by Ridgel and colleagues may work by challenging the participant to integrate complex sensory information into their movement. However, as Parkinson's disease symptoms reveal, emotional, sensory and cognitive context all matter. So how about the community context created in these spaces: the presence of others, the support and the responsibility?

Recent approaches such as dance classes (Bek et al., 2020) and rock climbing (Langer et al., 2021) also appear viable and effective (and probably great for many to be a part of, regardless of a particular diagnosis). Yet pinpointing one component of the training regime that promotes learning and neural restoration is not straightforward. This is in some ways the whole point. I have posited that the basal ganglia contribute to movement by filtering complex sensory environments by drawing on and combining sources from elsewhere in the brain and across the environment. Thus, the more aspects of an experience that can be connected to the movement, the more the basal ganglia enters the frame.

However, once such aspects become a standard part of initiating movement, basal ganglia involvement may diminish. Part of the function of the basal ganglia appears to the search for otherwise subtle cues, and the group of nuclei is thus active in obscure tasks like timekeeping in the absence of clear time information (see section 2.5 in Chapter 1). Similarly, the cerebellum garners more attention in sensory attenuation paradigms that use a simple sensory trigger to initiate movement (see section 3.1 in Chapter 1). Tasks requiring "self-generated movement" instead highlight basal ganglia involvement. Thus, a search is needed to involve the basal ganglia.

As the experiments in Chapter 3 demonstrate, adaptation occurs in response to sensory manipulations. A fixed approach may therefore not achieve the desired effects upon reuse. As suggested in the brief explication of neuroplasticity in Chapter 5, the notion of receiving form and giving form highlights the interplay of the roles of agent and environment. This dynamic creates an endless stream of novelty and improvisation. Future investigations could explore this further, particularly considering training approaches in living environments that grow and change with interaction, overcoming any habituation effects. Participants would then be required to find ways to be present and explore the new (but familiar).

Epilogue

Neuroscience, theology and who we are

1. Introduction

What follows is an exploration of place, environment and context to further understand the human brain. This thesis has delved into the principles of movement restoration, specifically in the context of Parkinson's disease. This has, however, prompted wider questions around what constitutes movement and how the brain is conceptualised. It has very much been an interdisciplinary approach to make sense of other researchers' neuroscientific findings, and those of the experiments I have led.

Regarding the significance of these findings for movement and for Parkinson's training, wider questions of the brain and of movement have involved inquiries into identity formation which relate to societal issues of racism and climate breakdown. These appear to evoke a consensus of condemnation with a shortage of action that goes far enough to grasp the issues at the roots. Both crises concern how we see ourselves: as humans in relation to each other and humans in relation to the rest of the world. As an endeavour to understand the biology of the human mind, neuroscience is a discipline where these issues can be seen and perpetuated. Could it also be a site for rethinking who we are and providing tools to help overcome these issues?

2. Isolated cognition

> We changed the world from the fifteenth century onwards; while Christian doctrines of creation did not account for that change, they were in fact crucial to that change. Like an essential enzyme that catalyzes change at an organic level, Christians reframed the world and bodies and in so doing reframed thought itself as an act upon the world rather than an act of the world. (p.389, Jennings, 2019)

> The deep-seated assumption that mind is an internal property of human individuals that can be studied in isolation from their involvement with one another or with the wider environment continues to reverberate within the field of psychology. (p.236, Tim Ingold, *The Perception of the Environment*).

Anderson, Richardson & Chemero (2012) posit that the cognitive sciences have often provided the forum for the examination of cognitive faculties, but treated in relative isolation. Studies about attention, for instance, fail to also be about memory and emotion. Further, cognition itself has largely been considered to be localised in the brain alone, immune from bodily and environmental processes. There are findings that suggest that the brain-body-environment interdependencies of motor control on language and bodily warmth (temperature) impinge directly on interpersonal judgment; Anderson and colleagues point out that the exercise of cognitive faculties cannot be localised to an area within the brain, or to the brain, alone.

The importance of context and environment on cognition can be argued further. In Godden & Baddeley's (1975) classic study, scuba divers demonstrated better memory for words learnt and recalled in the same location than in separate sites (underwater or on land). The lines-on-the-floor effect in Parkinson's (Morris et al., 1994, 1996; Beck et al., 2015) also demonstrates the significance of environment in movement. Despite these findings, the recent currents of research into the interrelationships of behaviour, bodily form and environment in cognition "questions some of the most deeply held beliefs in the cognitive sciences" (Anderson et al., 2012, p.718). How have beliefs in both an insulated cognition and in isolated cognitive faculties taken such deep root?

3. Two opposing world views

> The point that matters here is that they are modern versions of a powerful but not specially rational vision, derived from the atomists, of the natural worlds as somehow radically foreign to us and of ourselves as radically foreign to that world – a vision that is still influential in our thinking today. (p.35, Mary Midgley, *Science and Poetry*)

In *God of the Oppressed*, the theologian James Cone describes aspects of his life that informed him: his upbringing, his church, the cultural context and communities. He does this, he says, because most theologians will instead tell you about themselves through books they have read rather than via the social context which shapes their ideas. Cone is considered the founding father of a theological tradition known as Black Liberation Theology, which takes seriously the lived experience of black people as a starting point for framing questions about concerning divinity. Such an approach is a significant challenge to the assumption of knowledge being achieved abstractly through reason alone, a legacy of Descartes' mind-body dualism. Cone's work demonstrates that mainstream theology was itself a form of perspectival theology, stemming from often unnamed frameworks of whiteness, Western modernity and colonial power. Subsequent work in this field, such as that by Emilie Townes and Anthony Reddie consolidates the embodiment principles highlighted by Anderson et al. Knowledge is revealed to be inseparable from lived experience.

According to theologian Willie James Jennings, two opposing world views are evident when considering the scholarship of Christian intellectuals like José De Acosta who lived and worked in colonial Peru. De Acosta deemed Andeans in Peru to be idolatrous for their recognition the animate nature and possibilities for communication of plants and animals. His colonialist view of life was instead one in which:

> …the world sits silently, passively waiting to give itself up and give up what lies within it. Only in its surrender and in its role as divinely given gift can its life be honored by bringing that life to maturity through occupation, examination, manipulation, fragmentation and extraction. (p.397, Jennings, 2019)

This opposes a vision of life where the world is instead:

> …never silent, never passive, but always already actuality, speaking in and through creatures, including the human creature, and making intelligible life itself as both resource and source. Life in this regard cannot be conceived abstracted or extracted from land an animal, because that is simply not life. (p.397, Jennings, 2019)

My argument here is that neuroscience still displays the 'potentiality' world view, where humans are separate from the world, and the world's worth and life finds its meaning in the context of human consumption. As I discuss in the sections on motor control theories and neuroplasticity, a view of a passive world still shapes how we conceptualise the brain. This is important when considering questions as to why cognition is thought to be insulated from the world. However, I do not wrestle with the distortions in the cognitive sciences simply for the attainment of a more accurate conceptualisation of the brain, but instead to demonstrate that neuroscience is a site that perpetuates both the 'potentiality' and 'actuality' visions of life.

4. The role of neuroscience in societal inequality

> The vagaries of power affect the lives of each and every one of us, regardless of our awareness of this. Yet these power structures in which we are forever caught are, in themselves, human-made. While they may feel, much of the time, anonymous and institutional, they are composed of complex human relationships, and can only be transformed, unmade, and remade, by

> corporate retellings of collective stories. (p.50, Alison Webster, *You Are Mine*).

> It is remarkably hard for us to break out of this circle of increasing needs because our age is remarkably preoccupied with the vision of continually improving means rather than saving ourselves trouble by reflecting on ends. (p.36, Mary Midgley, *Science and Poetry*).

Recent critiques of neuroscience by Victoria Pitts-Taylor and Oliver Rollins' highlight the risks of perpetuating cycles of inequality by disregarding the social, environmental and cultural complexities that interact with the neurobiological factors we give most attention to (Pitts-Taylor, 2016; Rollins, 2021a). Historically, the shortcomings of neuroscience are perhaps easier to pinpoint. Francis Gall's reduction of cognitive faculties into specific, clearly demarcated areas of the brain reflects both aspects of the argument by Anderson and colleagues' (2012): the division of different cognitive faculties, and the reduction of cognition to the brain alone. With race being an issue of identity, and racism being fuelled through geographical enclosures and the reduction of human identity to that which can wholly be carried on skin-bounded selves (Jennings, 2010, p.226), neuroscience plays a bigger role in the struggle for justice than simply needing to account for race as a demographic factor (Rollins, 2021a, p.108-110).

As long as neuroscience predominantly subscribes to a view of the world as largely silent, passive, waiting to be used and extracted, we will continue to tell stories of human identity enclosed neatly inside the body – even inside the skull – and thus continue to perpetuate cycles of inequality. For instance, Rollins (2021a) examines the neuroscientific inquiries into what makes some individuals violent and others not. In attempting to establish the neurobiological basis for violence, within a vision of a more just and safe society, Rollins argues that the current framework that explains violence primarily focuses on the individual and their brain. Part of the problem is not "empirical ineptness, but a clue that certain social meanings, complexities and lives are being meticulously overlooked and erased from these biosocial equations of life" (p.155). Inspired by Wittgenstein's 'forms of life' concept and Crenshaw's concept of intersectionality, Bryson writes that people are not bodies but instead are lives (p.219, 2021). Such an argument demands a far more complex explanation than just "their brain made them do it". Irrespective of the depth and detail of study into matters concerning neurons, synapses and neurotransmitters, this demand rather asks us to consider the connectedness of the brain to the landscapes in which it is situated.

Similarly, Victoria Pitts-Taylor's (2016) critique of inquiries into how poverty affects the brain highlights not only the potential for targeted investment, but also the risk of divestment in programmes that address poverty itself. She describes one programme which provides "brain training" for participants, one that targets particular parts of the brain previously linked to the experience of poverty. Such an approach has a dual outcome: it aims to improve the life chances of participants, but also solidifies a particular phenotype of poverty, which dulls our attention to both the effects of poverty beyond the brain and the forces fuelling poverty and inequality. Neurobiology is an interesting part of these equations, but it is not the whole equation. Also overlooked is the relational aspect of similar interventions: the presence and attention of another person delivering an intervention (O'Connor & Nagel, 2017), and the reality of a brain that is not just "trained" with the puzzle-type tasks we associate with cognition and mind. A single model will not achieve all epistemic ends (Potochnik, 2022); the failure to recognise the obscuring of environmental, social and cultural complexities is symptomatic of a neuroscience that attempts to consider the mind and the brain in isolation, rather than embedded in a relational world.

In clinical neurological research, representation is important. It offers routes which improve access to treatments in marginalised communities and better tailor healthcare activity (Ojukwu et al., 2021). It is important to note the often unscrutinised WEIRDness (western, educated, industrialised, rich and democratic) of research populations (Henrich et al., 2010), which may go unquestioned because of the invisible normativity of whiteness as the reference point (Dyer, 2017, p.3; hooks, 2009, p.93, Reddie, 2009). Two further arguments must be made here.

First, there already exists a general consensus pushing for better inclusion of groups both under-represented in neurological research, and over-represented in health statistics. As Rollins (2021a) notes, organisations such as the National Institute for Health have abandoned a "one size fits all" model and require racial and ethnicity information in more representational samples. This does not result, however, in the destructive dynamics of race being discussed beyond it simply being a demographic variable to control for (Rollins, 2021a, p.108-110, 2021b).

Secondly, emphasising the addition of under-represented groups into the same clinical trials within the same paradigm of healthcare negates a double opportunity: firstly to both reimagine our approaches to health, and secondly to question the role of racialised existence and hyper-separated states of humans from the natural world in modern diseases, as we continue to treat the brain as the sole source of brain disorders (Fried, 2022; Hari, 2020; see also Ahsan, 2022).

5. Theories of motor control and sensory attenuation

The great philosophical question goes: if a tree falls in a forest and no one is

> around to hear, does it make a sound? But this is a troubling question, exalting one kind of being above all others. What then of the ears of snakes, or wood frogs, or mice, or bugs? Do they not count? What then of grass, of stone of earth? Does their witness not matter? If a man flies in Jamaica, and only the poor will admit to seeing it, has he still flown? […] Always – always – there are witnesses. (Kei Miller, *Augustown*)

One of my main arguments so far is that sensory attenuation can be understood as context-dependent processing, not necessarily the cancellation of sensory input by motor commands. Predictive models of motor control that underpin the cancellation accounts do not readily explain the variety of effective rehabilitation approaches. The lines-on-the-floor effect also revealed a deeper involvement of the environment in movement, one not captured by motor control theories which begin the story of movement with an outward (or downward) projection of predictive signals. These accounts paint a picture of an optional, rather than unceasing, interaction with the environment. They play down the role of context in eliciting a predictive signal in the first place, and thus resonate more with a 'potentiality' world view than an 'actuality' perspective.

Classic nerve conduction experiments reduced movement to reflex (Bennett, 1999), so recent motor control theories have successfully imagined a more complex interaction of agent and environment, but they still sit inside an imagination limited by the 'potentiality' world view. Falandays (2021) draws on Eastern philosophies to challenge the predominantly Western 'substance ontology', where everything can be considered as *things* in isolation, as opposed to processes with 'fuzzy' boundaries between entities. Falandays proposes that nothing exists without interaction, and the brain is in perpetual exchange with its environment as a complex open system far-from-equilibrium. Falandays' and Raja et al.'s, (2021) critiques of Karl Friston's free-energy principle – the prominent theory of the brain and movement (and everything, see Sun & Firestone, 2020) – focus on the sharp and arbitrary delineation between agent and environment. Such delineation draws on this same atomistic tradition in the sciences that Mary Midgley points out to us: the belief that we can best study things in isolation.

A favourite anecdote: even the best basketball players in the world do not make one hundred percent of their free-throws. Why not? A free-throw is taken from behind the same line that is the same distance from a rim that is the same size and same height off the ground. The ball is the same size, weight and is inflated to the same air pressure; each aspect is controlled as tightly as possible by professional leagues in the interests of sporting integrity. An alternative question might be to ask how would anyone be able to make one hundred percent of their free throws? Certain variables can be highlighted from one attempt to the next; the crowd noise could be different, muscle fatigue could have increased, game context (task information) could be new, attention might be drawn toward another aspect in an infinitely complex scene: the ball, the floor, heart rate, perspiration, interaction with the referee, a painful right wrist… The longest stretches of made free-throws are perhaps achieved by the skilful navigation of these variables, an attentiveness to the world symptomatic of a self who recognises their inseparable part of it, and of course lots of practice.

As highlighted in Chapter 1 and demonstrated in subsequent chapters, altering characteristics of the environment can shape movement in the present but also evoke beneficial adaptations and improvements. PD-SAFEx (Sage & Almeida, 2009, 2010) and forced-exercise cycling programmes (Ridgel et al., 2009, 2015; Ridgel & Ault, 2019) succeed in long-term symptom alleviation by focusing on tasks and qualities of the sensory environment, and not a reductive attempt to manipulate limb trajectory in isolation. If the nature of place is important in prompting positive neural adaptation, the question also arises: what role does the nature of place and environment have on worsening neural capacity in the first place? This question has not been thoroughly explored in the case of Parkinson's disease. There have been some investigations: tentative links between Parkinson's and pesticides and similar pollutants have been articulated (Ball et al., 2019; Hong et al., 2014; Jayaraj et al., 2016; Meredith & Totterdell, 2010), with varied prevalence according to geographic region (Gordon et al., 2012; Rusiecki et al., 2008; Wermuth et al., 2002). Additionally nutritional risk factors and buffers have been reviewed (Bianchi et al., 2022). Yet there is need to both tie these findings together and not leave out of the discussion how risk factors have become prevalent and sometimes unavoidable. We are not so good, it seems, at looking at cause in more than one place at a time. As Fried (2022) argues, medical scientists are prone to mistaking mental illnesses for the diagnostic criteria they are classified by, and we study isolated parts of an illness in the brain rather than the illness as a complex system of interacting biological and social processes.

6. The intriguing case of neuroplasticity

> This 'whole person' of whom we have been talking is not, then, a solitary self-sufficient unit. It belongs essentially within a larger whole, indeed within an interlocking pattern by a great range of such wholes. These wider systems are not an alien interference with its identity. They are its home, its native climate. The soil from which is grows, the atmosphere… (p.14, Mary Midgeley, *Science and Poetry*)

Neuroplasticity – the ability of the brain to change and adapt to the environment – is increasingly recognised as a key characteristic of the brain (Füchs & Flugge, 2014). The brain is far from fixed, but is rather adaptive and responsive to a range of environmental conditions: it is able to grow new neurons (neurogenesis), and alter connectivity between neuronal populations depending on situational demands and nourishing factors such exercise, sleep and proper nutrition (Shaffer, 2016). According to Papadopoulos (2011), plasticity is the possibility of recombining brain-body matter which draws focus to the relations between brain, body and environment. The brain may no longer be understood as a "self-contained, decontextualized entity" (p.432). Plasticity as a concept thus presents an image of a brain connected to the conditions of the world.

Neuroplasticity was first described in neuroscience by Santiago Ramón y Cajal and William James in the late 1800s (Berlucchi & Buchtel, 2009). However, it has only in the last several decades become widely accepted and discussed by neuroscientists. There has been a fierce debate about the existence of neuronal plasticity (the non-pathological change in neuronal structure in adult brains). There are many who have rejected the coherence of plasticity. As one psychologist questioned, "Why does the protoplasm stretch towards one neighbouring neuron when the organism happens to be in one situation, towards another neuron when the organism is in another situation? General silence on the part of the neurologists" (Berlucchi & Buchtel, 2009, p.315). Situation and context were overlooked as playing any meaningful role in the neuron's behaviour. The confusion around the seemingly erratic characteristics of neuronal response led to further questions as to who or what agent controlled such changes, as it was understood that situational factors could not possibly play active roles.

More recently it has been recognised that neurons do not respond uniformly to one type of stimulation, where response is also mediated by factors such as expectation, instruction and time of day (Sanes & Lichtman, 1999). Plasticity reveals living systems situated in contexts that explain how experiences come to be variegated. This powerful idea, described by Malabou (2008) as the ability to give form and receive form, has the potential to resist reductionism and determinism attributed to the neurosciences (Pitts-Taylor, 2016, p.122-123). Even though we are more than just our brains, plasticity conveys how we exist in the world: are we insulated and distant with optional interactions, or never existing without interaction and learning? Yet the prevalence of plasticity has only recently been confirmed in the adult brain (Eriksson et al., 1998). There is also a risk that plasticity comes to be misconstrued as a demand for a docile flexibility and a desire for endless self-enhancement (Malabou, 2008; Papadopoulos, 2011). That this concept did not find traction until recently is symptomatic of a neuroscience built on the 'potentiality' world view, but the notion of plasticity challenges how we see the world, and also how we see ourselves.

7. Conclusion

There is plenty of recognition within neuroscience of a more embodied and embedded cognition to challenge notions of an isolated cognition. Borrowing first from Black Liberation Theology, I linked Cone's contextual theology work to neuroscience research that recognises an embedded and plastic brain. What Cone's work did was highlight the perspective and context of mainstream theology that was otherwise considered 'correct', positionless and immune from social context. I thus subsequently borrowed from Jennings' work that points to the legacies of colonialism and mission Christianity as part of the context that uninvitingly shapes our world view.

Neuroscience exhibits strands of work that resonate with both the 'potentiality' and the 'actuality' perspectives. Using critiques from Pitts-Taylor and Rollins, I argued that the work we do in neuroscience plays out and intersects with societal issues. Research programmes affect societal inequalities, and the theories we form have traction in debates concerning identity. Neuroplasticity offers an interesting and potentially fruitful account of the human brain. Neuroplasticity is also a story to tell ourselves that nurtures loving and not exploitative attitudes, but its history reveals the skepticism and ignorance such stories can face. What other stories are we telling in neuroscience, where do they come from and what difference are they making?

Fin

Supplementary material

Supplementary Information 1 The Activities of Daily Living questionnaire in the experiments described in Chapters 2 and 3. For each statement below, participants selected "Never done", "Stopped doing" or "Still do", having been given the instruction: "For each activity below, please choose the response that best indicates your engagement with the activity".

1) Visit other people's houses
2) Receive visitors at your house
3) Go to religious building(s) for rituals or social activities connected with religion
4) Take part in social gatherings
5) Take part in cultural events such as concerts, shows, exhibitions, theatre plays or movies at the cinema
6) Drive a car
7) Take short trips out of town
8) Take longer trips out of town or out of the country
9) Do voluntary work
10) Do paid work
11) Sit on boards or committees of associations, clubs, schools, unions, cooperatives, or community centres, or engage in political activities
12) Take part in refresher courses or any type of university course
13) Participate in community centres or groups specifically for the elderly

Supplementary Table 1 Model comparisons for Experiment 1 in Chapter 3.

	DF	**AIC**	**BIC**	**LogLikelihood**	**Deviance**	**LRTstat**	**Change in DF**	**p-value**
Full model: incorrect ~ 1 + block*group + (1 ∣ ID) + (1 ∣ bl)	18	-3422.5	-3321.5	1729.3	-3458.5	-	-	-
Full model vs **null** (incorrect ~ 1)	2	-1463.7	-1452.5	733.87	-1467.7	1990.8	16	0
Full model vs **reduced model 1** incorrect ~ 1 + group + (1 ∣ ID) + (1 ∣ bl)	6	-2456.8	-2422.8	1234.2	-2468.5	990.07	12	0

Reduced model 3 (incorrect ~ 1 + block + group + (1 | ID) + (1 | bl)) vs **reduced model 1** (incorrect ~ 1 + group + (1 | ID) + (1 | bl))	6	as above	as above	as above	as above	41.82	4	<.001
Full model vs **reduced model 2** incorrect ~ 1 + block + (1 | ID) + (1 | bl)	8	-2442.8	-2397.9	1229.4	-2458.8	999.73	10	0
Reduced model 3 (incorrect ~ 1 + block + group + (1 | ID) + (1 | bl)) vs **reduced model 2** (incorrect ~ 1 + block + (1 | ID) + (1 | bl))	8	as above	as above	as above	as above	51.481	2	<.001
Full model vs **reduced model 3** incorrect ~ 1 + block + group + (1 | ID) + (1 | bl)	10	-2490.3	-2434.1	1255.1	-2510.3	948.25	8	0
Full model vs **reduced model 4** incorrect ~ 1 + block*group + (1 | ID)	17	-3387.4	-3291.9	1710.7	-3421.4	37.172	1	<.001
Full model vs **reduced model 5** incorrect ~ 1 + block*group + (1 | bl)	17	-3162.1	-3066.6	1598	-3196.1	262.47	1	0
Full model vs **alternative model 1** incorrect ~ 1 + block*group + (1 | ID) + (1 | bl) + (1 | RT)	19	-3420.5	-3313.9	1729.3	-3488.5	0.00000019179	-1	NaN

Supplementary Table 2 Model comparisons for Experiment 2 in Chapter 3.

	DF	**AIC**	**BIC**	**LogLikelihood**	**Deviance**	**LRTstat**	**Change in DF**	**p-value**
Full model: incorrect ~ group + block + (group:block) + (1 | ID) + (1 | bl:group:block)	23	-3838.9	-3705.3	1942.5	-3884.9	-	-	-

Full model vs **null** (incorrect ~ 1)	2	-1787	-1775.3	895.48	-1791	2068.8	22	0
Starting model (incorrect ~ 1 + group*block + 1 | ID) vs **reduced model 3** incorrect ~ 1 + group + block + (1 | ID)	10	-3766.3	-3638.5	1905.2	-3114.9	695.44	12	0
Reduced model 3 (incorrect ~ 1 + group + block + (1 | ID)) vs **reduced model 1** (incorrect ~ 1 + group + (1 | ID) + (1 | bl))	6	-3097	-3062.1	1554.5	-3109	5.901	4	0.207
Reduced model 3 (incorrect ~ 1 + group + block + (1 | ID)) vs **reduced model 2** (incorrect ~ 1 + block + (1 | ID))	7	-3077.4	-3036.7	1545.7	-3091.4	23.486	3	<.001
Starting model (incorrect ~ 1 + group*block + 1 | ID) vs **alternative model 1** incorrect ~ 1 + block*group + (1 | ID) + (1 | bl)	23	-3813.8	-3680.1	1929.9	-3859.8	49.433	1	<.001
Alternative model 2 (incorrect ~ 1 + group*block + (1 | ID) + (1 | RT)) vs starting model (incorrect ~ 1 + group*block + 1 | ID)	23	-3766.3	-3638.5	1905.2	-3810.3	0.0000004031	1	NaN
Alternative model 3 (incorrect ~ 1 + group*block + (1 | ID) + (1 | age)) vs starting model (incorrect ~ 1 + group*block + 1 | ID)	23	-3764.7	-3631.1	1905.4	-3810.7	0.3786	1	0.53835

Alternative model 1 (incorrect ~ 1 + block*group + (1 ǀ ID) + (1 ǀ bl)) vs **alternative model 6** incorrect ~ group + block + (group:block) + (1 ǀ ID) + (1 ǀ bl:group:block)	23	-3838.9	-3705.3	1942.5	-3884.9	25.147	0	0

Supplementary Table 3 Model comparisons for Experiment 3 in Chapter 3.

	DF	**AIC**	**BIC**	**LogLikelihood**	**Deviance**	**LRTstat**	**Change in DF**	**p-value**
Full model: incorrect ~ group + block + (group:block) + (1 ǀ ID) + (1 ǀ bl:group:block) + (1 ǀ bl) + (1 ǀ group) + (1 ǀ block)	21	-3205.7	-3088.7	1623.8	-3247.7	-	-	-
Full model vs **null** (incorrect ~ 1)	2	-768.52	-757.39	386.26	-772.52	2475.1	19	0
Starting model (incorrect ~ 1 + group*block + (1 ǀ ID)) vs **reduced model 3** incorrect ~ 1 + group + block + (1 ǀ ID)	9	-1909.9	-1859.7	963.93	-1927.9	1069.3	8	0
Reduced model 3 (incorrect ~ 1 + group + block + (1 ǀ ID)) vs **reduced model 1** (incorrect ~ 1 + group + (1 ǀ ID) + (1 ǀ bl))	5	-1850	-1822.1	929.99	-1860	67.866	4	<.001
Reduced model 3 (incorrect ~ 1 + group + block + (1 ǀ ID)) vs **reduced model 2** (incorrect ~ 1 + block + (1 ǀ ID))	7	-1852.7	-1813.8	933.37	-1866.7	61.111	2	<.001
Starting model (incorrect ~ 1 + group*block + (1 ǀ ID)) vs full model	17	-2963.2	-2868.5	1498.6	-2997.2	250.47	4	0

Starting model (incorrect ~ 1 + group*block + 1 | ID) vs **alternative model 1** incorrect ~ 1 + block*group + (1 | ID) + (1 | bl)	18	-2977.5	-2877.3	1506.8	-3013.5	16.341	1	<.001
Alternative model 2 (incorrect ~ 1 + group*block + (1 | ID) + (1 | age)) vs starting model (incorrect ~ 1 + group*block + 1 | ID)	18	-2961.2	-2861	1498.6	-2997.2	<.001	-1	NaN
Alternative model 3 (incorrect ~ 1 + group*block + (1 | ID) + (1 | keyTap)) vs starting model (incorrect ~ 1 + group*block + 1 | ID)	18	-2961.2	-2861	1498.6	-2997.2	<.001	-1	NaN
Alternative model 4 (incorrect ~ 1 + group*block + (1 | ID) + (1 | ADL)) vs starting model (incorrect ~ 1 + group*block + 1 | ID)	18	-2961.2	-2861	1498.6	-2997.2	<.001	-1	NaN
Alternative model 5 (incorrect ~ 1 + group*block + (1 | ID) + (1 | RT)) vs starting model (incorrect ~ 1 + group*block + 1 | ID)	18	-2961.2	-2861	1498.6	-2997.2	<.001	-1	NaN
Alternative model 1 (incorrect ~ 1 + block*group + (1 | ID) + (1 | bl)) vs **alternative model 9** incorrect ~ group + block + (group:block) + (1 | ID) + (1 | bl:group:block) + (1 | bl) + (1 | group) + (1 | block)	21	-3205.7	-3088.7	1623.8	-3247.7	234.13	3	0

Supplementary Table 4 Model comparisons for Experiment 4 in Chapter 3.

	DF	**AIC**	**BIC**	**LogLikelihood**	**Deviance**	**LRTstat**	**Change in DF**	**p-value**
Full model: incorrect ~ group + block + (group:block) + (1 | ID) + (1 | bl:group:block) + (1 | bl) + (1 | group) + (1 | block)	21	-1220.6	-1123.1	631.32	-1262.6	-	-	-
Full model vs **null** (incorrect ~ 1)	2	-252.23	-242.94	128.12	-256.23	1006.4	19	0
Starting model (incorrect ~ 1 + group*block + (1 | ID)) vs **reduced model 3** incorrect ~ 1 + group + block + (1 | ID)	9	-727.42	-685.6	372.71	-745.42	448.78	8	0
Reduced model 3 (incorrect ~ 1 + group + block + (1 | ID)) vs **reduced model 1** (incorrect ~ 1 + group + (1 | ID) + (1 | bl))	5	-727.42	-685.6	372.71	-716.01	29.406	4	<.001
Reduced model 3 (incorrect ~ 1 + group + block + (1 | ID)) vs **reduced model 2** (incorrect ~ 1 + block + (1 | ID))	7	-716.09	-683.56	365.04	-730.09	15.332	2	<.001
Starting model (incorrect ~ 1 + group*block + (1 | ID)) vs full model	17	-1160.2	-1081.2	597.1	-1194.2	68.447	4	<.001
Starting model (incorrect ~ 1 + group*block + 1 | ID) vs **alternative model 1** incorrect ~ 1 + block*group + (1 | ID) + (1 | bl)	18	-1165.7	-1082	600.83	-1201.7	7.4584	1	0.006
Alternative model 2 (incorrect ~ 1 + group*block + (1 | ID) + (1 | timeSinceDiagnosis)) vs starting model (incorrect ~ 1 + group*block + 1 | ID)	18	-1158.2	-1074.6	597.1	-1194.2	0.012	1	0.913
Alternative model 3 (incorrect ~ 1 + group*block + (1 | ID) + (1 | keyTap)) vs starting model (incorrect ~ 1 + group*block + 1 | ID)	18	-1158.2	-1074.6	597.1	-1194.2	<.001	-1	NaN

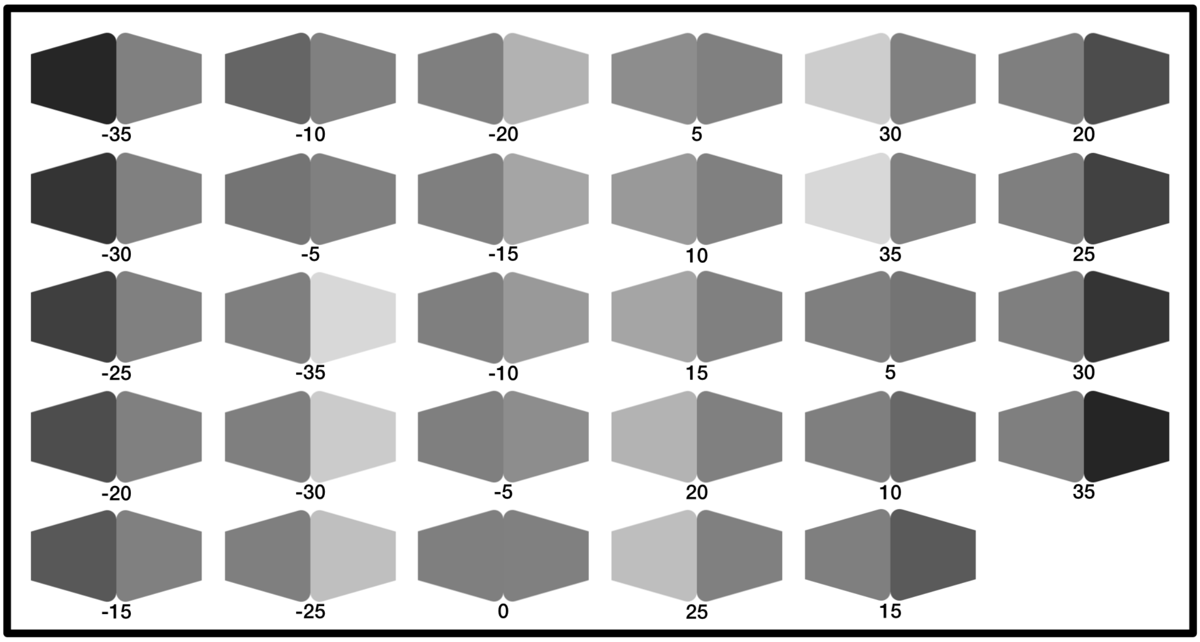
Alternative model 4 (incorrect ~ 1 + group*block + (1 | ID) + (1 | ADL)) vs starting model (incorrect ~ 1 + group*block + 1 | ID)	18	-1158.2	-1074.6	597.1	-1194.2	<.001	-1	NaN
Alternative model 5 (incorrect ~ 1 + group*block + (1 | ID) + (1 | RT)) vs starting model (incorrect ~ 1 + group*block + 1 | ID)	18	-1158.2	-1074.6	597.1	-1194.2	<.001	-1	NaN
Alternative model 6 (incorrect ~ 1 + group*block + (1 | ID) + (1 | LEDcurrent)) vs starting model (incorrect ~ 1 + group*block + 1 | ID)	18	-1160.3	-1076.7	598.15	-1196.3	2.106	1	0.147
Alternative model 10 (incorrect ~ 1 + group*block + (1 | ID) + (1 | RT)) vs starting model (incorrect ~ 1 + group*block + 1 | ID)	18	-1159.4	-1075.8	597.7	-1195.4	1.192	1	0.275
Alternative model 1 (incorrect ~ 1 + block*group + (1 | ID) + (1 | bl)) vs **alternative model 7** incorrect ~ group + block + (group:block) + (1 | ID) + (1 | bl:group:block) + (1 | bl) + (1 | group) + (1 | block)	21	-1220.6	-1123.1	63.32	-1262.6	60.989	3	<.001

Supplementary Table 5 Model comparisons for pooled data from experiments 1, 3 and 4 in Chapter 3.

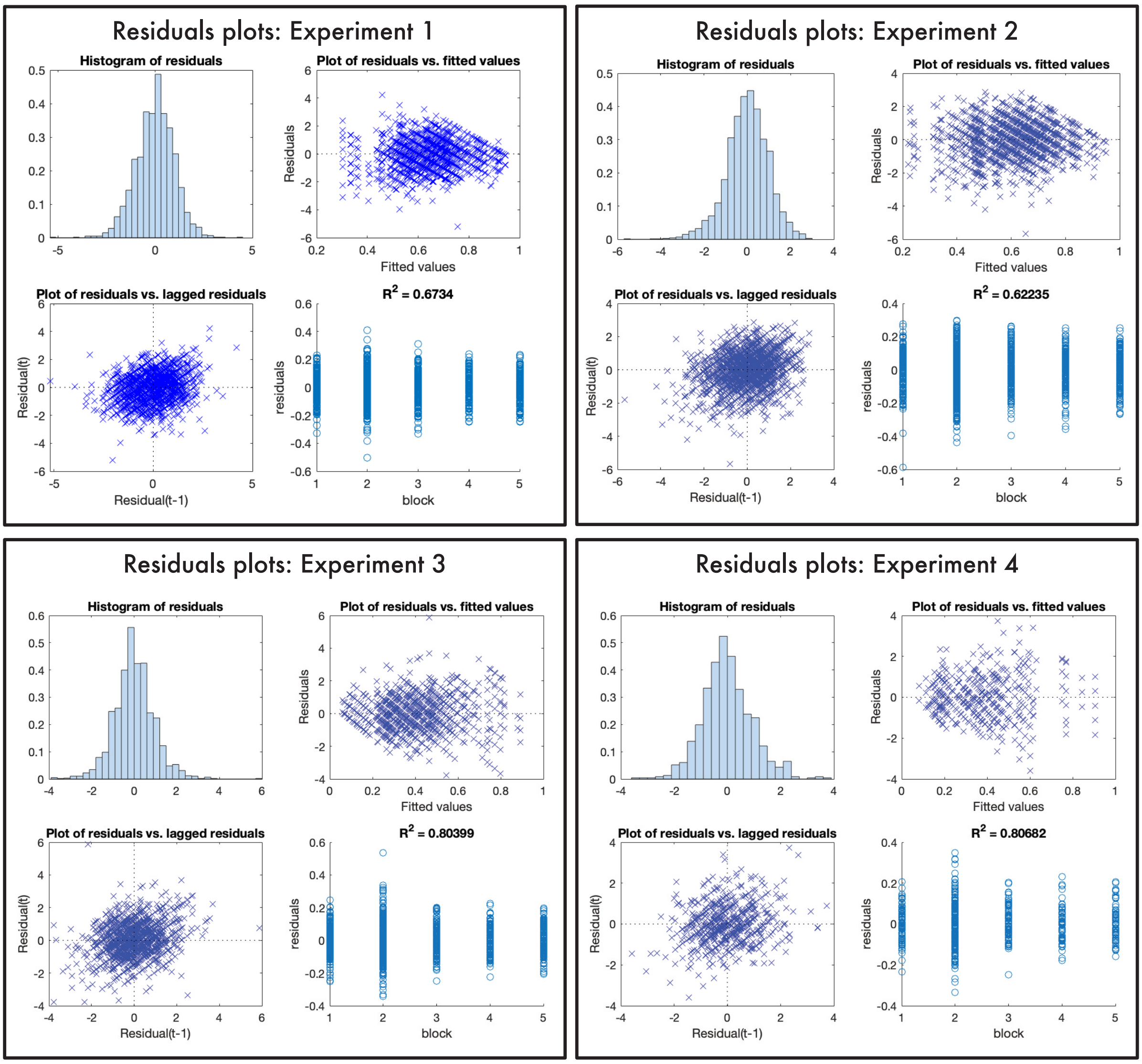
	DF	**AIC**	**BIC**	**LogLikelihood**	**LRTstat**	**Change in DF**	**p-value**
Full model: incorrect ~ 1 + block*group + (1 | ID) + (1 | bl)	18	-7529.2	-7412.9	3782.6	-	-	-
Full model vs **null** (incorrect ~ 1)	2	-2383.9	-2371	1194	5177.3	16	0

Starting model (incorrect ~ 1 + group*block*population + (1 ∣ ID) + (1 ∣ bl) vs **reduced model 1** incorrect ~ 1 + group + block + population + group:block + (1 ∣ ID) + (1 ∣ bl) [to assess if interaction benefits from population as a third term]	20	-7526.3	-7397.1	3783.2	947.43	-8	NaN
New starting model with no interaction to assess main effects (incorrect ~ 1 + group + block + population + (1 ∣ ID) + (1 ∣ bl)) vs **reduced model 2** (incorrect ~ 1 + group + population + (1 ∣ ID) + (1 ∣ bl)) [to assess block main effect]	8	-5023.3	-4971.6	2519.7	88.582	4	<.001
New starting model with no interaction to assess main effects (incorrect ~ 1 + group + block + population + (1 ∣ ID) + (1 ∣ bl)) vs **reduced model 3** (incorrect ~ 1 + block + population + (1 ∣ ID) + (1 ∣ bl)) [to assess group main effect]	10	-4944.9	-4880.2	2482.4	163.04	2	<.001
New starting model with no interaction to assess main effects (incorrect ~ 1 + group + block + population + (1 ∣ ID) + (1 ∣ bl)) vs **reduced model 4** (incorrect ~ 1 + group + block + (1 ∣ ID) + (1 ∣ bl)) [to assess population main effect]	10	-5107.3	-5042.7	2563.6	0.61832	2	.73406
Reduced model 4 (incorrect ~ 1 + group + block + (1 ∣ ID) + (1 ∣ bl)) vs **alternative model 1** (incorrect ~ 1 + block*group + (1 ∣ ID) + (1 ∣ bl)) [to assess block:group interaction]	18	-7529.2	-7412.9	3782.6	2438	8	<.001

Supplementary Figure 1 Stimuli used in Chapters 2 and 3, but with the Mach bands hidden to more clearly show underlying panel contrast.



Supplementary Figure 2 Closer inspection of models described in Chapter 3.



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Abstract

People with Parkinson’s disease experience motor symptoms that are affected by sensory information in the environment. Sensory attenuation is a phenomenon that describes the modulation of sensory input caused by motor intent. This appears to be altered in Parkinson’s and may index important sensorimotor processes underpinning Parkinsonian symptoms. Seemingly disparate results in sensory attenuation experiments are reconciled with an emphasis on task-relevance in the modulation of sensory input.

Additionally, findings from original psychophysics and motor learning experiments are presented. A Cornsweet illusion task is used to elucidate context-dependent perception, which increases with age. Adaptation effects also occur in response to contextual cue manipulation, with implications further afield for training techniques. The subsequent motor learning experiment altered sensory information availability during a pegboard task. The results demonstrated that altered sensory input prompts strategy change, but no unique enhancements in motor skill performance. An interdisciplinary approach is then used critique some of the broader themes in neuroscience that relate to the questions explored in this thesis.

Collectively, this work illuminates the dual effect of basal ganglia dysfunction in Parkinson’s disease: a reduced capacity to filter task-relevant signals harms the ability to integrate contextual cues, just when such cues are required to effectively navigate an environment. Further, the interdependencies of action, perception and cognition are highlighted. Current motor control theories are brought into question, whereby sensory attenuation is reframed as context-dependent perception instead of a result of probabilistic integration. A move toward effective training principles is attempted in this context.

For Flip

First thanks goes to my supervisors – John-Stuart Brittain and Ned Jenkinson. Thank you Ned for being open to listening to a probably slightly annoying and previously unknown-to-you undergraduate student knocking on your door and asking about a PhD in neuroscience and remembering me in the year or two that followed to let me know about the opportunity with John. Thank you John for the opportunity, for entertaining various wacky ideas while we waited for that mythical brain-stimulation device to one day arrive from a faraway land. I am grateful for you getting me in the lab so early on, especially given the absence of lab time that ensued amidst a pandemic. It is a shame we did not get more opportunities to scribble all over your whiteboard, but I am glad we had opportunities nonetheless, and I am proud of the work that has emerged.

I had a lot of help with data collection for the younger adult groups in Chapters 2 and 3 from Emily Warren, Megan Platts, Jackie Chow and Jack Richards, who were brilliant and a joy to teach and work with. Benjamin Hart helped me with the study described in Chapter 4, helping with study design by trying out different variations in piloting and then in collecting data. Chapter 5 stems from a paper written with friend and colleague Morgan Mitchell of Oxford University for a special issue of Frontiers, which at the time of writing is under review. Chapter 1 is a very slightly edited version of a paper originally published in the journal *Brain Sciences* under the name *Sensory Attenuation in Sport and Rehabilitation: Perspective from Research in Parkinson's*, where authorship is shared with John who provided thorough editing, guidance along the way and the suggestion for a review in the first place (which I learnt so much from writing – who knew there was so much out there to make sense of in neuroscience already!).

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It has often felt like there is an expectation and duty to go into isolation, finish writing up the thesis and then reemerge into society. I found myself half-way down that rabbit hole a few times, but however stoic and necessary it felt initially, each phase ended in exhaustion and loneliness. I am grateful to the communities who have welcomed me in and kept me connected, from basketball and football, to church and its surrounding activities like Lauda, STS Community Project, Action Potential and to Les, Wendy and my grandparents who provided a space to explore more deeply the meaning of all the writing that follows and

some Friday afternoon training to look forward to and reflect on. Amidst it all, I am grateful to God who connects all things to all things to make each thing less thing-like.

Finally, though. Money. My PhD was funded internally by the University of Birmingham via John-Stuart Brittain. We were also awarded two small grants from the School of Psychology which contributed toward research participation costs. Thank you, and thanks University of Birmingham for having me.

Contents

Introduction

Lines on the floor

In one scenario, a person shuffles forward, moving gradually towards the far end of the room. Steps are short and stuttered. The delicacy of the skill of walking is suddenly very apparent. In a second scenario, lines of tape are stuck down on the floor, arranged like a ladder along the path the person just travelled. This time, they stride confidently and smoothly across the room, feet landing precisely on each line of tape. In the first scenario, walking stutters, but in another, the many years of walking practice are gracefully revealed. The difference between the two is sticky tape.

Shuffling gait can be symptomatic of Parkinson's disease, a movement disorder affecting the basal ganglia in the brain. Cues, such as lines on the floor, can alleviate such motor impairments (Beck et al., 2015; Morris et al., 1994, 1996; Nonnekes et al., 2019; Quintyn & Cross, 1984). The lines-on-the-floor effect on gait has been a source of fascination for me, and a recurring image throughout the investigations described in the chapters that follow: how can changing the content of the environment so dramatically change the ease of movement? What does it tell us about how we all move, what does it reveal about the basal ganglia and how can it inform our understanding of approaches to Parkinson's treatment?

Ever since James Parkinson's description of a 'shaking palsy' in 1817, Parkinson's disease has primarily been considered a movement disorder. Its non-motor symptoms are becoming increasingly recognised, including emotion- and cognition-related changes (Aarsland et al., 2013; MacDonald et al., 2019), challenging the motor-only emphasis of Parkinson's categorisation (with four motor cardinal symptoms). However, as I will explore, the challenge goes beyond just the inclusion of non-motor symptoms into the diagnosis of Parkinson's. How might motor and non-motor symptoms be linked beyond just occupying the now-longer list of diagnostic criteria?

I had the exciting opportunity to help out with exercise classes for people with Parkinson's and other movement disorders at the Movement Disorder Research and Rehabilitation Centre in Waterloo, Canada. It was exciting to me because of my life-long obsession with sport, movement, how to improve movement in sport, my general joy of learning and the thrill of communal exercise in shared spaces. It was here that I got an insight into the approaches that form part of the Parkinson's disease sensory attention focused exercise (PD-SAFEx) programme. In PD-SAFEx, the lights in the gym where it takes place are sometimes turned down during exercise sessions and participants perform some exercises with their eyes closed. Participants often demonstrate improved symptom severity scores at the end of a 12-week programme, and even after a further 6-week washout period (Sage & Almeida, 2009, 2010).

The unique effects of varied sensory environments during the same movements fascinate me. One of the draws was the chance to rethink movement and imagine connections across the conceptual divide between action and perception. I was drawn to the basal ganglia, the system damaged in Parkinson's, and the possibility that it might be combining a variety of information signals from across the brain to contribute to movement. At the start of this doctorate, already with a focus on the links between sensory stimulation and motor control, Ned Jenkinson pointed out to John-Stuart Brittain (my two supervisors) and I some papers on sensory attenuation. It was the phenomenon of sensory attenuation that helped us grapple a little more deeply the symptoms of Parkinson's, whilst placing centre-stage the links between movement and sensation.

The Basal Ganglia

The basal ganglia are groups of subcortical nuclei, clusters of neurons, near the centre and the base of the brain. They are highly interconnected, hence the frequent grouping of them as "the basal ganglia", but are also connected to nearly the whole of the cortex (Miall, 2013). The dorsal striatum, made up of the caudate nucleus and putamen receives input from limbic, associative, sensory and motor areas converging from across the brain while serving as the primary input into the rest of the basal ganglia. The globus pallidus (often divided into its external and internal segments), the subthalamic nucleus, ventral striatum (nucleus accumbens and olfactory tubercle) and the substantia nigra (pars reticulata and pars compacta) make up the other main components of the basal ganglia.

A vast array of different neurotransmitters and neuromodulators adds to the complexity of the basal ganglia's intrinsic loops (Figure 1a), though these are often simplified into two parallel pathways: direct and indirect (Gale et al., 2008; Miall, 2013). As an oversimplification, the direct pathway (from striatum, straight to the globus pallidus internal and the substantia nigra pars reticulata, out to the thalamus, on to the cortex and back around to the striatum) is suggested to facilitate movements and the indirect pathway (from the striatum to the substantia nigra pars reticulata via the globus pallidus external and the subthalamic nucleus, and out to the cortex again via the thalamus) is said to suppress movements. An imbalance between the two pathways is often used to model how basal ganglia damage leads to different symptoms, or to understand the chain reaction of damage to just one region of the basal ganglia, though this and other models (e.g. the centre-surround and firing-rate model) should be held loosely as no one model adequately describes every feature of basal ganglia dysfunction in Parkinson's by itself (Gale et al., 2008).

The key attributes of Parkinson's disease's pathophysiology include the loss of dopaminergic neurons in the substantia nigra as well as the aggregation of Lewy bodies and Lewy neurites which contribute to the loss of neural function (Simon et al., 2020). The loss of dopaminergic terminals in the striatum (which receives input from the substantia nigra pars compacta, Figure 1a) is suggested to be the crucial event underlying the onset of motor symptoms in Parkinson's disease. Insufficient dopamine can be considered to reduce the capacity to enable new voluntary actions (Jenkinson & Brown, 2011). The very particular organisation of the striatum which consists of some separate regions that remain in distinct channels along corticostriatal loops, in addition to some overlapping regions thanks to dendrites that cross over, may be key to integrating disparate signals into ongoing movement, ensuring motor responses are appropriate to the creature's current motivational and behavioural state (Miall, 2013).

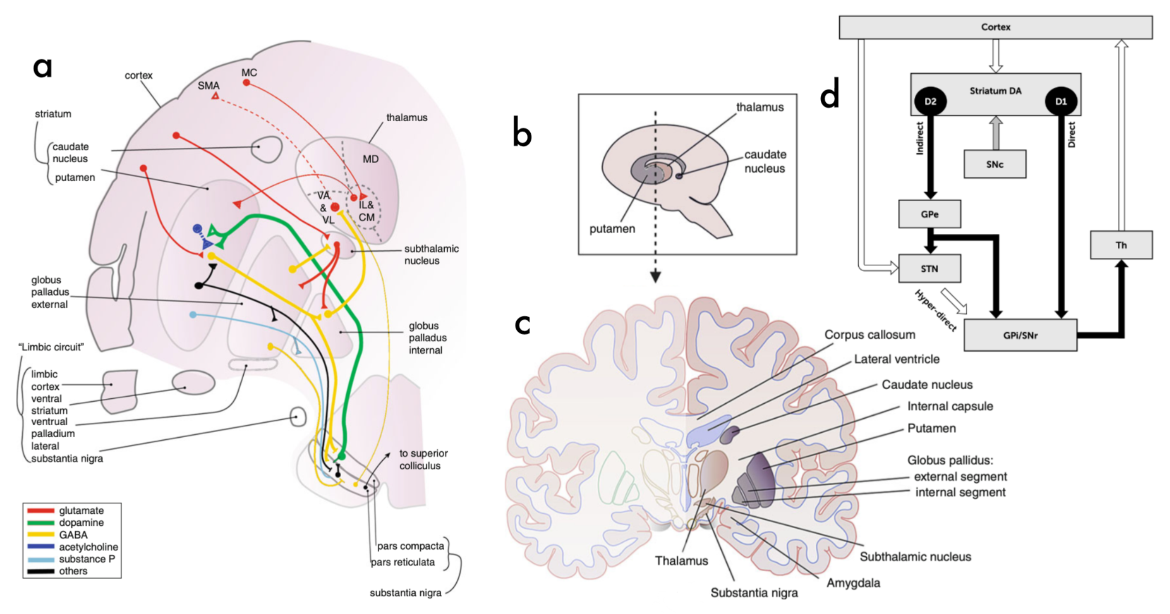


Figure 1 Diagrams of the basal ganglia from Miall (2013) – a, b and c – and Andres & Darbin (2018) – d. (a) The basal ganglia are highly connected to other parts of the brain, including the cortex and thalamus, with an array of mediating neurotransmitters. (b) Depiction of the basal ganglia along the sagittal plane. (c) depiction of the basal ganglia along the frontal plane. The basal ganglia form a complex web of structures, with many interconnections (a), contributing to the reasons why the basal ganglia is difficult to understand (Miall, 2013). (d) A schematic diagram of the direct and indirect pathways, commonly used to make sense of basal

ganglia dysfunction.

Sensory attenuation

Sensory attenuation classically describes why you cannot tickle yourself. When someone tickles my palm, it is ticklish, but when I tickle my palm, it is not (Blakemore et al., 1998, 2000). This phenomenon demonstrates how the same stimulus – the same tickling motion in the same place – leads to different sensations depending on the source of the tickling. Similarly, participants in the force-matching task (Figure 2), when attempting to match a target force, typically press harder onto their finger when they press directly with their other hand compared to when they generate the force with a slider (Kilteni et al., 2017; Parthasharathy et al., 2021; Walsh et al., 2011; Wolpe et al., 2016, 2018). The prominent explanation for these findings has been the cancellation of sensory input because of motor involvement.

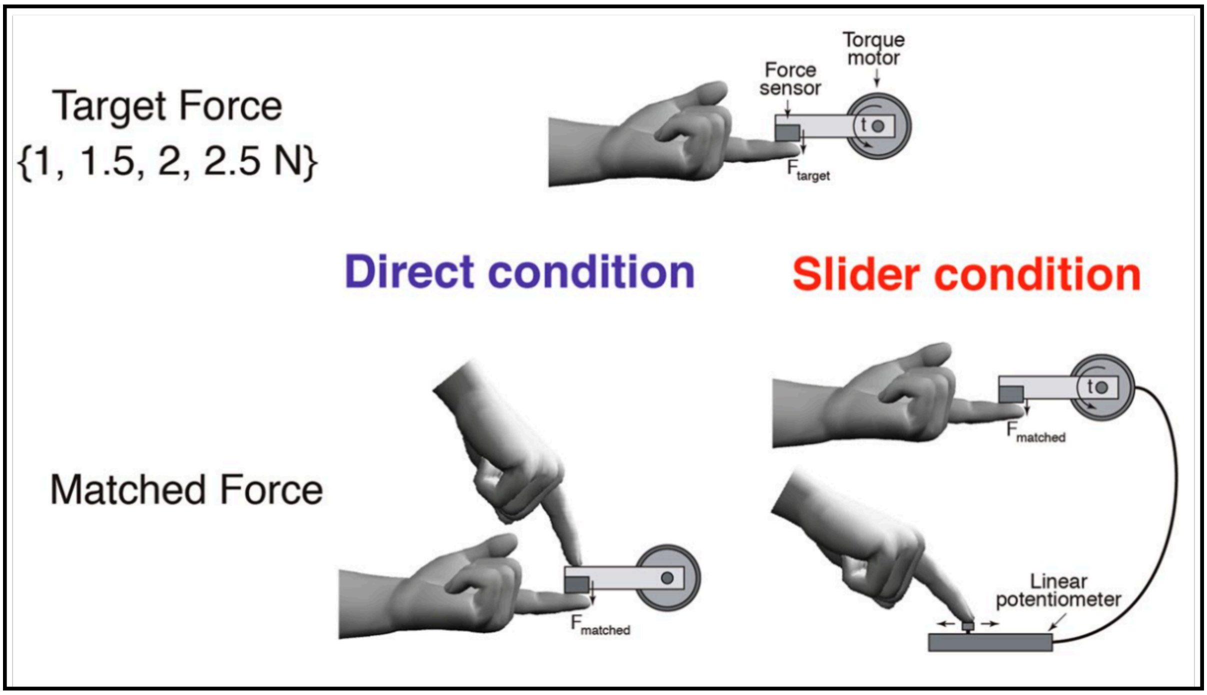


Figure 2 A typical force-matching task protocol, this one from Wolpe and colleagues (2018). Here, a motorised lever presses down onto a participant's finger with a set amount of force; this force is the target force (top). Next, the participant must match the target force in one of two matching conditions. In the direct condition (bottom left) the participant, with their free hand, presses the lever down onto the the receiving hand in an attempt to replicate the sensation felt in the target condition. In the slider condition (bottom right), the participant instead uses a slider to recreate the same sensation using the torque motor. Participants tend to press harder than they need to in the direct condition, but reproduce the force accurately in the slider condition. Pressing harder in the direct condition is believed to result

from the cancellation of sensory input because of direct motor involvement of the free hand. The mismatch between direct and slider matching conditions is thus an index of sensory attenuation.

Another way to measure sensory attenuation is with sensory evoked potentials (SEPs, sometimes referred to as event-related potentials – ERPs). An SEP is generated from electrical signals recorded at the scalp, elicited by a stimulus such as electrical stimulation of the finger. Lots of trials are performed and then averaged in search of a particular pattern that relates to the stimulus. This technique offers a way to measure how a stimulus is being processed, probably at a cortical level (Passmore et al., 2014). Thus, sensory attenuation can be measured by contrasting SEPs elicited from self-generated stimuli and externally generated stimuli. SEPs tend to be of bigger magnitude when externally generated, and smaller magnitude when self-generated, but people with Parkinson's demonstrate a reduced difference between the two conditions (Macerollo et al., 2016, 2019; Railo et al., 2020). Indeed, Parkinson's disease appears to reduce sensory attenuation, as revealed in the force-matching task too (Wolpe et al., 2018). Intriguingly, while sensory attenuation is reduced in people with Parkinson's, it appears to steadily increase with healthy ageing (Parthasharathy et al., 2021; Wolpe et al., 2016). The reason for this disparity was unclear but it demonstrated that sensory attenuation is sensitive enough to track change, and also potentially alterable. *Could it be possible to alter the sensorimotor processes revealed in the sensory attenuation paradigm and would that be of any use in Parkinson's-focused training?*

Pilot study: subthreshold and suprathreshold SEPs

To explore the usefulness of SEPs as a measure of sensory attenuation, we performed a small pilot study. The purpose was to tentatively explore the potential to track changes in the sensorimotor processing capacity of individuals that might also be affected by training. I learnt a lot from this study, but not what I expected. To keep things simple, we performed a partial replication of the Nierhaus et al. (2015) and Forschack et al. (2017) paradigm. In those studies, peripheral nerve stimulation (PNS) was delivered to the participant's finger and SEPs were measured using electroencephalography (EEG) (Figure 3). PNS was delivered either covertly or overtly, meaning the intensity of the stimulation was either slightly below a detection threshold or above a detection threshold.

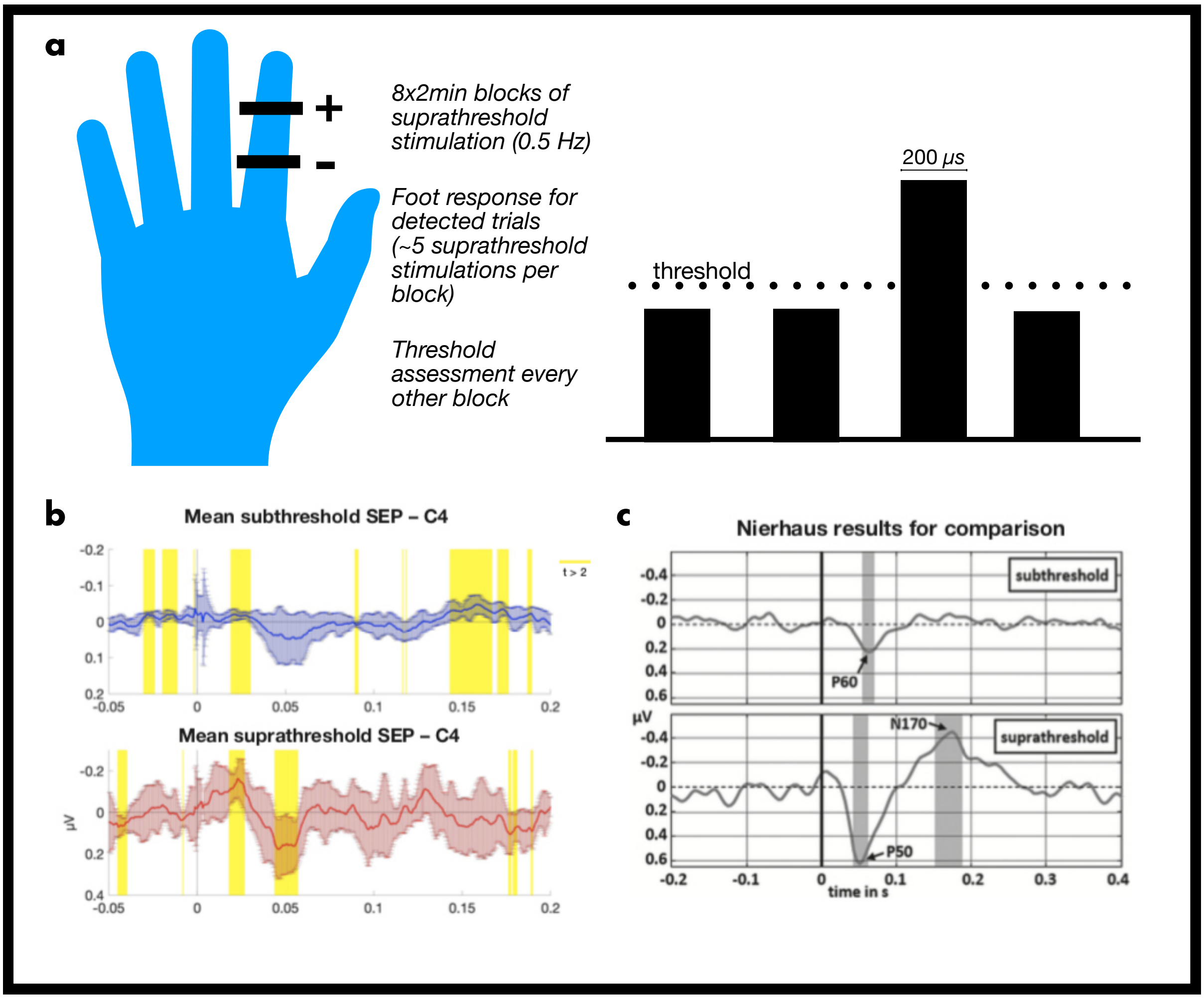


Figure 3 (a) Experiment set up. Peripheral nerve stimulation was delivered using a Digitimer DS5 current stimulation and a CED 1401 interface, operated by Spike2 software (CED). The participants stepped on a squeaky toy to indicate that they felt the suprathreshold stimulation. (b) Afterwards, we compared the responses recorded at the C4 electrode for sub- and suprathreshold stimulation. Red or blue shading around the line (the mean) indicates standard error of the mean. Timepoints where voltage is more than two t-statistics from zero. $N = 5$. (c) Figure from Nierhaus et al. (2015), one of the studies we partially replicated. We likewise found distinct patterns for sub- and suprathreshold stimulation, but the possible N20 component in our data was more akin to Macerollo et al. (2016). More curious, was the change in detection thresholds (Figure 4).

We successfully replicated the difference between subthreshold and suprathreshold PNS conditions, albeit with noisier SEPs that may have smoothed out with more participants (Figure 3). The spikes are also located earlier on in time, closer to the patterns found by Macerollo and colleagues (2016) and consistent with the N20 component which responds to tactile stimuli (Passmore et al., 2014). It was interesting to see that subthreshold stimulation – information that was not consciously detectable – still elicited a cortical response, pointing to the involvement of more than just one brain area in the processing of sensory input (Forschack et al., 2017).

However, there were two aspects of our pilot study that I found more interesting and which guided parts of the subsequent work, described in the chapters that follow. Firstly, the detection threshold – the lowest intensity in milliamps at which the PNS could be detected – changed each time it was measured (Figure 4). The detection threshold at the fifth and last time of measuring was higher than the first time of measuring, indicating a reduced sensitivity over time. Whether this was due to peripheral changes such as reduced impedance of the skin or more central factors such as attention, it highlighted either the inability of measuring without interfering, or, an effect of the task we had devised. The task was simple: lots of subthreshold stimuli were presented about two seconds apart (slightly staggered to be less uniform) with an occasional suprathreshold stimulus. Participants were required to stamp on a squeaky (dog) toy when they felt the suprathreshold stimulus, just to ensure they were engaged in the task. I could not help but wonder, were the task's set-up and instructions guiding the participants toward the suprathreshold stimulation and away from the subthreshold stimulation and thus dulling their tactile sensitivity?

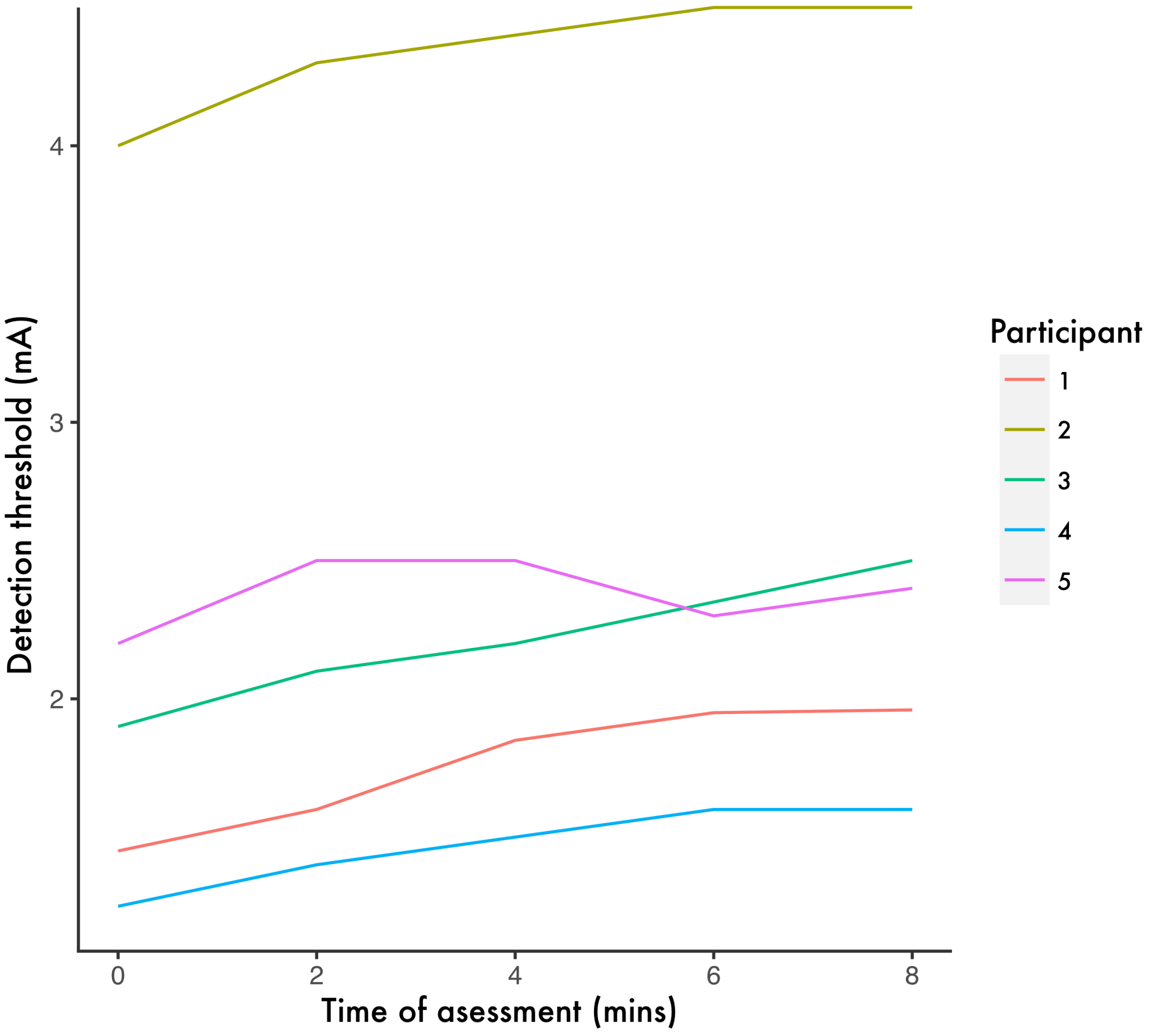


Figure 4 Detection thresholds for peripheral nerve stimulation (PNS) in an early pilot study. Thresholds indicate the lowest PNS intensity that the participant could detect, measured through a simple yes/no response protocol at five timepoints throughout the experiment. Sensitivity to the PNS pulses reduced over the course of the experiment, indicated by higher thresholds at the last timepoint compared to the first: $t(4) = -6.125$, $p = .004$.

As I discuss in Chapter 1, task set-up does indeed make a difference in how stimuli are attended. In a key study, Riley and colleagues (1999) measure the postural sway of participants on a force-plate. In one condition, participants are instructed to pinch a curtain and in another, participants are instructed to pinch the curtain but keep it as still as possible. In the latter, postural sway is significantly better, demonstrating that the sensory input from pinching a curtain does not have a uniform effect on behaviour, but depends on how and why it is being attended to. In Chapter 1, I review the sensory attenuation literature and use this principle of task-relevance in an attempt to reconcile contradictory findings in the field. Some studies demonstrate a sensory suppression effect consistent with the traditional cancellation account of sensory attenuation, whereas others find a sensory enhancement effect. I thus argue for a slight reframing of sensory attenuation, describing it as context-dependent processing, moving beyond rigid cancellation accounts. I go on to explore what sensory attenuation paradigms reveal about the roles of the basal ganglia and the cerebellum in movement and draw on a strand of research (Kaji, 2001; Robbe, 2018; Schneider, 1984) that postulates a sensory-filtering role for the basal ganglia that best explains its contribution to motor control. In the interests of informing approaches to Parkinson's-focused rehabilitation training, I bring together my conclusions on sensory attenuation and the basal ganglia for a holistic account of the symptoms of Parkinson's disease and suggest principles for effective rehabilitation approaches.

The task-relevance principle, highlighted by Riley et al. (1999), is important when considering the lines-on-the-floor effect during gait. The lines help to simplify the environment being navigated but are they being used in a way to aid the learning of the ability to navigate complex environments? To further explore principles of effective rehabilitation, I present findings of an experiment in Chapter 3 that point to how sensory cues are used and how adaptation effects emerge through repeated use. The experiments in Chapter 3 – that suggest the use of bold, salient cues can have a negative effect on cue sensitivity – utilise the same task described in Chapter 2. This task is a simple visual illusion task, where participants make one of two keyboard responses depending on how they perceive the onscreen stimuli. We demonstrate a clear effect of contextual information on participants' perception in a similar fashion to the force-matching task, pointing to a multi-sensory (not just somatosensory) nature of sensory attenuation and supporting the framing of sensory attenuation as a form of context-dependent sensation. We also compare illusion strength across three populations – older adults with and without Parkinson's, and younger adults – to further explore the reported increase of sensory attenuation with age and decrease in disease.

Chapter 4 is an account of a rather different experiment. Instead of pressing a keyboard in response to onscreen stimuli, participants completed a two-day pegboard task that involved placing pegs as quickly as possible under different sensory conditions. The interventions that alter sensory conditions (a blindfold and latex gloves) serve as an attempt to mimic approaches to rehabilitation that reduce a form of sensory input, such as the PD-SAFEx programme, but in a non-Parkinsonian population group. By using participants without a neurological disorder, we ask if the PD-SAFEx approach enacts a general principle of motor learning beyond participants who are overly reliant on visual sensory input to move. Further, we bring into question theories of motor control prominent in the field of neuroscience that offer an explanation for the lines-on-the-floor effect and even aspects of the PD-SAFEx approach, but do not so easily handle the more diverse array of training techniques that depend on the need to navigate complex environments.

Chapter 5 is written in a different style to the rest of the chapters. The style is reflective of the variety of sources drawn on to make the arguments, as I discuss literature beyond the neurosciences that have been important and fruitful to consider throughout the duration of my PhD. As such, the essay is somewhat unusual, and draws on quotations as much as quantitative evidence from experiments, and demonstrates the somewhat broader interdisciplinary approach I have taken to make sense of the central findings in Chapters 1 to 4, even if our experiments themselves have subscribed to a typical cognitive neuroscience framework (of course itself multi-faceted). I reflect more broadly on the brain, ultimately arguing that things do not make sense in isolation. That is, in spite of the silos inside which we have traditionally examined the brain, action, perception and cognition cannot be properly understood without reference to their dependence on each other (Cisek, 2019; Guo & Song, 2022). Just as a motor skill is dependent on characteristics of the environment, thought is not solely an act of the brain but rather arises as an act of a world the brain is a part of. This idea (of thought as an act of the world, not an act upon the world (Jennings, 2019, p.389)) is a destination of the work that takes seriously the interplay of action, perception and cognition, because the sensory characteristics of past and present environments come to be recognised as playing an active role in shaping thought. Rather than the basal ganglia containing, all by itself, motor programmes, the story is rather one where movement emerges from the connections between things and the basal ganglia grapples with the complexity of the brain's surroundings by drawing on other brain regions and snippets from the body and wider environment. Recognising the intimate interplay of agent and environment also challenges our approaches to rehabilitation, seeing movement as interaction and training as the shaping of environment to facilitate learning and the capacity to navigate complex environments that prompts even further learning.

The mind then, is not a self-sufficient unit, but rather intimately embedded and connected to the rest of the world. The utter absence of isolation is evident in the effects of task and context on action and perception. Recognising how we move and filter sensory information becomes crucial in approaches to Parkinson's-focused training. Further, the revelation of context-dependent movement in people with Parkinson's discloses the intricacy of motor skill more generally – why and where we move matters to us all.

> Every organism is like a melody that resonates and harmonises with living things around it.

M.R. O'Connor, summarising Jakob von Uexküll, *Wayfinding*, p.75

Chapter 1

Task-relevant sensory filtering by the basal ganglia in Parkinson's disease and in sensory attenuation experiments

1. Introduction

People with Parkinson's Disease face debilitating symptoms that often begin years before disease diagnosis (Gaenslen et al., 2011), worsen over time and significantly affect quality of life. Dopamine replacement therapy is used to treat Parkinson's and can be effective for long periods (Jost & Bausch, 2017), though it does not improve all cardinal symptoms of this neurodegenerative disorder (Sangarapillai et al., 2020), with high levels of wearing off over time and considerable dissatisfaction among patients (Jost & Bausch, 2017). While techniques such as deep brain stimulation can be employed with relative success (Bratsos et al., 2018), they are still associated with significant shortfalls (di Biase & Fasano, 2016), not least of which are the narrow inclusion criteria deemed necessary for high efficacy (Antonini et al., 2018), and the significant investment in time required for effective stimulator titration. This means there is a need for effective therapies that can be utilised in prodromal and early-stage Parkinson's in a preventative capacity, which may delay, or even complement later stage medical or surgical options. Various exercise therapies have been developed which have involved the manipulation of sensory feedback (Sage & Almeida, 2009, 2010), manipulation of movement amplitude (Ebersbach et al., 2010), multi-sensory cueing strategies (Chawla et al., 2020; del Olmo & Cudeiro, 2005; Morris et al., 1994, 1996; Spaulding et al., 2013), action-observation and motor imagery (Caligiore et al., 2017), resistance training (Corcos et al., 2013), forced-exercise protocols (Ridgel & Ault, 2019; Ridgel et al., 2009, 2015; Miner et al., 2020) and dance (Bek et al., 2020; Foster et al., 2013). Whilst varying degrees of success have been reported, an optimal strategy has not been identified (Spaulding et al., 2013) and underpinning mechanistic principles for effective rehabilitation remain elusive.

Parkinson's involves gross degeneration of midbrain dopaminergic nuclei which innervate the basal ganglia, leading to abnormal patterns of activity in basal ganglia pathways. However, it is not so straightforward how such abnormal patterns of activity give rise to the wide-ranging motor and non-motor symptoms of Parkinson's, and yet it is important in the development of effective treatments. Here, we first investigate the phenomenon of sensory attenuation which traditionally describes the suppression of sensory input resulting from motor intent. We re-examine the literature with an explicit consideration of Task-Relevance and reframe sensory attenuation as the distinct context-dependent perception of two identical stimuli. We propose that this novel framing reconciles a previously contradictory literature whilst still incorporating the concept of movement modulating sensory input. Such reframing presents sensory attenuation paradigms as a useful means to gain insight into how people monitor task-relevant signals and utilise contextual cues during movement, a concept not well captured by current sensory attenuation theory.

Next, we explore the neural substrates of sensory attenuation and their somewhat paradoxical conjunctions with Parkinson's, which implicate the basal ganglia. Non-motor symptoms of Parkinson's are increasingly gaining recognition as an intrinsic part of the disease (Armstrong & Okun, 2020; MacDonald et al., 2019; Van Laar & Jain, 2004). This is supported by the recognition that basal ganglia circuits contribute to a plethora of non-motor as well as motor functions in a sensory capacity (Kaji, 2001; Lidsky et al., 1985; Nakajima et al., 2019; Robbe, 2018). Indeed, the true function of the basal ganglia eludes any single abstract model (Gale et al., 2008; Utter & Basso, 2008). However, by exploring sensory attenuation through the lens of Parkinson's, we begin to see that a reduced ability to filter environmental signals based on task-relevance creates a more complex landscape for the attendance to salient signals, just as such signals might be more beneficial to enhance movement and perception.

Finally, we examine current exercise rehabilitation techniques for further support of this notion, and consider how the most effective techniques might be working within this framework to place increasing demands on the processing capacity of depleted neurons in the basal ganglia rather than by bypassing them, and hence provide only a short-term solution. Implications for rehabilitation design are considered, pointing to sensory attenuation paradigms of a particular design to help monitor changes in important sensorimotor processing throughout an exercise programme.

2. Sensory Attenuation and Task-Relevance

2.1. Recent and Relevant Findings

Sensory attenuation usually describes the phenomenon whereby sensory input elicited by self-generated actions is reduced compared to sensory input generated externally. Anecdotally, the inability to tickle oneself has captured this phenomenon well. Elsewhere a force-matching task has been used to demonstrate that we appear to experience external forces as more intense than self-generated equivalents (Shergill et al., 2003; Walsh et al., 2011; Wolpe et al., 2018). Sensory attenuation can also be demonstrated using electrophysiological and brain imaging techniques whereby self-generated versus externally provided cues result in attenuation of somatosensory, auditory or visual evoked potentials (Horváth, 2015; Macerollo et al., 2016; Mifsud et al., 2018). Sensory attenuation has proved an interesting and robust phenomenon that appears to index selective information processing within multiple modalities. In addition to being used to explain why self-tickle is ineffective (Blakemore et al., 1998; Kilteni et al., 2019), sensory attenuation has been demonstrated when simply observing actions (Heins et al., 2020; Sato, 2008).

Some researchers have distinguished between the attenuation of sensory evoked potentials (SEPs) at the cortical level and behavioural outcomes that indicate altered perception of a stimulus (Macerollo et al., 2016, 2019). There is good reason for acknowledging the neurophysiological responses and the behavioural measures as the two do not always present harmoniously. For instance, in healthy older adults, sensory attenuation appears to increase with age when measured with a force-matching task (Wolpe et al., 2016), but the picture is a little more complex when investigating the neurophysiological data (Ogata et al., 2009). Furthermore, behavioural measures indicated equally good distinction by participants of smooth and rough surfaces in two conditions: active touch, where the participant moves their finger across the surface; and dynamic passive touch, where the participant's finger remains still while the surface is moved. However, fMRI analysis revealed distinct brain activation patterns for the two touch conditions (Simões-Franklin et al., 2011). Across different measures and studies, the common pattern is that identical stimuli have the potential to elicit different, context-dependent responses.

Sensory attenuation appears to be reduced in people with Parkinson's, displaying diminished differences between the intensity of self-generated and externally generated sensations. When comparing sensory evoked potentials from electrical stimulation of the thumb during movement and rest, people with Parkinson's who were off medication displayed reduced attenuation of the movement-initiated stimuli compared to healthy controls (Macerollo et al., 2016, 2019). Furthermore, in the same studies, dopaminergic medication restored sensory attenuation in participants with Parkinson's. In a Parkinson's-ON group, Wolpe and colleagues (2018) found that the amount of sensory attenuation was negatively related to motor symptom severity, but positively related to dopamine dose in a force-matching task. Parkinson's symptoms are of course a problematic confound when making assessments in movement-based paradigms such as the force-matching task, especially in the OFF-state, but the link between higher dopamine dose equivalent and increased sensory attenuation reinforces the connection to dopamine and its alteration in Parkinson's disease. In a speech task, people with Parkinson's also demonstrate reduced attenuation of auditory evoked activity 100 ms after sound onset when the participant speaks as compared to when the sound is externally produced (Railo et al., 2020).

2.2. Reconsidering Sensory Attenuation Theory

Prominent theories of motor control emphasise the role of predicted sensory consequences in sensory attenuation. It is believed that we construct an internal model of the world around us which is built-up through experience, and which allows us to make predictions about the results of our movements (Figure 1a). In optimal control theory, an efference copy of a motor command is used to predict its sensory consequence to overcome sensory delays, cancelling out self-generated feedback to better detect sensory information in the environment (Franklin & Wolpert, 2011). In active inference, which subsumes predictive processing theory, the prediction itself acts as a motor command and descends further down the neural hierarchy. It is compared to the current position of the body, which gives rise to a prediction error. The overall goal is to reduce prediction error, and therefore this prediction error can either travel back up to inform higher centres of the lack of movement and update the internal model, or the prediction error is attenuated and fulfilled by reflex arcs bringing about the movement (Brown et al., 2013). Perhaps confusingly, whilst sensory attenuation has previously been used to describe the resultant phenomenon of perceived intensity for self-generated sensations, here it describes the halting of an ascending prediction error. This halted ascension is enabled by lowering the precision of the prediction error.

Both theories utilise a Bayesian-like framework, where weighting of prior and current evidence is altered based on precision (Figure 1b). Using prior knowledge provides a way to estimate and better navigate an environment (Körding & Wolpert, 2004). Moving in an uncertain environment, such as playing sport at dusk, increases the reliance on prior information, and the Bayesian framework specifies how we can optimally combine multiple sources of information to better estimate an uncertain event (Körding & Wolpert, 2005). Learning a new skill or navigating a new environment naturally involves novel unknown information, but useful information can be better extracted using predictive signals formed in a Bayesian manner from previous experience (Wolpert et al., 2010).

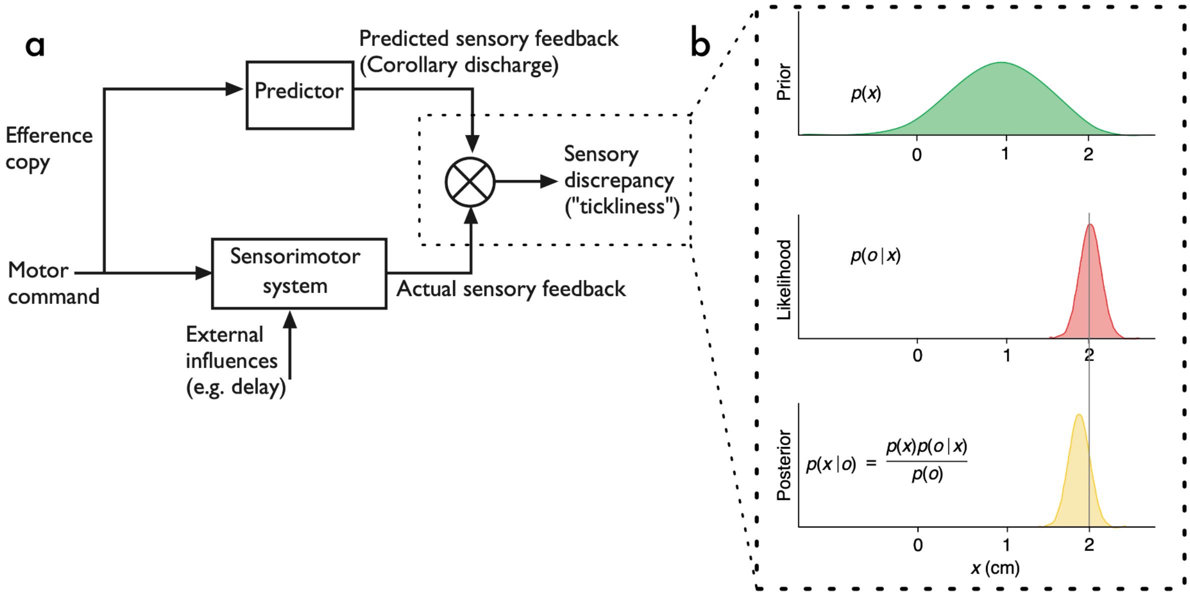


Figure 1 Schematics of the sensorimotor integration models used to explain sensory attenuation. **(a)** The diagram from Blakemore, Wolpert and Frith (2000) represents a typical internal forward model that underpins optimal control theory, proposes how a sensation, ticklishness, arises. Starting from a motor command, an efference copy is used to predict upcoming feedback to overcome noise and delay in the system, and is then compared to actual sensory feedback. The comparison of the two signals gives rise to the final sensation. **(b)** Bayesian integration is often used in optimal control and active inference accounts to model how this final sensation – ticklishness in this case – arises from the integration of predictive and sensory signals. The more certain the signal, the more influence it has on perception. The prior signal (*green curve, top, p(x)*) is the prediction or internal signal; the likelihood (*red curve, middle, p(o | x)*) is the new information, the sensory input. The resulting integration of the two, the posterior (*yellow curve, bottom, p(x | o)*), is informed by the noisiness of each signal, or the spread of the curves, and is determined here by Bayes' theorem ($p(x \mid o) = p(x)p(o \mid x)^{*}p(o)^{-1}$). Thus, the posterior (yellow curve) in this case more closely resembles the likelihood (red curve), though the estimate is still informed by the prior (green curve). Diagram from Körding & Wolpert (2006). To illustrate which part of the forward model Bayesian integration is used to describe, images in **(a)** and **(b)** have been connected with dashed lines added by the current author. The integration of a prior signal into sensation is a crucial concept when considering sensory attenuation: sensory input is integrated differently due to priors which can include motor involvement.

While the optimal control and active inference theories similarly predict a wide array of empirical findings, they do differ in the way that sensory attenuation during movement is described. In optimal control theory, sensory attenuation is a result of accurately predicting the sensory consequences of movement. The predictions are made with the efference copy of the motor command, providing an informative internal signal (Kilteni et al., 2020). This underpins various benefits such as overcoming noise and delays in the sensorimotor system, and heightens detection of unpredicted and potentially useful/dangerous stimuli. In active inference, sensory attenuation is not just a beneficial by-product of movement, but essential in bringing it about (Brown et al., 2013). Here sensory attenuation refers to the down-weighting of the precision of sensory signals to facilitate the fulfilment of predictions by reflex arcs. The reduced precision of a sensory signal means a reduced perception of it at higher levels during movement onset; or, put another way, reduced sensory attenuation.

Evidence from studies of people with schizophrenia suggests sensory attenuation is altered across different modalities (Shergill et al., 2014), and so measures may capture some phenomenon resulting from the fundamental way our brains engage in perception (Clark, 2015). However, the presence of non-motor contributors to sensory attenuation (Saradjian, 2015) challenges optimal control theory which ultimately only describes a perception dependent on action. It has been maintained that self-generated sensations are attenuated, making way for externally-generated sensations to be facilitated (Blakemore et al., 2000) but this neat distinction does not sufficiently explain the specificity of selective sensory modulation amongst self-generated signals based on factors such as spatial location (Chapman et al., 1987) or task-relevance (Saradjian, 2015). And active inference, which places gating of sensory afference at an inseparable level from movement does not comfortably explain why sensation can often be enhanced by movement (e.g., Simões-Franklin et al., 2011; Saradjian, 2015), though predictive processing more generally does make room for non-motor influences on perception (Clark, 2015; Hohwy, 2016).

Action, even when including imagined and observed action, is not the only factor that modifies perception. In a cleverly designed experiment, Heins and colleagues (2020) trained participants in hurdling and tap dancing—two complex movements that generate sounds as a consequence of foot contact with the floor. After an extended period of training, participants watched point-light videos of themselves during an fMRI recording, being tasked with rating the subjective quality of their performance. Scrambled video and audio were used to gauge sensitivity to errors. More sensory attenuation, as indicated by reduced activation of the auditory cortex and more reactive ratings to sounds when scrambled, occurred in the tap-dancing condition. This was argued to be due to the different relationships that sound posed to the performance of the different tasks. The authors argue the importance of sounds elicited by tap-dancing is greater to task performance and are therefore goal-related, unlike the by-product sounds of hurdling. Whilst active modulation of sensory input likely occurred in both conditions, evidence of stronger modulation for tap-dancing supports the notion that factors other than self-generation mediate sensory attenuation.

Reduced neural responses in the ventral visual stream to images based on learned regularities—that is, only the expectedness of the image was manipulated—support the view that sensory input is modulated by non-motor factors also (Dogge et al., 2019; Kaiser & Schütz-Bosbach, 2018; Richter & de Lange, 2019). There has also been criticism of efference copy models for characterising motor commands as context-independent (Gandolla et al., 2014) with studies demonstrating motor cortex excitability changes with sensory stimulation (Léonard et al., 2013; Roy & Gorassini, 2008). Furthermore, self-generation can actually heighten as well as attenuate neural responses to sensory stimuli (Reznik & Mukamel, 2019; Saradjian, 2015; Saradjian et al., 2013), which also challenges active inference as a model to explain all aspects of sensory attenuation. Whilst predictive processing accounts are flexible enough to incorporate various signals from the current context, a "generalised and multi-modal suppression of sensory input from the effector to enable movement" (Limanowski et al., 2020, p. 8) does not lend itself to the differential attenuation or augmentation of sensory gain, nor do models arguing for inflexible sharpening effects from movement (Yon et al., 2018).

2.3. Scope of the Dominant Theories

While the active inference and optimal control models are useful, and appear anatomically viable (e.g., Adams et al., 2013; Holland et al., 2020), they so-far lack a solid specification in regards to the neural substrates involved in sensory attenuation itself. Rather, the behaviour consequence of sensory attenuation has been used to explain certain Parkinson's symptoms, centred on a global decrease in sensory precision of internal predictive signals which increases reliance on external sensory signals (Brown et al., 2013; Wolpe et al., 2018). This explains how increasing the salience of external cues—such as lines on the floor to improve gait (Beck et al., 2015; Morris et al., 1994, 1996)—are needed to overcome movement deficits. However, succesful longer-term rehabilitation programmes have also taken, in some ways, the opposite approach by reducing visual input during training sessions (Sage & Almeida, 2009, 2010). And while reduced sensory attenuation in Parkinson's (Wolpe et al., 2018; Macerollo et al., 2016, 2019) indicates a deficit in successfully modulating sensory input, it is not clear, without further work at least, how this principle could inform therapeutic approaches. As we discuss in the final section, such theories do not entirely explain the rehabilitation effects of all therapies.

Such models may be limited in scope but are still useful in describing a mechanism that explains motor-related attenuation that need not be constrained to a single neural circuit. As far back as 1964, Giblin reported reduced SEPs during voluntary movement and the gating of sensory afferent signals during movement is well documented (for a review, see Saradjian, 2015). The presence of such gating does not mean worsened perception during movement though, as many tasks have since shown. The classic definition describes sensory attenuation as resulting only as a consequence of self-generation, emphasising a suppression effect, which is itself limiting. Across the literature in the sensory attenuation field though, what the tasks do is measure how sensory stimuli are being modulated by organisms.

2.4. Factors Affecting Sensory Attenuation

Sensory attenuation measures the distinct context-dependent perception of two identical stimuli and, in doing so, captures not only our internal model of prediction, but also the salience and task relevance ascribed to each sensory input. As sensory attenuation is diminished in Parkinson's, this raises the question of which aspect of this multi-faceted process is affected by basal ganglia dysfunction: from sensorimotor integration, to salience attribution, through to predicting sensory consequences. Intriguingly, while sensory attenuation is reduced in Parkinson's, it appears to steadily increase with healthy ageing (Wolpe et al., 2016). The reason for this remains unclear, but it shows that sensory attenuation is both sensitive enough to track change over time, and also potentially alterable: might it be possible to alter the sensorimotor processes captured in a sensory attenuation paradigm?

What factors do affect sensory attenuation, and what insights might they offer? The feeling of body ownership has been investigated using the rubber hand illusion where a participant is led to believe a fake hand belongs to them. Body ownership was shown to have a sensory attenuation effect, whereby somatosensory stimulation triggered by the fake hand was experienced comparably to stimulation triggered by the participant's own hand, both of which were experienced less intensely than a standard externally-generated condition (Pyasik et al., 2019). Ehrsson et al. (2004) argues body ownership arises from multi-sensory signals from the body occurring synchronously. Likewise, Kilteni and Ehrsson (2017) found that sensory attenuation was diminished in a self-generated force-match when the hands were held apart from one other, demonstrating the importance of congruence between visuospatial context and action. Sense of agency, while strongly connected to body ownership, arises from a movement feeling like it has been controlled by the self (Pyasik et al., 2019). Sensory attenuation is often assumed to give rise to sense of agency; that is, processing self-generated stimuli differently to externally-generated stimuli contributes to the sense of agency (Kilteni & Ehrsson, 2017). Indeed, sense of agency and sensory attenuation are both seen to be altered in schizophrenia (Jeannerod, 2009; Shergill et al., 2005).

Of course, movement and sensation are intrinsically linked, and the context-dependent motor symptoms in Parkinson's support this notion: freezing-of-gait can be exacerbated by changing door-frame width (Almeida & Lebold, 2010), tactile triggers can help overcome akinesia (Quintyn & Cross, 1986), and visual and auditory cues can enhance gait (del Olmo & Cudeiro, 2005). Sensory attenuation experiments tend to focus on the attenuation of sensation due to movement, but other forms of perception can also be heightened as a result of movement. For instance, the execution of actions can benefit visual perception (Miall et al., 2006), and movement training, which results in improved action fluency, enhanced subsequent visual discrimination (Guo & Song, 2019). Sherwin and Sajda (2013) found that expert musicians are better than novices at detecting anomalous sounds when listening to music; they recorded cortical activity corresponding to the playing hand giving rise to the possibility that imagined movement that mimicked the music enhanced auditory perception. Evidence for the dependence of perception on action (in addition to the descriptions of motor symptoms in Parkinson's being dependent on perception) support codependent and bidirectional links (Bosch, 2020; Guo & Song, 2019; Wykowska & Schubö, 2012).

It might be logical, given the above, to assume that a deficit in sensation such as body awareness would be a crucial factor affecting movement in Parkinson's (Quintyn & Cross, 1986). However, a deficit in proprioception is not itself enough to explain the motor symptoms of Parkinson's. Kammers and colleagues (2009) found motor control to be unaffected when using the rubber hand illusion to create false information about the hand position. Here, it is possible movements were far from complex, and accurate proprioception may have been restored the moment movement was initiated. However, perception may arise from different levels of the neuraxis, whereby a sense of agency may be experienced at a conscious level while action adjustments occur automatically (Jeannerod, 2009; Wolpe et al., 2020). This is indeed consistent with the notion of low-level attenuation of sensory precision to fulfil actions described in active inference, while other predictive processes can still influence perception in higher regions (Brown et al., 2013; Wolpe et al., 2020). In fact, predictive processing accounts might even explain both sense of ownership and sense of agency, whereby the former arises from reducing prediction error by updating the internal model (perceptual inference), and the latter arises from reducing prediction error with action (active inference) (Braun et al., 2018). So, while body awareness can interact with sensory attenuation, movement need not invariably be disrupted by disturbances occurring in parallel that involve separate regions (Humprhies et al., 2007).

Finally, Redgrave and colleagues (2010) distinguish between forms of motor control enacted by the basal ganglia that support the idea of layered control, maintaining the notion of bidirectional links between movement and sensation. It was argued that the basal ganglia loops are involved in distinct functions of goal-directed and habitual motor control, of which the latter is most affected in Parkinson's. In Redgrave and colleagues' analysis, goal-directed control describes the conscious, cognitive control of movement, which might then be more easily disrupted when one's attention is diverted. Habitual control describes the lower level, more inflexible, stimulus-response movements. This distinction is important in explaining why movement in some contexts, often more demanding ones, is worsened in Parkinson's. However, goal-directed behaviour should not be confined to describing only that performed under conscious, attentional control; movement can arise from subcortical circuits to achieve a goal, without the movement being controlled cognitively. Rather, there is surely the capacity for a goal encoded at a cortical level to have the general effect of filtering the environment for fast, responsive movements to then achieve (e.g., "walk up the stairs"), in addition to a specific cognitive control (e.g., "move my leg") (Nakajima et al., 2019; Robbe, 2018). It is the effect of this concept of sensory filtering by goal—or task—that we now examine.

2.5. Task-Relevance in Sensory Attenuation

Often overlooked in sensory attenuation studies are the effects of task demands on sensory processing. It might even seem obvious that task demands affect how we interact with our environment; the need to filter through a vastly complex and dynamic environment is crucial for an organism's survival, and it is often considered in ecological psychology that we have evolved to do this in a task-relevant manner (Cisek, 2007; Cisek & Pastor-Bernier, 2014). Proponents of the constraints-based approach in sports coaching strongly emphasise the importance of the three interacting elements of task, environment and organism (Bosch, 2020) (Figure 2). However, sensory attenuation experiments largely only consider organism and environment interactions, and explain changes in sensory processing in terms relating to organism-centred factors such as movement, expectation and attention.

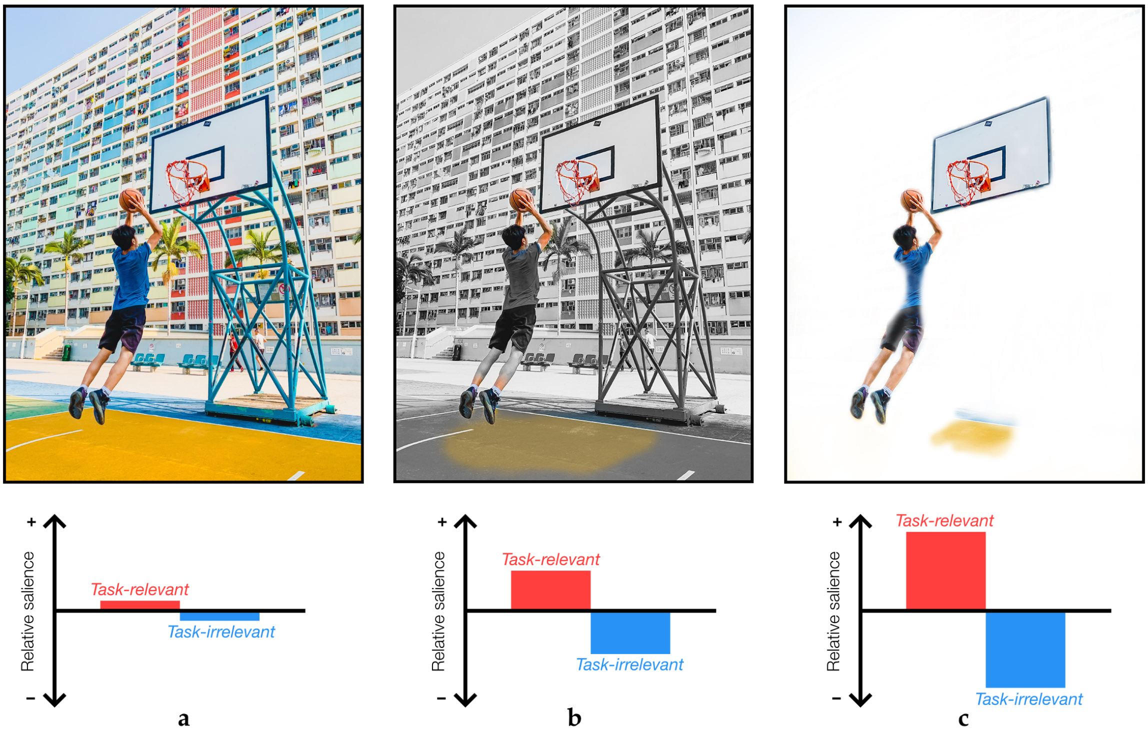


Figure 2. Visualising the effects of normal sensory attenuation when attempting to score in basketball, with schematic plots of the relative salience of task-relevant and task-irrelevant features: (**a**) the full, unfiltered scene is full of information, with little difference between relevant and irrelevant features; (**b**) but we are able to selectively filter information relevant to the task such as the ball, the basket, sense of the body in space relative to the ground and backboard; (**c**) salience of important stimuli may then be further enhanced through the use of contextual information; for example, using the proximity of the ball to the basket. The distance to the floor is not immediately as important, but will be once the ball has been released and the player lands. Original photo provided by Fahrul Azmi.

Task conditions affect our responses to stimuli. Staines and colleagues (2002) measured responses in the human brain using fMRI, finding that during simultaneous tactile stimulation to both hands, only task-relevant stimulation increased activity in contralateral primary somatosensory cortex. In a more complex task, Riley and colleagues (1999) demonstrated improved postural sway when participants were instructed to pinch and stabilise a curtain as opposed to simply making contact with it, indicating altered behavioural use of a similar tactile input when it becomes more important for the task at hand. Task complexity itself can affect the neural response to stimuli; Reiser and colleagues (2019) used a mobile EEG set-up to show that auditory evoked potentials during an oddball paradigm, as well as performance of the task, were altered when participants walked an obstacle course as compared to when they walked without obstacles. Though a small motor response was required for target sounds, it does suggest that there is competition for attentional resources in a cognitive-motor dual-task paradigm, and that more complex motor tasks may depend more on such task-relevant filtering, especially in real-world environments.

The force-matching paradigm reveals the use of distinct contextual information in perceiving and responding to an identical target stimulus. The task in both the direct matching condition and the indirect matching condition is to match a target force, so the objective remains consistent. It has been suggested that the direct condition benefits from predictive mechanisms more so than the unusual indirect condition where the hand generates the force with a joystick or slider (Shergill et al., 2003). Interestingly, people with schizophrenia have been suggested to display increased weighting of internal predictions (Teufel & Fletcher, 2020; Teufel et al., 2015), whereas internal predictive signals are of reduced precision in Parkinson's (Brown et al., 2013; Wolpe et al., 2018), yet both appear to show less force-overcompensation in the force-matching task compared to healthy controls (Wolpe et al., 2018; Shergill et al., 2005, 2014). The key pattern here then is that two stimuli in two distinct contexts are perceived less differently in a disease state—that is, they converge—and this difference results from contextual information once task has been controlled for, pointing to compounding effects on sensory processing (Figure 2 and Figure 3).

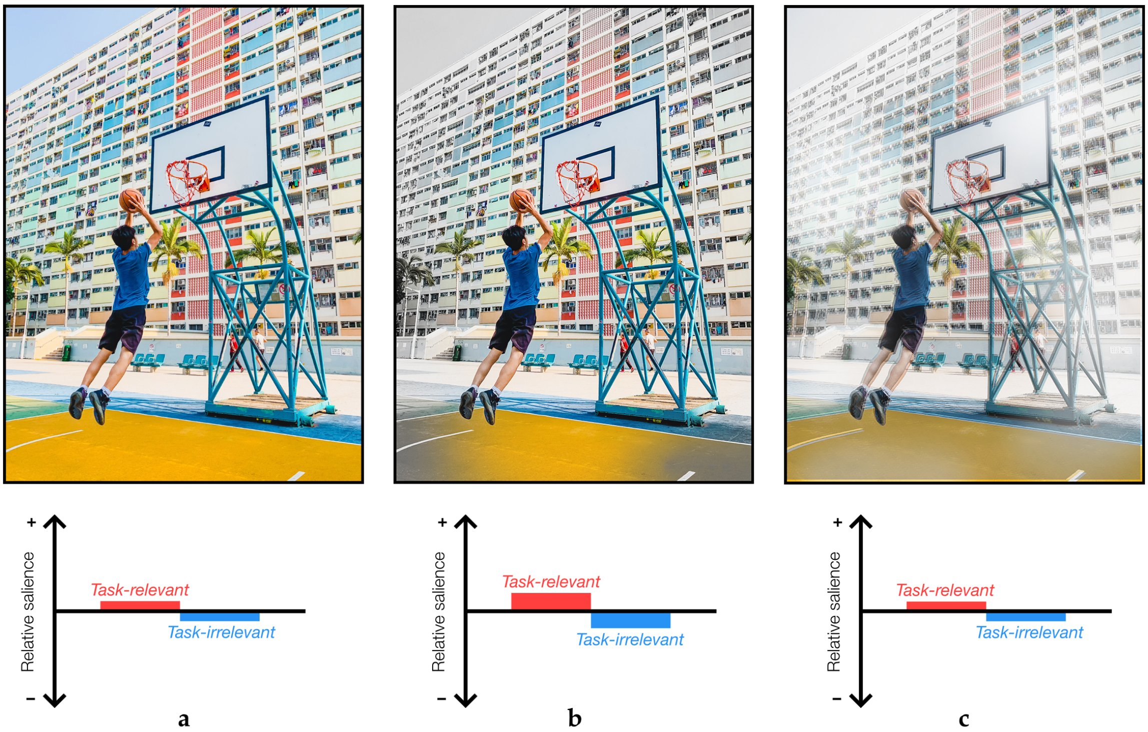


Figure 3. Visualising pathological sensory attenuation when attempting to score in basketball with deficits in task-relevant filtering and the utilisation of contextual information, with schematic plots of the relative salience of features

important for the task: (**a**) the full, unfiltered scene is full of information; (**b**) task-relevant filtering is only partially effective, failing to filter out information irrelevant to the task and leaving little difference between task-relevant and task-irrelevant information; (**c**) this makes it harder to use contextual information to further enhance sensation, and irrelevant information remains similarly salient. The illustration made might also be considered with other examples, from everyday tasks such as the oft-considered 'picking up a mug to drink' example, to dance moves and other sporting scenarios.

Further to this point, Bolton and Staines (2012) found reduced task-relevant modulation of sensory input during a tactile discrimination task in older adults compared to young adults. However, force-overcompensation—the sensory attenuation index in a force-matching task—was found to increase with age (Parthasharathy et al., 2021; Wolpe et al., 2016). This supports the notion of the force-matching task capturing the ability to utilise contextual information, such as hand position, to perceive a target stimulus and guide movement.

Perhaps this ability to utilise a contextual cue is captured by pre-pulse inhibition (PPI) and temporal discrimination tasks. In PPI paradigms, people with Parkinson's show reduced gating of auditory stimuli whereby a preceding stimulus normally attenuates the response of a subsequent stimulus when they are presented at a higher frequency (Gulberti et al., 2015). Somatosensory temporal discrimination threshold (STDT) tests have also revealed people with Parkinson's have higher thresholds when discriminating between two tactile stimuli presented in close succession (Conte et al., 2013). Researchers have pointed to a role of the basal ganglia in timekeeping operations (Bradley et al., 2012; Rao et al., 2001). Perhaps in the absence of explicit time information, the basal ganglia utilise disparate signals from across the brain to "stand-in" (Turner & Anderson, 2005), form a "consensus" (Beeler & Dreyer, 2019), and modulate a response accordingly. Indeed, the striatal networks appear to outperform the prefrontal cortex in timekeeping (Bakhurin et al., 2017). This points to the capacity to integrate useful contextual information for optimal behaviour and, in Parkinson's, could underpin performance deficits in PPI and STDT paradigms.

3. Neural Substrate

3.1. Reconciling Discrepancies in Studies Investigating the Neural Substrates of Sensory Attenuation

With the basal ganglia heavily associated with sensorimotor control, it is no surprise that sensory attenuation is affected in both Parkinson's and schizophrenia (Shergill et al., 2005, 2014), both of which are disorders of the basal ganglia. It has even been postulated that fronto-striatal circuits may help explain changes of sensory attenuation in healthy older adults (Wolpe et al., 2016, 2018). However, cortical regions such as the supplementary motor area have also been implicated (Jo et al., 2019), as has the cerebellum (Blakemore et al., 2000; Kilteni & Ehrsson, 2020), and the thalamus (Staines et al., 2002). Initially this may point to a non-specific cross-modal sensory attenuation phenomenon that describes a generalisable principle of perception and, while this may hold some truth, there is an important role for the basal ganglia in actively modulating sensory input. In fact, by examining the available literature concerning the neural basis of sensory attenuation, there appears to be a striking discrepancy that relies on the variety of tasks being used.

The findings from fMRI studies investigating sensory attenuation can broadly be split into those that show involvement of the cerebellum, those that demonstrate basal ganglia involvement, and those that show both. Pointing to cerebellar involvement, Kilteni and Ehrsson (2020) demonstrated attenuated activity of the cerebellum and secondary somatosensory cortex, and increased functional connectivity of the two structures, in healthy young adults for self-generated sensations compared to externally generated sensations, replicating some of the findings of Blakemore and colleagues (2000). Likewise, Boehme and colleagues (2020) compared people with ADHD and neurotypical controls in a self- vs. other-touch task, finding not only a difference between groups in the primary somatosensory cortex, but also an increased BOLD signal of the cerebellum and prefrontal cortex amongst other areas when the experimenter administered touch compared to self-touch.

Capturing a combination of both basal ganglia and cerebellum involvement, a comparison of people with schizophrenia and healthy controls (Shergill et al., 2014) demonstrated that the cerebellum was active in both groups during a modified force-matching task. They speculated that the cerebellum seemed to be performing a comparator function. However, they also found increased activation of the caudate for healthy controls when sensation was synchronous with movement, and increased cerebellar activation when sensation was delayed (along with other differences across condition and group). Simões-Franklin and colleagues (2011) compared active, passive and dynamic-passive touch for rough surface detection, reporting greater activation of the cerebellum and lentiform nucleus for the active condition compared to the passive conditions.

Supporting basal ganglia involvement, Leube et al. (2010) compared people with schizophrenia to healthy controls during a task comparing visual consequences of self-generated actions in conditions of delay and no delay. They found reduced activation of the putamen in patients which accompanied a reduced ability to discriminate the delayed action consequences. Nonetheless, to add to the assortment of findings, Ackerley and colleagues (2012) reported altered activations across a range of sensory areas elicited by a paint brush on the arm under self-touch and passive touch conditions, but not the basal ganglia or the cerebellum.

This somewhat mixed set of findings may best be explained by the variety of tasks used. The studies attempting to recreate the force-matching tasks have needed to heavily modify the task for use in (usually) an MRI scanner, and the constraints of such neuroimaging techniques make altered paradigms necessary. Movement may also be controlled differently in such paradigms, and is often triggered by a very simple visual cue, without the clear task goal in the behaviour-only paradigms where matching a previous force in a more complex environment demands active selective filtering using memory and task information in the absence of simple visual cues.

The self- vs. other-touch paradigms appear more consistent in design (Blakemore et al., 2000; Boehme et al., 2020; Ackerley et al., 2012) with some commonalities in findings such as modulation of primary somatosensory cortex, but also differences. Movement is still instructed with an on-screen cue which might not be so problematic in this case, but there is no clear task goal and therefore no monitoring of performance or control of attention which may affect perception as well as the way movement is being initiated (Ackerley et al., 2012).

Perhaps the most informative designs are those which embrace the reality of a different set up and use videos of participants' movements in the scanner, and/or manipulate visual or auditory information to alter its predictability (Heins et al., 2020; Leube et al., 2010). This builds on the assumption that there is an attenuation effect from observing action as well as performing it (Sato, 2008).

Heins and colleagues (2020) only compared conditions where a strong sensory attenuation effect was expected, but Leube et al. (2010) compared healthy controls and people with schizophrenia. Participants opened and closed their hands which was filmed and played back for them to see in the scanner with no delay or with small delays to create congruent and incongruent action consequences. Not dissimilar to Heins et al. (2020) where participants rated movement quality which worsened with scrambled videos, participants were tasked with detecting the synchrony of the video with their movements (Leube et al., 2010). Those with schizophrenia were more likely to incorrectly perceive movements as asynchronous, and sometimes also incorrectly perceived asynchronous movements as synchronous. Such error detection paradigms used in these two studies index the ability to distinguish self from externally generated stimuli captured in sensory attenuation measures, with better detection thresholds during related movement (Chapman et al., 1987; Eliades & Wang, 2008; Synofzik et al., 2010). Activation of putamen and thalamus was reduced in patients compared to controls during this error detection task during distinct delay and no-delay conditions (Leube et al., 2010).

There are of course challenges in collecting this type of data in those with movement disorders, but considerations should be made for the different types of motor control that are likely being invoked in these designs. Externally triggered movements, such as when a finger-tap is elicited by an on-screen stimulus (Kilteni & Ehrsson, 2020), have been strongly associated with cerebellar circuits, whereas internally generated movement—that is, movement elicited and guided more so by memory signals—are associated with basal ganglia circuits (Turner & Anderson, 2005; Martinu & Monchi, 2013; van Donkelaar et al., 2000). If the basal ganglia are predominantly involved in memory-guided movement, and filter information for action in a task-relevant manner (Robbe, 2018), then investigation of sensory attenuation in basal ganglia disorders should consider task design, including sensory cues, carefully. Cerebellar circuits are also altered in Parkinson's though, which is thought to be pathophysiological rather than compensatory (Martinu & Monchi, 2013). Perhaps these systems might work in a complementary fashion whereby global task-dependent filtering decomposes a complex environment into smaller and simple components that can be responded to with other more appropriate systems such as the cerebellum (Yamazaki & Lennon, 2019). A future direction for research in sensory attenuation might be to compare attenuation during different forms of motor control for further insight into its neural underpinnings.

3.2. The basal ganglia through a Sensory Lens: Task-Relevant Signalling

Movement can vary across environments, perhaps radically demonstrated by athletes in the phenomenon of choking in sport (Bosch, 2015) and even sports-related dystonia with its variety of quirky alleviating manoeuvres (Sadnicka et al., 2018; Lenka & Jankovic, 2021). Motor symptoms in Parkinson's are also responsive to sensory environment and task demand, which are exacerbated in more challenging environments (Almeida & Lebold, 2010; Ehgoetz Martens et al., 2014, 2015; Klockgether & Dichgans, 1994; Quintyn & Cross, 1986) but alleviated when aided by sensory cues that help navigate an environment (Beck et al., 2015; Chawla et al., 2020; Morris et al., 1994, 1996; Spaulding et al., 2013). This leaves a narrow set of often impractical environments where free-flowing movement is possible. Importantly though, this demonstrates that Parkinson's is not purely a kinetic disorder, and rather that the basal ganglia has a sensory processing function that heavily impacts movement (Kaji, 2001; Lidsky et al., 1985; Robbe, 2018; Schneider, 1984).

Before movement is even considered, the basal ganglia appear influential in task-relevant sensory filtering to achieve behavioural goals. Nakajima and colleagues (Nakajima et al., 2019) describe a need for animals to filter relevant stimuli through sensory noise. It has been shown that the need to engage sensory filtering can depend on the amount of sensory noise and also behavioural goals (Gilbert & Li, 2013). Goal-related movement has often been functionally linked to the basal ganglia (Gale et al., 2008), but such behaviourally-relevant sensory filtering has also been demonstrated in non-motor aspects of behaviour. McNab and Klingberg (2008) demonstrated basal ganglia involvement in filtering visual stimuli, and suggested that working memory capacity may be related to how well (ir)relevant information is filtered, finding that increased globus pallidus activity correlated with increased working memory capacity. It has also been demonstrated that memory for deep-encoded words is impaired in Parkinson's compared to shallow-encoded words, with higher beta oscillations (an indicator of reduced novel processing) during deep-semantic processing, suggesting a difference in the initial encoding phase (MacDonald et al., 2019). In a recent study, evidence was found for a pathway between the prefrontal cortex and the basal ganglia which mediates top-down filtering of irrelevant stimuli based on task demand and not movement (Nakajima et al., 2019).

Considering a task-dependent sensory processing role appears fruitful in motor control studies too. Neuronal recordings have shown that the basal ganglia respond to sensory stimulation more prominently when they are relevant for upcoming motor control (Kaji, 2001). This may provide a mechanism to explain how basal ganglia lesions mostly affect automatic movements that require sensory guidance (Kaji, 2001). Schneider (1987) meanwhile argues for a transient and adaptable system which respond differently to stimulation during different tasks. Schneider found that in cats, neurons in the entopeduncular nucleus (homologous to the internal segment of the globus pallidus in humans) and the caudate nucleus do not respond to facial stimulation or jaw movement, but those cells do become responsive if they are stimulated during ingestion-related jaw movements. These findings suggest a more complex and dynamic relationship to movement, and the basal ganglia system is well placed to monitor internal signals relevant to task demands with input from across the cortex (Andres & Darbin, 2018).

Understanding the role of the basal ganglia in a sensory capacity begins to make sense of some of the context-specific motor symptoms in Parkinson's, and lays a foundation for the existence of a common mechanism to underlie the vast array of motor and non-motor symptoms. Basal ganglia disorders are themselves diverse, expressing a range of motor, cognitive and emotional symptoms (Andres & Darbin, 2018; Schneider, 1984; Utter & Basso, 2008). It is worth considering then, that damage to the basal ganglia in Parkinson's affects processes that underpin environment-specific motor symptoms, in addition to non-motor symptoms. A viable alternative might be that non-motor symptoms arise from the overload of more cognitive pathways in Parkinson's which may be required to control movement due to degeneration of circuits involved in habitual (lower-level, stimulus-response) control of movement (Redgrave et al., 2010). There is evidence however of both reduced storage capacity and an impaired ability to filter out irrelevant information that underlies such non-motor functions as visual working-memory (Lee et al., 2010), which hints at a more general sensory filtering function of the basal ganglia that could underpin some motor and non-motor Parkinsonian symptoms.

3.3. Sensation to Action

How might impaired sensory filtering be important not just in enhancing movement more generally, but the initiation of actions? A possible mechanism has been demonstrated in early animal experiments. Researchers showed that electrically stimulating the lateral hypothalamus of a cat would sensitise the perioral area, so that touching the area around the mouth would cause the animal to orient toward the stimulus and open its mouth. This reflex would only work when the hypothalamus was stimulated (Flynn et al., 1971), so by modulating sensory processing, movement was initiated. In an excellent review, Robbe (2018) argues against the basal ganglia as an action selector. Instead, the basal ganglia continuously track sensorimotor signals, which can contribute to action production. Such a sensorimotor transformation is demonstrated in membrane potential recordings of medium spiny neurons (MSNs) in mice trained to lick a reward spout following a whisker deflection (Sippy et al., 2015). The MSNs depolarised during whisker deflection after training, and optogenetic stimulation of those neurons was able to substitute for the whisker deflection and elicit the licking action. During whisker deflection though, the MSNs were more active for successful trials compared to unsuccessful, indicating that a motor response could be elicited with a predictive sensory stimuli (Robbe, 2018). Interestingly, it was the MSNs in the direct pathway—the pathway that is underactive in Parkinson's—that depolarised with the whiskers and predicted a licking response (Sippy et al., 2015).

3.4. Sensorimotor Integration

The basal ganglia are strongly positioned to monitor internal and external signals, contributing to motor responses. The generation of actions appropriate to task and environment requires integration of signals from multiple sources (Robbe, 2018; Haber & Calzavara, 2009). Motor symptoms in Parkinson's reveal deficits in sensorimotor integration. Consider the finding that people with Parkinson's display difficulty tracking a visual target on screen by using jaw movements to control another onscreen signal (Connor & Abbs, 1991). There are multiple sources of information that require monitoring and integration to successfully perform the task, both internal and external, across modalities. However visually guiding movement is often helpful or even necessary in Parkinson's, and motor deficits can be overcome with visual cues (Beck et al., 2015; Morris et al., 1994, 1996). One explanation might be that reducing the demands on integration processes of the basal ganglia, achieved by using only vision to guide the foot to a line on the floor for example, restore functionality (Vitório et al., 2014). In support, bilateral integration from whisker stimulation by MSN was found to be diminished in dopamine-depleted mice (Ketzef et al., 2017). Alternatively, visual cueing strategies might make use of alternative and more intact pathways (Martinu & Monchi, 2013; Sage & Almeida, 2010), but it is intriguing that using visual information during movement in different ways can have opposing effects on movement quality.

With a wide range of inputs to the basal ganglia and a role integrating multimodal information for action, studying oscillatory activity across neural systems can prove useful to track complex processing dynamics. Oscillatory changes in Parkinson's have been well established, notably in the basal ganglia (Brittain et al., 2014; Jenkinson & Brown, 2011; Brown, 2006) but also in cortex (Pollok et al., 2012; Marsden et al., 2001). Of particular interest, there has been a focus on the modulation of activity within the alpha/mu (8–12 Hz) and beta (13–30 Hz) frequency bands (Brittain et al., 2014). Focussing on Parkinson's, the time-course of beta has been shown to index movement kinematics (Little et al., 2012), the severity of motor impairment (Chen et al., 2010), and cortico-muscular coupling at beta frequencies is reduced in both early and late stages of Parkinson's (Pollok et al., 2012; Roeder et al., 2020). These observations reinforce arguments we have made about the role of the basal ganglia, as well as offering insight into changes in sensorimotor processing in Parkinson's. Changes in neural synchrony, by means of phase-resetting or neural entrainment, offer potential mechanisms for instigating differential responses to sensory stimuli (Bauer et al., 2020). Beta synchrony in the basal ganglia is reduced during movement, but also in response to cues that are predictive of movement (Brittain & Brown, 2014). Whilst it has been argued that beta synchrony indexes the likelihood for a need for a new action (Jenkinson & Brown, 2011), it might more fundamentally signify the capacity for processing new information (Brittain et al., 2014) which resultantly may facilitate action. Excessive beta synchrony impedes response to novel demands, creating a neural landscape unable to match the complexity of surrounding environments (Andres & Darbin, 2018; Brittain et al., 2014), harming vital task-dependent sensory filtering and sensorimotor integration processes necessary for appropriate behavioural responses (Figure 3).

4. Establishing Principles for Rehabilitation

How do we enhance such vital task-dependent sensory filtering and sensorimotor integration processes? Returning to the motor control theories which point to an imbalance between predictive and sensory signals, we can see how altering information in the sensory environment can affect movement. Sensory cues such as lines on the floor or sounds can alleviate symptoms during walking (Beck et al., 2015; Quintyn & Cross, 1986). Rudimentary sensory cues often simplify and contextualise the perceived environment and can be a useful tactic to improve motor performance, possibly by improving the precision of the sensory input and reducing the demand on "priors" (Figure 1). Such rudimentary cues which simplify the environment, however, do not necessarily train the ability of the nervous system to filter and extract useful information in more complex surroundings. Some attempts at cueing have been promising as a form of rehabilitation (Badarny et al., 2014; de Oliveira et al., 2021; Morris et al., 1994, 1996) but the long term benefits are not clear (Nieuwboer et al., 2007; Spaulding et al., 2013). I have thus far argued that the basal ganglia play a role in task-relevant filtering and then also in utilising useful signals for ongoing behaviour: how then, might we exercise this system and how else can we consider rehabilitation approaches, beyond cueing strategies that more obviously and immediately alleviate symptoms?

In one approach, Sage and Almeida (2009, 2010) utilised a form of exercise called PD-SAFEx where limb movements and gait exercises were performed in low-light conditions, increasing attention to proprioceptive input for guiding movement, forcibly shifting it away from visual input. The researchers found the programme improved symptom severity scores at the end of the programme and after a non-exercise washout period of 6 weeks. Another example of a promising rehabilitation method is forced-exercise cycling (Ridgel & Ault, 2019). An early example of this illustrates the concept well; Ridgel and colleagues (2009) had participants perform tandem cycling where they had to maintain the same high cadence dictated by the other cyclist. Participants with Parkinson's improved their symptom severity scores after an 8-week training programme.

There is a deficit in Parkinson's first of using task-relevance to filter complex environments which is mediated by the basal ganglia (Cisek, 2007; Nakajima et al., 2019; Robbe, 2018; Brown et al., 1997) and then to use this information as useful contextual cues for behaviour (MacDonald et al., 2019; Turner & Anderson, 2005; Beeler & Dreyer, 2019; Schneider, 1984). The two rehabilitation approaches described here – low-light proprioceptive and walking training (Sage & Almeida, 2009, 2010) and forced-exercise cycling (Ridgel & Ault, 2019; Ridgel et al., 2009) – may be training task-relevant filtering and contextual cue integration reliant on basal ganglia function. PD-SAFEx participants have reasonably clear task-goals to make use of during sessions such as gait training involving one high knee each step and opposite hand touching ear. Participants complete these movements in low-light conditions where vision can be excessively relied upon (Abbruzzese & Berardelli, 2003).

Similarly, participants in Ridgel and colleagues' forced-exercise protocol have a very clear task goal to match the cadence of the paired cyclist, which cultivates skilled sensorimotor integration of one's own and another's movement in a dynamic situation. Other approaches to exercise rehabilitation may be more naturally training sensory filtering capacities, such as rock-climbing (Langer et al., 2021) and dance (Bek et al., 2020). Crucially, a route to effective recovery (or slowing disease progression) that involves movement in complex sensory conditions can at least be fruitful. A variety of routes are worth considering, especially when strategies do not have the same effect for every person and cueing tricks can lose effectiveness over time (Nonnekes et al., 2019).

Nonnekes and colleagues (2019) emphasised the inventiveness of people with Parkinson's in developing effective compensatory strategies to overcome gait deficits. Such strategies might be considered more effective because they are developed within the specific environment that the person navigates. As the context of an event affects our response to it, rehabilitation in daily-life settings might be appealing. However, this could highlight the importance of the compatibility of a strategy, and not necessarily the concept of transfer specificity. When considering specificity, it is important to recognise not just that we are better at recalling something in the same physical space it was encoded (Godden & Baddeley, 1975), but also that internal factors such as attentional context can affect motor learning (Song & Bédard, 2015). In sport, specificity considerations underline factors such as muscle fatigue, force landscapes and speed of movement, all of which form a context that may affect transfer from practice to competition (Bosch, 2020). Furthermore, the evidence actually points to a reduced ability of people with Parkinson's to make use of such contextual factors during recall (MacDonald et al., 2019). This poses a challenge, but as no two contexts of a movement are ever the same, perhaps it is better to train the underlying ability to identify and utilise contextual cues and to do so in a range of interesting environments that invite exploration and the use of task-relevant filtering to draw out cues to enhance movement.

With the short-term success of simple sensory cues, there might be a temptation to bombard a patient with cues to overcome motor deficits. However, in the absence of simple cues the basal ganglia are required to incorporate other internal signals relating to task and context to make sense of a complex environment (Beeler & Dreyer, 2019; Turner & Anderson, 2005) and this can be a useful tool in training. Finally, task will alter what signals are relevant and irrelevant, meaning a movement may look the same but still affect the brain's response to that movement (Bek et al., 2021; Staines et al., 2002), which is ultimately the principle underpinning sensory attenuation—active modulation of sensory input. In an exercise programme, determining sensory input in terms of which artificial cues are provided is not sufficient, as controlling sensory experience is not possible. A coach or facilitator can provide a stimulus, but that will only be part of the experience, as task and environment critically alter our response to each sensory event, and therefore inform our unpredictable experiences and capacities to engage with the world as a whole.

5. Conclusions

We have reviewed sensory attenuation through the lens of Parkinson's research with a particular interest in sport and rehabilitation. Studies investigating sensory attenuation measure the distinct responses that can emerge from two identical stimuli presented under different contexts. Differences in these responses indicate that contextual information has been utilised in active modulation of the sensory input, captured by a facilitation or suppression of the response to a stimulus. Diseased states appear to cause a convergence of responses that are more differentiable in healthy populations, indicating a reduced ability to integrate relevant sensory signals for perception or to enact appropriate movements. However, a crucial step precedes the utilisation of contextual cues, and we have considered the importance of task-relevance in both reconciling seemingly conflicting findings in sensory attenuation research and simultaneously informing on the symptoms of Parkinson's disease. There is a dual effect of basal ganglia dysfunction in Parkinson's where a reduced ability to filter relevant signals from a complex environment overwhelms a basal ganglia system already at reduced capacity, just when contextual cues might be used to enhance movement and perception (Figure 2 and Figure 3). Sensory attenuation paradigms may capture this process and offer a useful tool to track changes elicited by effective interventions and may even form the foundations of effective rehabilitation strategies themselves. Regardless, examining the sensorimotor processes that underpin sensory attenuation through the lens of Parkinson's research paves the way for establishing key principles that may be useful in guiding the design of effective rehabilitation.

Context

context is a powerful thing.
not because of what it is, but because of the
relations it represents.

it reveals an inseparability,
a connectedness of all things
a dynamism because for something to have context

it must relate,

it moves us between things
to consider the relations

Chapter 2

Sensory attenuation as context-dependent processing

1. Introduction

We argued in Chapter 1 that sensory attenuation paradigms, beyond just assessing the involvement of movement and sometimes expectation, measure context-dependent sensation. For instance, the oft-used force-matching task (Kilteni et al., 2020; Walsh et al., 2011; Wolpe et al., 2016, 2018) requires participants to replicate an experienced target force on one finger delivered by a computer-controlled lever. When they attempt to replicate this force using a removed dial or slider, they are quite accurate. However, when attempting to replicate the target force by pressing down on top of the lever with a finger from the other hand, participants significantly overcompensate. The differences seen between matching conditions requiring different motor output is compatible with the view that motor involvement attenuates sensory input, but it is also consistent with the notion that the presence of a finger from the other hand creates a unique context in which to perceive the force. As such, creating a 25 cm gap between the force-exerting finger and the force-receiving finger was enough to reduce the overcompensation effect (Kilteni & Ehrsson, 2017, 2020). Additionally, a context-dependent perception explanation of sensory attenuation measures also helps make sense of findings where sensation of a stimulus is heightened because of motor involvement (Guo & Song, 2019; Miall et al., 2006; Sherwin & Sajda, 2013). This alternative perspective thus helped to make sense of some contradictory findings in the literature, whereby some studies report a motor-induced sensory suppression and others report an enhancement of sensory input.

Sensory attenuation then, is not simply a uniform dampening of sensory input during movement. Rather, it is crucial to consider what exactly is the sensory input being measured, how it is needed to perform the set task, and what factors create a unique context to perceive the target stimulus. Even classic sensory gating studies (Chapman et al., 1987; Flynn et al., 1971) can be interpreted in this way, where concurrent stimuli and other more global factors such as attention alter the characteristics of sensory evoked potentials. We cannot therefore assume that the gating effects of movement are uniform and absolute. Additionally, as Riley and colleagues (1999) demonstrated, as discussed in the previous chapter, simple physical alterations to the task set up can change how sensory information is being used.

Framing sensory attenuation as a form of context-dependent perception, that may involve self-generation of the stimuli, is compatible with the task-relevant sensory processing role the basal ganglia play in movement (Kaji, 2001; Robbe, 2018; Schneider, 1984). As such, information, or signals, continually flow in and out of the brain (not solely when, say, an electrical stimulus is delivered), and influence how a target stimulus is perceived. Support for the involvement of the basal ganglia is seen in the fact that this ability appears harmed in Parkinson's, in both experiments using sensory attenuation paradigms such as the force-matching task (Wolpe et al., 2018) and in the way heightened sensory cues that simplify a complex environment such as lines on the floor can instantaneously alleviate some motor symptoms (Morris et al., 1996; Beck et al., 2015). Even in word recall tasks, people with Parkinson's have demonstrated a reduced ability to utilise the usual memory benefits of deep-semantic encoding compared to shallow-non-semantic encoding (MacDonald et al., 2019); similarly, Parkinson's may impair integration in the basal ganglia of sensory and motor activity to help process action-verbs while object-noun processing is spared (Cousins & Grossman, 2017). Thus we can argue that people with Parkinson's exhibit a a reduced capacity to utilise contextual information to guide action and perception.

The Craik-O'Brien-Cornsweet effect is a visual illusion where we perceive one of two panels to be lighter in colour than the other despite them being identical. This "error" is made because of the shading lines, also known as Mach bands (after Ernst Mach, see Lotto et al., 1999), which give the impression of a particular lighting context (Figure 1). The effect of Mach bands in this Cornsweet illusion is akin to how we see light illuminate and shadows darken colours in our environment which we know are actually the same base colour (e.g. a wall painted with the same pot of paint being lit by sunlight in parts and shaded elsewhere). The illusory effect can be eliminated by covering the Mach bands revealing the panels to be identical in colour. The mistake we make is thus evidence of context-dependent perception: we do not perceive the panel colours in isolation but as part of a whole, integrating other signals.

In the experiment I describe in this chapter, we used the Cornsweet illusion as a way of assessing context-dependent perception. We first confirmed a significant illusion effect does take place by varying the contrast of the panels over multiple trials to quantify illusion strength. We then compared illusion strength – as an index of context-dependent processing – across three groups: adults with Parkinson's, and younger and older adults without Parkinson's. Sensory attenuation, as demonstrated with the force-matching task, has been shown to increase with age (Parthasharathy et al., 2021; Wolpe et al., 2016). We therefore expected older adults to experience greater illusion strength than younger adults. In the group with Parkinson's, similar to Wolpe and colleagues (2018), we sought to demonstrate a positive correlation between Levodopa Equivalent Dose and illusion strength. Participants were not required to refrain from taking their usual dopaminergic medication for this study and thus the effect of Parkinson's disease on context-dependent perception was expected to be detected in this relationships of illusion strength with dopamine level estimate and also disease severity.

2. Methods

2.1 Participants

Three hundred and fifty-six adults participated in this study approved by The University of Birmingham Ethics Committee after giving informed consent. Two hundred and twelve younger adults without Parkinson's (95.9% of original sample; 18-35 years), eighty-five healthy older adults without Parkinson's (91.4%; 64-86 years) and forty-one adults diagnosed with Parkinson's (97.6%; 47-76 years) met the task-performance inclusion criteria outlined below and were included in our analysis. The younger adults group were recruited through the University of Birmingham Research Participation Scheme, the older adults group were recruited through Prolific (an online recruitment platform), and the Parkinson's group via a lab database of volunteers with Parkinson's disease. Table 1 shows a breakdown of group characteristics for participants included in the analysis.

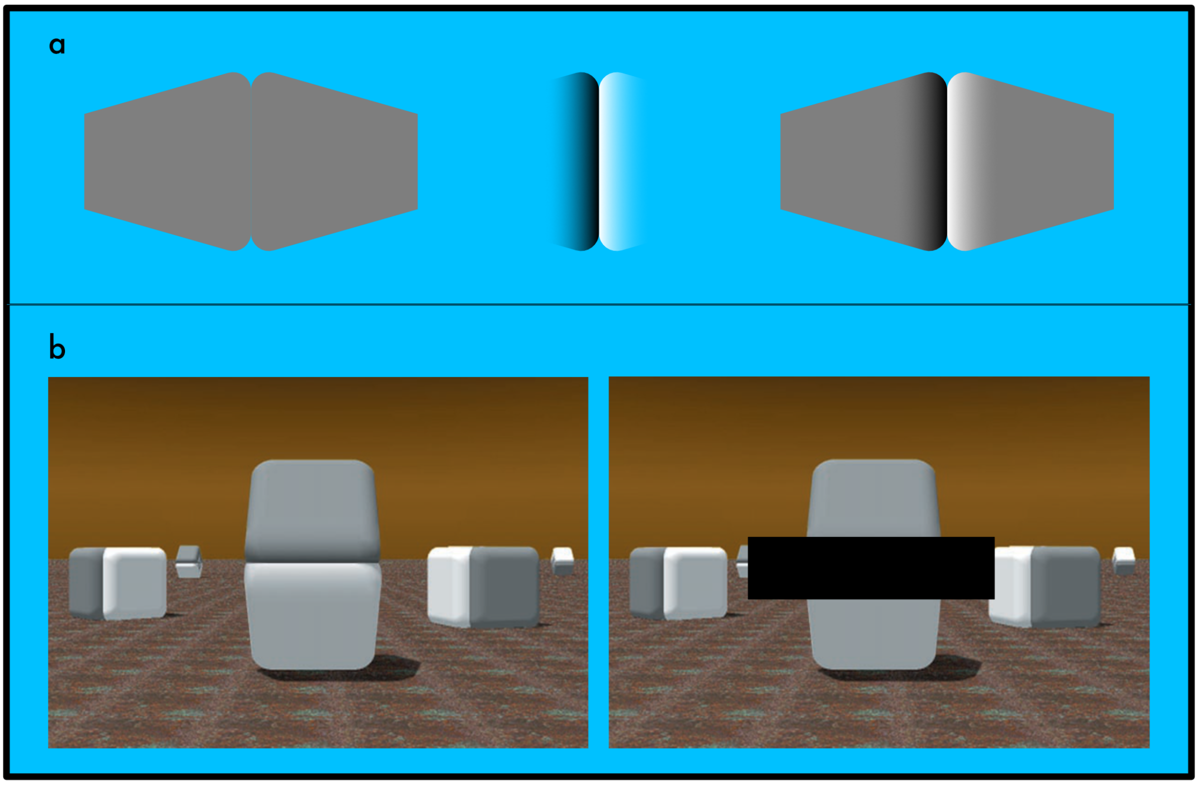


Figure 1 (a) Composition of the Cornsweet illusion stimulus used in the

present study, shown here on a blue background to make the Mach bands visible. Even in this simple arrangement, the Cornsweet effect should still occur where the same panels (left), appear to be different colours (right) when combined with the Mach bands (middle). (b) A more complex arrangement of the Cornsweet illusion from Purves et al., (1999, p. 8549). Purves and colleagues found the extra elements in this arrangement (such as vertical arrangement of panels, 3D effects and additional object) contributed to a stronger illusion effect. The key to the illusion is the presence of Mach bands in the middle of the panels (see image on left versus image on right), which provide contextual information to suggest a particular lighting arrangement shaping how we perceive the base colour.

2.2 Task and stimulus design

All experiments featured the main Cornsweet illusion task (Figure 2). In this task, a Cornsweet illusion stimulus was presented, which consists of two panels connected at the middle as if part of the same, somewhat unusual object (Figure 1a). Vertically arranging the panels in a complex 3D-looking environment creates a stronger illusion effect (Purves et al., 1999) but we used a simpler arrangement of what we considered the essential elements for an illusion to occur. In this case, an illusion is defined as incorrectly judging the right panel to be lighter despite it being the same (as in Figure 1) or darker. The reader may want to test this themselves by looking at the right-hand image in Figure 1 and deciding which panel appears lighter. Then, covering the central Mach bands with a finger, pen or piece of paper, notice that the panels—just as in the left-hand image in Figure 1—are the same lightness.

The task required participants to simply select which panel they thought was lighter. To assess the strength of the illusion, 29 combinations of panel colours (Figure 3) with 15 different contrast levels in total were presented to explore how often the illusion occurred when the right panel was darker than the left. Larger contrasts—that is, one panel is much lighter than the other—should be less susceptible to the illusion effect, and smaller contrasts should be more susceptible. Through repeated presentations of different contrasts in a random order, we were able to see how strong the illusion effect was based on participant responses.

The stimuli were designed using Affinity Designer, and the contrasts were formed by changing the colours of the panels using a HSL (hue, saturation, lightness) colour wheel where hue and saturation were set at 0, and lightness was varied on a scale of 0 (white) to 100 (black). Contrast between panels ranged from -35 (where the left panel was 35 points lighter than the right) to 35 (where the left panel was 35 points darker), and included 0 where panels were identical in colour.

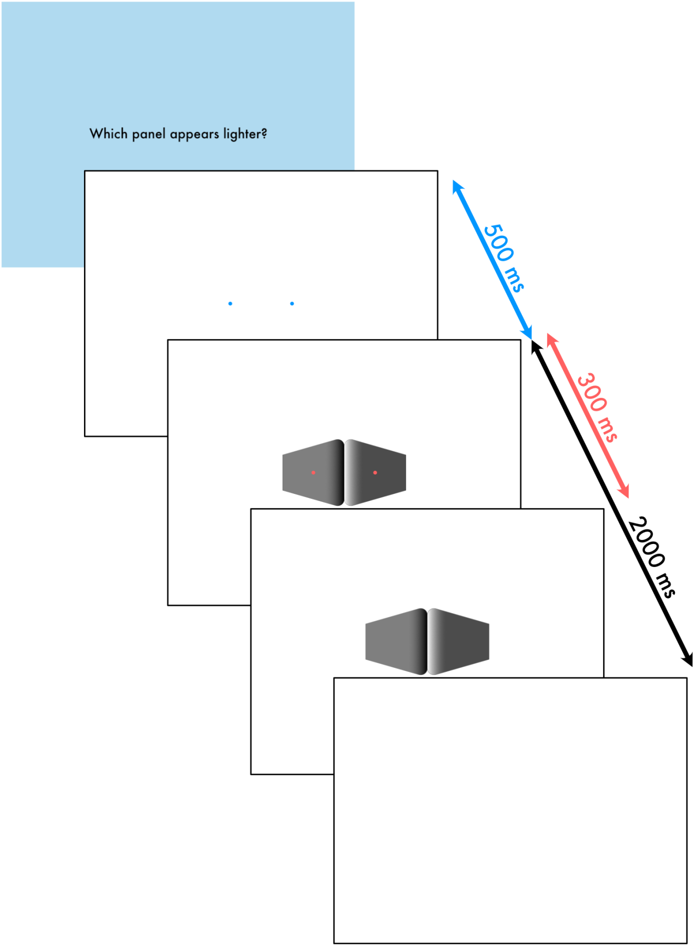


Figure 2 After being asked which panel appears lighter, blue fixation dots cued the appearance of the Cornsweet stimulus, which was accompanied by red dots for 300 ms. The Cornsweet stimulus appeared on screen for a total of 2 seconds, but a response was possible after this.

The Mach bands were black on the left and white on the right, and faded from a solid colour on the inside edge of the panels to complete transparency (Figure 1). This composition gave the impression of shading and luminance, as if a light source was positioned to the right of the shape, with the panels contoured at the middle. For consistency, we kept the Mach bands arranged this way throughout, so as to reinforce a sense of permanence for the source of light. Continually randomising the location of the light source across trials risked having an effect on averaged illusion effect for each participant, as a more vacillating light source might weaken the priors underpinning the illusion (e.g. the light-from-above Cornsweet effect is stronger than a horizontal light source because we are so used to light coming from above in the form of sunlight). We preferred here the option of a fixed light source to maintain an illusion effect dependent on our experience of light and colour. Furthermore, variations in the direction of light have already been explored by Purves and colleagues (1999), and the focus here rested on assessing illusion strength between different populations (and within individual participants in Chapter 3), negating a need to control for any hemispatial bias that could be created from not randomising the location of the light source.

In each trial, red fixation dots indicated the area of the panel participants were to judge (Figure 2), responding with a left or right key press depending on which panel they thought looked lighter. The stimulus appeared at the centre of the screen for 2 seconds before disappearing, and participants could make their response during this or for an unlimited time after, maximising participant engagement by linking their response to the progression of trials. Response time was stored and used to exclude responses that took longer than 10 seconds in the analysis of reaction time (99.9% of trials kept). A long time window (10 seconds) simply meant extreme outliers were removed, allowing for participants to respond how they wished and using reaction time to characterise the nature of the illusion effect (Figure 5). Participants were still only exposed to the stimuli for 2 seconds, preventing excessive studying of the image and it prevailed that mean responses for all participants across every contrast were shorter than 2 seconds (Figure 5a). For the remaining analyses, we deemed the participant level inclusion criteria sufficient to ensure high quality response data.

It is important to note the difference between control trials and illusion trials in our experiment. As we are defining an illusion in this stimulus arrangement as incorrectly judging the right panel to be lighter when it is in fact the same or darker, this means illusions are only possible when the right panel is the same or darker than the left. What about stimuli where the left is darker than the right? Here, the Mach bands simply exacerbates the lightness of an already lighter panel and thus no illusion effect can be measured. A right arrow response to indicate the participant thinks the right panel is lighter is simply the correct response, and a left response would be incorrect, but not because of an illusion effect. These trials are control trials, and will be made up predominantly of correct responses. Hence, control trials were useful for assessing task performance, and participants' datasets were excluded from analysis if they fell below 95% accuracy in control trials. In illusion trials, we expected a mix of correct and incorrect responses, and the percentage of incorrect responses indexed illusion strength (Figure 4). Overall, we expected the illusion effect to make right responses more likely than left responses, as shown in Figure 5.

For the Cornsweet illusion task, participants completed 87 trials in total, across three bins, each comprising the 29 panel combinations and the 15 unique contrasts. The task was assembled in PsychoPy (Peirce et al., 2019) and made available to participants online via Pavlovia (https://pavlovia.org).

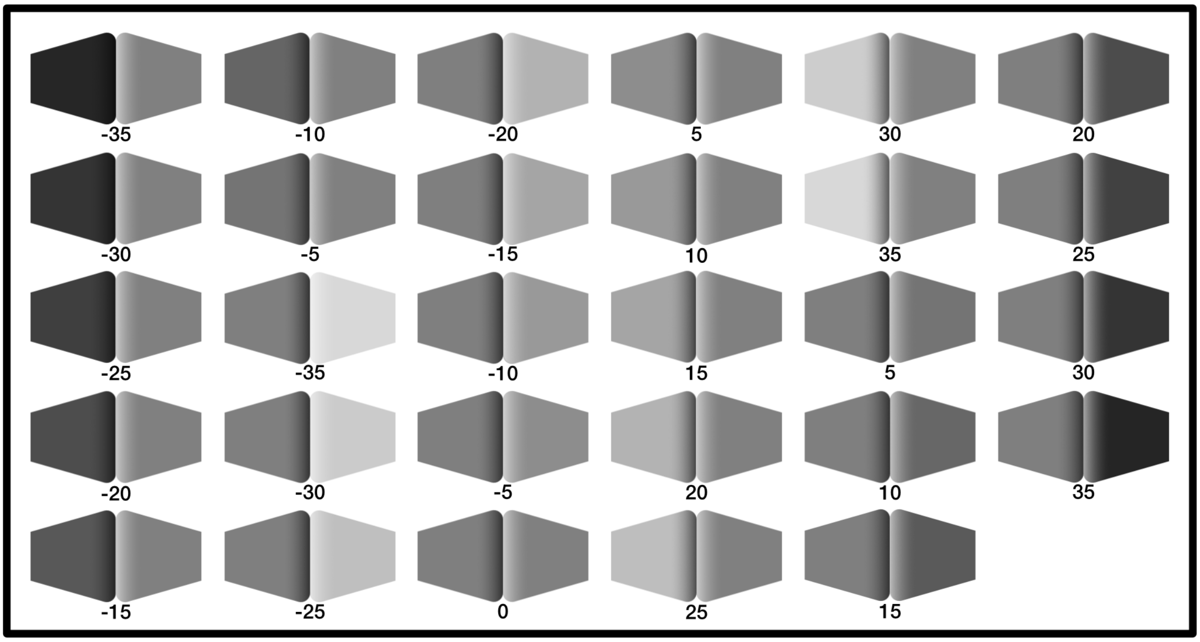


Figure 3 All the stimuli presented during one of three bins to assess illusion strength. The Mach bands were set at 60% opacity. There are 15 different contrasts, including the stimulus with panel contrast of 0.

2.3 Levodopa equivalent dose

A levodopa equivalent dosage (LED) calculator designed and openly provided by John Turner on the brilliant parkinsonsmeasurement.org was used to generate an LED (a well-accepted standard of measurement of dopamine intake) given the variety of medications used by participants with Parkinson's, aiding comparison. I referred to Tomlinson et al. (2010) and Schade et al. (2020) to check calculations and fill in gaps such as (COMT and MAO-B inhibitors), complying with the more recent publication at points of contradiction. Importantly, rather than calculating a daily dose, participants reported the dosage and time of medications taken in the last 6 hours, or the last taken medication, for a rough estimate of activity of the medication at the time of the study. We thus used Turner's programme to calculate a "Current LED" which takes into account LED, time taken for drug to reach max effectiveness, and the time taken for the drug to lose half its effectiveness. Turner's programme assumes multiple drugs do not interact and have additive effects when taken together, but helps in reaching a closer estimate of circulating dopamine levels for our attempt to assess its role in context-dependent action and perception in this study. Some participants also provided information on additional medications being taken for non-Parkinsonian co-morbidities. For consistency within, only medications being taken for Parkinson's were analysed in this study, which does of course highlight the heterogeneity of attempting to tease apart the effect of dopamine alongside other medications.

2.4 Activities of Daily Living and Key Tapping Score

Owing to the links established between sensory attenuation measures and movement competence, we anticipated the possibility that variability in motor skill and lifestyle might confound our investigation of age and dopamine related changes in context-dependent perception. All older adults were accordingly asked to complete a short Activities of Daily Living (ADL) Questionnaire as an indicator of activity levels, functional capacity and engagement with wider communities (Dias et al., 2019; Lawton & Brody, 1969; Reuben et al., 1990; Slachevsky et al., 2019). The version we used comprised 13 questions asking the participant if they have either: (a) never done, (b) stopped doing, or (c) still do the named activity, with each answer corresponding to 0, 1 or 2 points respectively. The maximum score was 26, indicating the highest possible level of activity. We complemented the ADL score with a Key Tapping Score, calculated as the number of times the space bar was pressed in a 30 second period where the participant was instructed to tap the key as fast possible. A 5 second practice was provided beforehand, and only the 30 second Key Tapping Score was included in our analysis as a second, more acute, indicator of motor ability. Both ADL score and Key Tapping Score were included in a model comparison as part of a Bayesian linear regression analysis with our main outcome measure illusion strength as the dependent variable.

2.5 Data analysis

The main outcome measure in this study was illusion effect, which we measured as the proportion of incorrect responses made during illusion trials. We thus split illusion trials from control trials, using the latter as inclusion criteria as outlined above, and calculated the percentage of incorrect responses from the remaining 45 trials for each participant. We compared illusion trials and control trials using a t-test to confirm the presence of an illusion effect. Illusion effect was then compared across groups in an ANOVA, and was also used in two Bayesian linear regression analyses (allowing for many model comparisons) to explore possible effects of LED in the group with Parkinson's, as well as motor ability and lifestyle activity indicators (ADL and Key Tapping Scores) in both older groups. Additionally, to visualise the illusion effect in greater detail in what is a novel task, we calculated reaction time for each contrast level and plotted each group separately. Finally, we fit a logistic regression curve using a binomial distribution to the binary response data of individual participants, displaying one example in Figure 5 to further elucidate the illusion effect and the ambiguity of perception at particular contrast levels. The majority of data processing and analysis was performed using MATLAB, with contributions in places from RStudio (reaction time plots) and JASP (linear and logistic regression analyses).

Table 1 Group characteristics for participants included in the analysis.

Group	**Young adults**	**Older adults**	**Adults with Parkinson's**
N	212	85	41
Mean age (SD)	19.7 (1.7) years	69.2 (4.6) years	63.6 (7.9) years
Key Tapping Score (SD)	n/a	153.6 (24.7)	156.2 (26.9
Activities of Daily Living Score (SD)	n/a	16.5 (4.0)	18.9 (3.2)
Levodopa Equivalent Dose current estimate (SD)	n/a	n/a	75.3 (67.1) mg
Years since Parkinson's diagnosis	n/a	n/a	9.4 (6.9) years

3. Results

3.1 Illusion effect

The mean percentage of incorrect responses during illusion trials was 39.8% (SD = 11.9%), whereas the mean proportion of incorrect responses during control trials was 0.3% (SD = 1.0%). An independent samples t-test unsurprisingly revealed this difference between incorrect responses for illusion and control trials to be significant ($t(337) = 60.949$, $p < .001$, $d = 3.315$), also shown in Figure 4. Thus, we replicated the Cornsweet effect with our task, demonstrating the influence of Mach bands as contextual cues on perception.

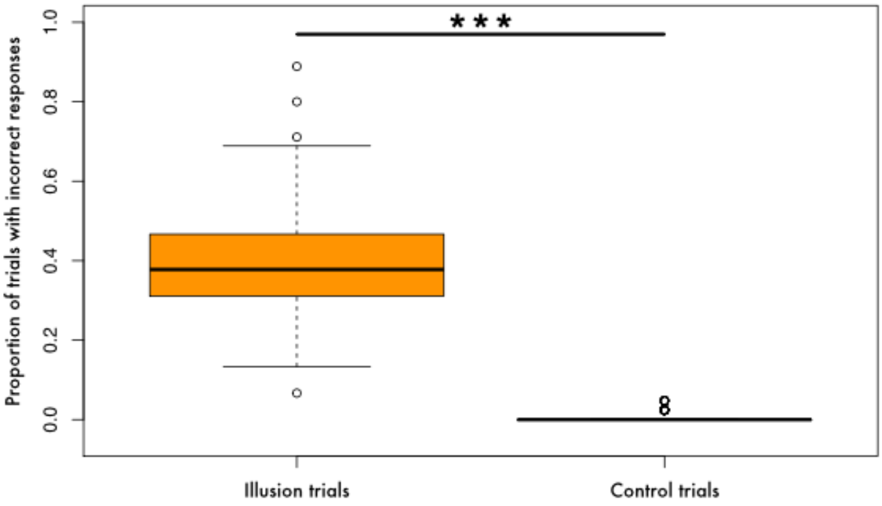


Figure 4 Boxplot of the proportion of incorrect responses during illusion trials vs control trials for all 356 participants. The bold horizontal line represents the

median, the upper and lower edges of the box represent the upper and lower quartiles, the horizontal lines at the ends of the whiskers the upper and lower extremes, with outliers marked by circles. ***$p < .001$.

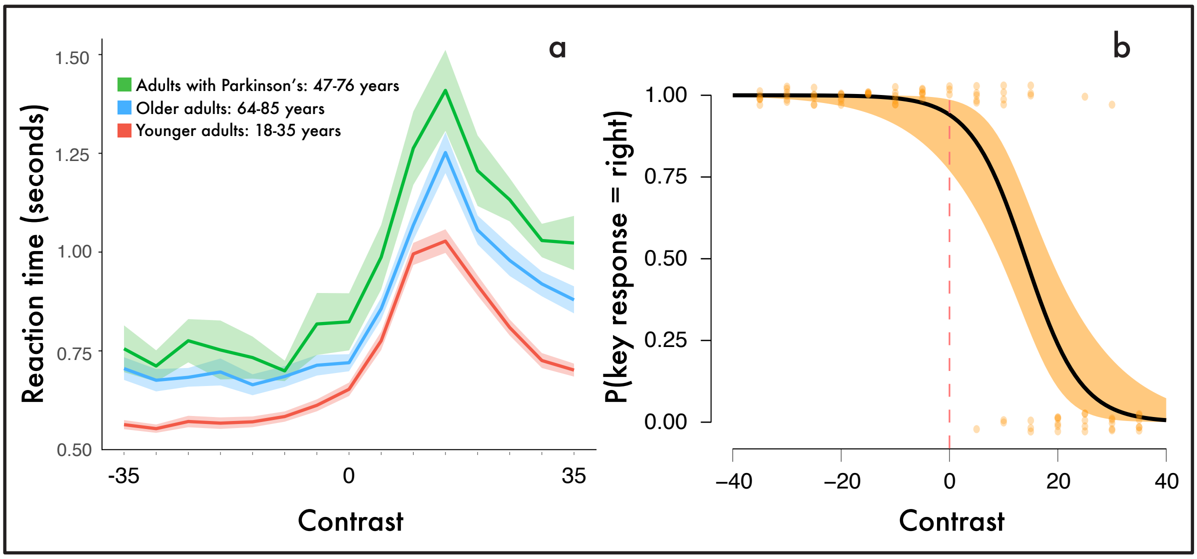


Figure 5 Participants' key responses are affected by the contrast of the panels. The contrast is calculated as the difference (on a grayscale of 0 to 100) the left and right panel. A positive value indicates the left panel is lighter, a negative value indicates that the right panel is lighter, and 0 that they are equal. (a) Mean reaction times across participants for each contrast level, with a line for each group and standard error of the means represented by the shading around each line. Younger participants were generally quicker responding, but all participants slow for positive contrasts where ambiguity created by the illusion effect increases. (b) Response data from a single participant, modelled with logistic regression using a binomial distribution (df = 85, BIC = 47.044, McFadden $R^2 = 0.651$, $p < .001$). The Y-axis represents the probability from 0 to 1 that the participant responds with the right arrow key. The curve is asymmetrical as the illusion effect creates more right key responses.

3.2 Illusion effect group comparison

To ensure no differences between groups in attention, a comparison of incorrect rates across control trials ANOVA revealed no effect of group ($F(2,335) = 1.007$, $p = .366$). An ANOVA revealed a significant main effect of group for illusion effect ($F(2,335) = 6.659$, $p = .001$, $\eta^2 = .038$), where older adults without Parkinson's demonstrated the strongest illusion effect with 43.5% (SD = 12.1%) of the responses to illusion trials being incorrect. Adults with Parkinson's were incorrect in 41.1% (SD = 12.1%) of illusion trials, and younger adults were incorrect 38.1% (SD = 11.4%) of illusion trials. Post-hoc tests with Bonferroni correction revealed only the difference between healthy older adults and younger adults to be significant ($p = .001$, $d = .461$;

older adults vs adults with Parkinson's: *p* = .844; adults with Parkinson's vs younger adults: *p* = .413), comparisons also shown in Figure 6 with 95% confidence intervals. We therefore demonstrated that illusion effect increases in healthy old age.

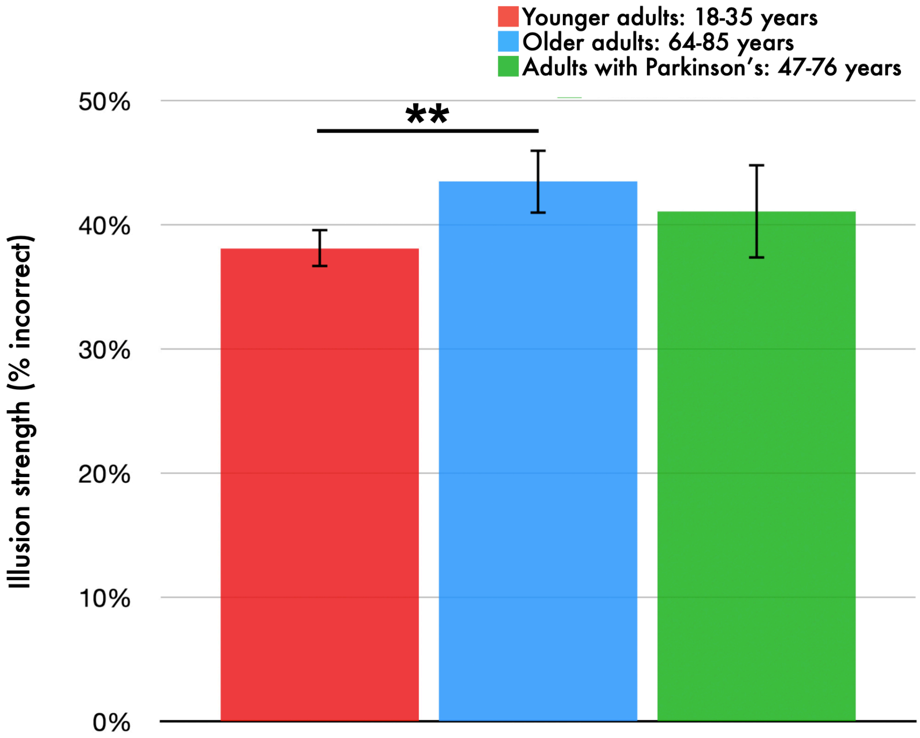


Figure 6 Illusion strength, as a measure of context-dependent processing (Mach bands as context inform the perception of panel contrast), is greater in older adults compared to younger adults. People with Parkinson's demonstrated an illusion strength in between that of the other two groups, but the difference was not significant. Error bars represent 95% confidence intervals. ***p* = .001.

3.3 Regression analysis

To assess the effect of dopamine levels on illusion strength, which has been linked to sensory attenuation in people with Parkinson's (Wolpe et al., 2018), we used a Bayesian Linear Regression to model the relationship between estimated Current LED at time of testing. The first model (Table 2) consisted of data only from participants with Parkinson's (*N* = 41). Table 2 shows the best eight models, out of 32. We included LED Current, Time Since Diagnosis, ADL Score, Key Tapping Score and Age as covariates, where illusion strength was the dependent variable. We found no evidence to reject the null model in favour of any of the possible model permutations, with no apparent relationship between LED Current and illusion strength (BF(10) = 0.357, R^2= 0.010), also shown in Figure 7.

In a second model (Table 3), we included only older adults without Parkinson's (*N* = 85) in another Bayesian Linear Regression. We included ADL Score, Key Tapping Score and Age as covariates. Table 3 shows all eight model permutations. We again found no evidence of a better model than the null model. Taken together, there was no observable correlation between estimated dopamine levels and illusion strength, nor generic motor ability and lifestyle variables.

Table 2 Model comparisons from a Bayesian Linear Regression with data from adults with Parkinson's (*N* = 41). Only the best 8 models are shown. Unexpectedly, LED Current was not predictive of illusion strength, at least insofar as the data are not explained by a linear relationship. Five covariates were included, with illusion strength as the dependent variable: ADL Score, Age, Key Tapping Score, LED Current and Time Since Diagnosis.

Models	P(M)	P(M | data)	BF_M	BF_{10}	R^2
Null model	0.167	0.505	5.108	1.000	0.000
Key Tapping Score	0.033	0.055	1.686	0.544	0.036
Age	0.033	0.050	1.539	0.499	0.031
Time Since Diagnosis + Key Tapping Score + Age + ADL Score + LED Current	0.167	0.038	0.195	0.074	0.095
LED Current	0.033	0.036	1.086	0.357	0.010
ADL Score	0.033	0.033	0.999	0.329	0.005
Time Since Diagnosis	0.033	0.033	0.982	0.324	0.004
Age + Key Tapping Score	0.017	0.023	1.417	0.464	0.082

Table 3 Model comparisons from a Bayesian Linear Regression with data from older adults without Parkinson's (*N* = 85). Only the best 8 models are shown. There is no evidence of a linear relationship between illusion strength and any of the three covariates: ADL score, Age, Key Tapping Score.

Models	P(M)	P(M | data)	BF_M	BF_{10}	R^2
Null model	0.250	0.674	6.190	1.000	0.000
Age	0.083	0.093	1.124	0.413	0.016
ADL	0.083	0.060	0.706	0.269	0.005
Key Tapping Score	0.083	0.052	0.602	0.231	0.001
Age + ADL Score + Key Tapping Score	0.250	0.038	0.120	0.057	0.019

Age + ADL Score	0.083	0.032	0.368	0.144	0.019
Age + Key Tapping Score	0.083	0.030	0.343	0.135	0.017
ADL Score + Key Tapping Score	0.083	0.021	0.231	0.091	0.006

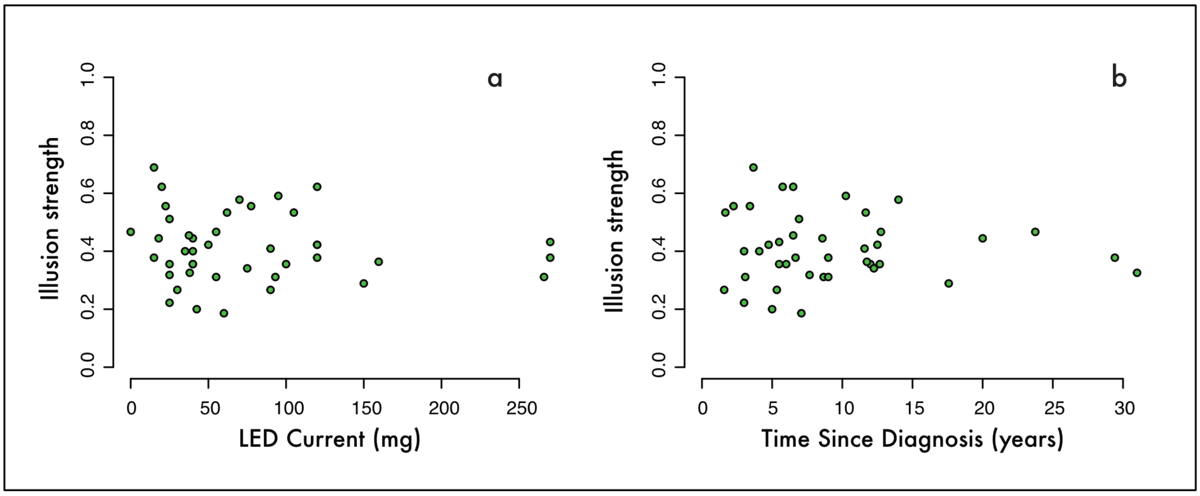


Figure 7 Scatter plots of illusion strength (proportion incorrect responses during illusion trials) and LED Current (a) and Time Since Diagnosis of Parkinson's (b), illustrating a lack of correlation between variables (Illusion Strength ~ LED Current: $R^2 = 0.010$; Illusion Strength ~ Time Since Diagnosis: $R^2 = 0.004$).

4. Discussion

4.1 Key findings

In this study, we demonstrate that context affects perception. In the illusion trials, the Mach bands have the effect of causing the participants to choose the darker panel when asked which one was lighter. Participants selected the incorrect panel in nearly forty percent of the trials, while selecting the correct panel near perfectly in control trials. The Cornsweet illusion task is thus a useful measure of context-dependent perception.

We demonstrated, in line with Wolpe and colleagues' (2016) findings from a force-matching task, that healthy older adults demonstrate greater levels of context-dependent perception than younger adults. Wolpe and colleagues (2016) suggest the increased force-overcompensation they found by older adults in the force-matching task is the result of worsened tactile sensitivity with age which thus requires greater weighting of prediction signals to guide behaviour consistent with Bayesian perception frameworks (Körding & Wolpert, 2004, 2006), thereby resulting in more sensory suppression and greater force-overcompensation. While plausible, this explanation has been disputed (Parthasharathy et al., 2021); alternatively, sensory attenuation could develop through experience (Idei et al., 2021, 2022) whereby infants may display an absence of sensory attenuation (Meyer & Hunnius, 2021) and responses become more context-specific through learning, indicative of a more complex nervous system, at least in places (Wolpe et al., 2016) and subject, of course, to experience (Konishi & Bohbot, 2013).

We did not find a difference in illusion strength in the Parkinson's group compared to the other groups. In the absence of any on/off medication requirements, we opted instead to explore the correlational relationship between estimated dopamine levels and illusion strength amongst the Parkinson's participants. Expecting to replicate Wolpe and colleagues' (2018) finding of a positive correlation between LED and force-overcompensation, we were surprised to find no relationship between LED and illusion strength in the present study (Figure 7), even when including additional factors such as Time Since Diagnosis, ADL Score and Key Tapping Score (Table 2). We opted for a slightly different LED measure, estimating current dopamine levels at the time of study rather than a daily dose, owing to the transient nature of many dopamine medications. We considered LED Current to be a sophisticated estimate of dopamine levels comparable to Wolpe and colleagues' (2018) approach to recording a daily LED (LEDD) and requiring participants to complete the study in a specified 2 hour window related to levodopa self-administration timing.

However, in the absence of a correlation between LED Current and illusion strength in the present study, four possibilities arise. Firstly, the combination of LEDD and a time-controlled approach to testing could more accurately gauge dopamine dose and its links to context-dependent processing. Secondly, illusion strength could be linked to LEDD and not LED Current, though this seems unlikely unless the first possibility is also true. Third, the positive correlation between dopamine dose and sensory attenuation found by Wolpe et al. (2018) could instead be reflective of disease severity, which was found to be negatively correlated with sensory attenuation (though many links elsewhere have been made to dopamine and sensory integration, cf. Beeler & Dreyer, 2019; Jenkinson & Brown, 2011; Ketzef et al., 2017; Petzinger et al., 2015). Fourth, it is possible that LED Current did gauge dopamine levels effectively but that illusion strength was unaffected. It is this final possibility I will discuss in more detail.

4.2 Context-dependent perception and task complexity

Jenkinson & Brown (2011) argue that sufficient dopamine levels uphold the capacity for effective movement, playing a role in coordinating oscillatory activity in preparation for action (see also Beeler & Dreyer, 2019; Brittain et al., 2014; Brittain & Brown, 2014). Crucially, dopamine levels are themselves modulated by salient input from internal or external cues. Thus, in the absence of salient cues, dopamine levels remain low (too low in Parkinson's), and there is a reduced ability to perform new movements. As argued in Chapter 1, in the absence of clear, salient cues, the basal ganglia are involved in searching for and integrating useful cues from elsewhere, and it is this ability that is harmed in Parkinson's. The lines-on-the-floor phenomenon illustrates that when clear, salient cues are available, movement becomes fluid, but breaks down stuttered in their absence, implicating the basal ganglia in navigating a complex environment. The force-matching task usefully lacks the clear, salient cues to inform perception that are part of this current Cornsweet illusion task. The Cornsweet illusion task, in this current form, despite being a measure of context-dependent perception where Mach bands and prior experience are integrated in the perception of panel colour, also comprises very simple, salient contextual cues that likely bypass any need for complex searching and integrative behaviours that depend on capable and dopamine-bountiful brain regions.

Complexity of the task and environment is important to consider, just as word memory in Parkinson's is only impaired when more complex integration is involved (MacDonald et al., 2019; Cousins & Grossman, 2017), and just as visual feedback can aid movement when it shortcuts the need to navigate a more complex environment (Beck et al., 2015; Morris et al., 1994, 1996) but can harm movement when the visual feedback itself is an additional source of information to integrate (Connor & Abbs, 1991). We provide further evidence here that while context-dependent action and perception is a useful concept to reframe sensory attenuation to make better sense of Parkinson's symptoms, contextual cue integration–when sufficiently salient and simple–is not impaired. As argued in Chapter 1, the basal ganglia affected by Parkinson's exhibits a reduced capacity to both filter complex environments in a complex environment and then integrate the resulting variety of contextual cues into ongoing movement. Therefore, context-dependent movement is a more useful concept than motor-induced sensory suppression for understanding Parkinson's, but it is still not, by itself, a complete explanation for Parkinsonian symptoms.

4.3 Future directions and implications

There are other ways of presenting the Cornsweet illusion, and Purves and colleagues (1999) found greater illusion strength with a more complex, visual scene (Figure 1). Some evidence, albeit inconsistent, in studies of people with Schizophrenia suggest visual illusions can be impaired in people with dopaminergic disorders affecting the basal ganglia (Grzeczkowski et al., 2018; Notredame et al., 2014). It would therefore be interesting to see if a more complex Cornsweet illusion scene similarly elicits a stronger illusion effect amongst people with Parkinson's, or if the image on screen is still too simple. Alternatively, the use of distractors could be used to require participants to filter out task-irrelevant information in conjunction with the Cornsweet illusion task to place greater demand on the basal ganglia (Lee et al., 2010; McNab & Klingberg, 2008).

For Parkinson's training approaches, it remains important to challenge and grow the ability to navigate complex environments. Many approaches to training, in Parkinson's rehabilitation and in sports, can involve a simple cue facilitated by the coach to help the participant or athlete initiate a particular action (O'Connor et al., 2017). While there may be benefits in terms of achieving action quickly, it also may not be demanding much from the nervous system to promote plastic growth and the skilful improvisation of movement in the absence of that simple cue.

4.4 Conclusion

In a novel Cornsweet illusion task, we demonstrated context-dependent perception in all participants, where Mach bands likely elicited the integration of prior knowledge with the perception of panel colours to dramatically shape the response profile. We further demonstrated a shift of illusion strength in healthy old age, possibly reflecting experience-related change over a lifespan. In the absence of a link between dopamine dose and illusion strength in the Parkinson's group, we argue for the usefulness of recognising context-dependent perception when coupled with a careful appreciation of task and environment complexity.

Chapter 3

Altered use of contextual cues with training

1. Introduction

Having observed observed no gross shift in task performance between the two older adult groups in the previous chapter – rather demonstrating a change in perception related to age – we now seek to perturb this sensory attenuation index through training. Can illusion strength be "trained" through exposure to different cue characteristics (e.g. the Mach bands) and, if so, how is this capacity altered in healthy ageing and Parkinson's disease? These questions are important because exercise-based approaches to neurological rehabilitation use cues in a variety of ways, but an understanding of the underlying mechanisms mediating their benefits is lacking (Nonnekes et al., 2019).

The symptoms of Parkinson's disease are remarkably context dependent. In many environments, patients may exhibit short, shuffling steps when walking. Cluttered (Tan, 2009) and precarious (Ehgoetz Martens et al., 2014) environments can exacerbate such symptoms. Even reducing the size of a door frame can elicit more episodes of freezing – a sudden inability to initiate or continue walking (Almeida & Lebold, 2010). However, such symptoms can be alleviated with simple cues: drawing lines on the floor enables much improved walking with bigger steps (Beck et al., 2015), and sounds and tactile cues (Nonnekes et al., 2019; Quintyn & Cross, 1986) can similarly be useful to enhance movement while the cues are present and even with some lasting effects (Morris et al., 1996). Such cues can be considered contextual cues: that is, sources of information that guide movement or perception of a target stimulus but, according to a particular task set-up, are not the target of perception themselves.

Far from negating the usefulness of augmented contextual cues in everyday life, it is unclear if such strategies restore function to damaged regions of the basal ganglia, or if they serve as a compensation mechanism (Nonnekes et al., 2019; Spaulding et al., 2013) with declining effectiveness over time when implemented in a long term programme (Nieuwboer et al., 2007). Morris and colleagues (1996) used lines on the floor to visually cue steps to help participants with Parkinson's walk with greater speed and bigger stride length. They found after-effects lasting the maximum period of two hours where stride length and velocity were improved after the removal of the visual cues. However, other approaches in weeks-long programmes have demonstrated promising effects on Parkinson's symptom severity while avoiding augmented contextual cues to guide movement (Ridgel et al., 2009, 2015; Ridgel & Ault, 2019; Sage & Almeida, 2009, 2010). PD-SAFEx for instance (Sage & Almeida, 2009, 2010) requires participants perform movement drills in low-light conditions, purposefully reducing visual input, with lasting improvements in symptom severity. How are salient cues being used during training and what effects might a lines-on-the-floor set up have – not just on gait kinematics, but on perceptual abilities important for moving in complex environments?

To find out how the perception of contextual cues change with training, we devised a simple task called the Cornsweet illusion task, using the Craik-O'Brien-Cornsweet effect (Kingdom & Moulden, 1988; Purves et al., 1999). The Cornsweet effect (for short) is a visual illusion that reveals that perception of target stimuli is dependent on its situated context. The effect is achieved when two panels of identical colour are judged to be different because the shading at the meeting point of the panels creates unique lighting contexts (see Figure 1, Chapter 2). The shading used here are Mach bands – gradients of black and white from 100% to 0% opacity.

Morris and colleagues (1996) measured walking characteristics in response to the introduction of visual cues. Here, with this task, rather than measuring any improvement in movement, we measure how cues are being perceived, indicated with a simple keyboard response, where the illusion effect results directly from the influence of Mach bands on perception. In the absence of salient cues, the basal ganglia play a role in finding and piecing together other sources of information to inform ongoing action and perception (Kearney & Brittain, 2021). Therefore we interpret the residual gait improvements in Morris et al. (1996) to result from a new compensatory stepping behaviour, rather than a renewed ability to search and use cues in a complex environment.

In the Cornsweet illusion task, we asked participants to pick which panel they thought was lighter while varying the panel contrast to establish how strong the illusion effect was at different time points. A stronger illusion effect indicated greater influence of the contextual cues (Mach bands) on perception. We sought to change the strength of the illusion effect through "training". As perception is tightly intertwined with action, as evidenced in the sensitivity to context of Parkinson's symptoms, and movement ability can be improved through training that manipulates the availability of sensory information (e.g. PD-SAFEx, Sage & Almeida, 2010), we expect such training to alter illusion strength. The training here involved repeated trials either with more prominent or more subdued Mach bands.

We expected participants repeatedly exposed to more prominent Mach bands in "Strong Mach Training" to both experience a stronger illusion effect and also to adapt to this level of cue salience. The result of this adaptation to prominent Mach bands would be a subsequent reduction in illusion strength indicative of a waning effect where relevant contextual information becomes integrated into perception with less vigour and relative influence. We similarly expected participants to adapt to subdued Mach bands in "Weak Mach Training", instead experiencing a weaker illusion effect in the training block but demonstrating a stronger subsequent illusion effect when returning to baseline conditions. We tested two variations of Strong Mach Training and Weak Mach training in Experiments 1 and 2 amongst younger adults to determine which aspects of the task induced adaptation. Experiment 1 involved a direct manipulation of Mach band opacity, whereas Experiment 2 involved a noise overlay to indirectly alter Mach band salience. We then extended this work by taking the most effective variant and repeating the experiments on groups on otherwise healthy older adults in Experiment 3, and adults with a Parkinson's disease diagnosis in Experiment 4.

2. Methods

2.1 Participants

A total of three-hundred and fifty participants took part in one of four experiments. Experiment 1 included young adults and comprised three different training conditions, where Mach band opacity was increased, decreased or left unchanged during the training block. Experiment 2 also involved young adults, but comprised four training conditions aiming at achieving a similar effect as Experiment 1 by layering the images with noise to obscure the Mach bands and panels rather than directly changing Mach band opacity and relative salience. Experiments 3 and 4 were the same as Experiment 1 but included adults without Parkinson's and with Parkinson's, respectively. The task-performance inclusion criteria required participants to respond correctly in at least 95% of the control trials, as in the previous chapter. Across Experiments 1 and 2, two-hundred and four adults met the task-performance inclusion criteria (92.3% of original sample; 18-35 years). In Experiment 3, eighty-eight participants met the inclusion criteria (94.6%; 64-86), and in Experiment 4, thirty-five participants did so (97.2%; 47-76 years). Participants were randomly assigned to the experimental conditions. The study was approved by the The University of Birmingham Ethics Committee and participants provided informed consent at the start of the study after reading the information sheet.

Table 1 Group characteristics across the four experiments of participants included in the analysis based on task-performance inclusion criteria requiring at least a 95% accuracy rates in control trials.

Experiment	1: Young adults	2: Young adults, noise manipulation	3: Older adults	4: Adults with Parkinson's
N	92	112	88	35

Mean age (SD)	19.5 (1.1) years	20.0 (2.1) years	69.1 (4.5) years	63.4 (8.0) years
Key Tapping Score (SD)	n/a	n/a	153.8 (24.5)	156.9 (26.8)
Activities of Daily Living Score (SD)	n/a	n/a	16.6 (3.9)	18.8 (3.2)
Levodopa Equivalent Dose current estimate (SD)	n/a	n/a	n/a	74.7 (62.5) mg
Years since Parkinson's diagnosis	n/a	n/a	n/a	8.3 (5.3) years

2.2 Task and stimulus design

This task used the stimuli as described in Chapter 2, with the addition of varied Mach band opacity during the training block, and partial and complete noise overlays shown in Figure 1 (i and j). The tasks were implemented in PsychoPy (version 2022.1.3) and participants took part in the study online using Pavlovia. The majority of the analysis was performed using Matlab (2021a) with some support from JASP (2020, version 0.14.1). As described in Chapter 2 (Sections 2.3 and 2.4), Key Tapping Score, Activities of Daily Living (ADL) Score and Current Levodopa Equivalent Dose (LED) were established for each participant at the start of the experiment.

2.3 Training

A novel aspect of this study is the attempt to "train" an index of sensory attenuation (distinct responses to identical stimuli in distinct contexts). In this case, we examined how changing the salience of the contextual cue altered illusion strength. To do this, we assessed illusion strength in a baseline block consisting of three bins of 29 trials each (87 trials total). Each bin consisted of two stimuli from each of the 15 contrast combinations, apart from contrast 0, which was only presented once due to being less informative than the other contrast levels. In every condition across each experiment, the baseline block remained the same. A longer "training" block followed, where the sensory information in the scene was altered. As displayed in Figure 2, the training block consisted of 12 bins (348 trials). The task —choosing the lighter-appearing side—remained the same throughout.

In Experiments 1, 3 and 4, we manipulated Mach band opacity in the training block across three conditions (Figure 3). In the Weak Mach condition, Mach band were reduced in opacity to 0.2; in the Medium Mach condition, Mach bands remained at the same 0.6 opacity, as in the baseline condition; in the Strong Mach condition, Mach bands were increased to 1.0 opacity. A test block and two washout blocks followed the training block which were identical to the baseline block.

In Experiment 2, we manipulated Mach band salience indirectly using noise overlays that targeted different parts of the scene across four conditions. In the

Gradation Noise condition, a noise overlay obscured only the Mach band. In the No Noise condition, the stimulus remained unchanged from baseline. In the Surround Noise condition, a noise overlay obscured everything in the scene except for the Mach bands. In the Solid noise condition, a noise overlay covered the whole scene. Each noise overlay was made from the same speckled white, black and grey image and was set at 0.5 opacity.

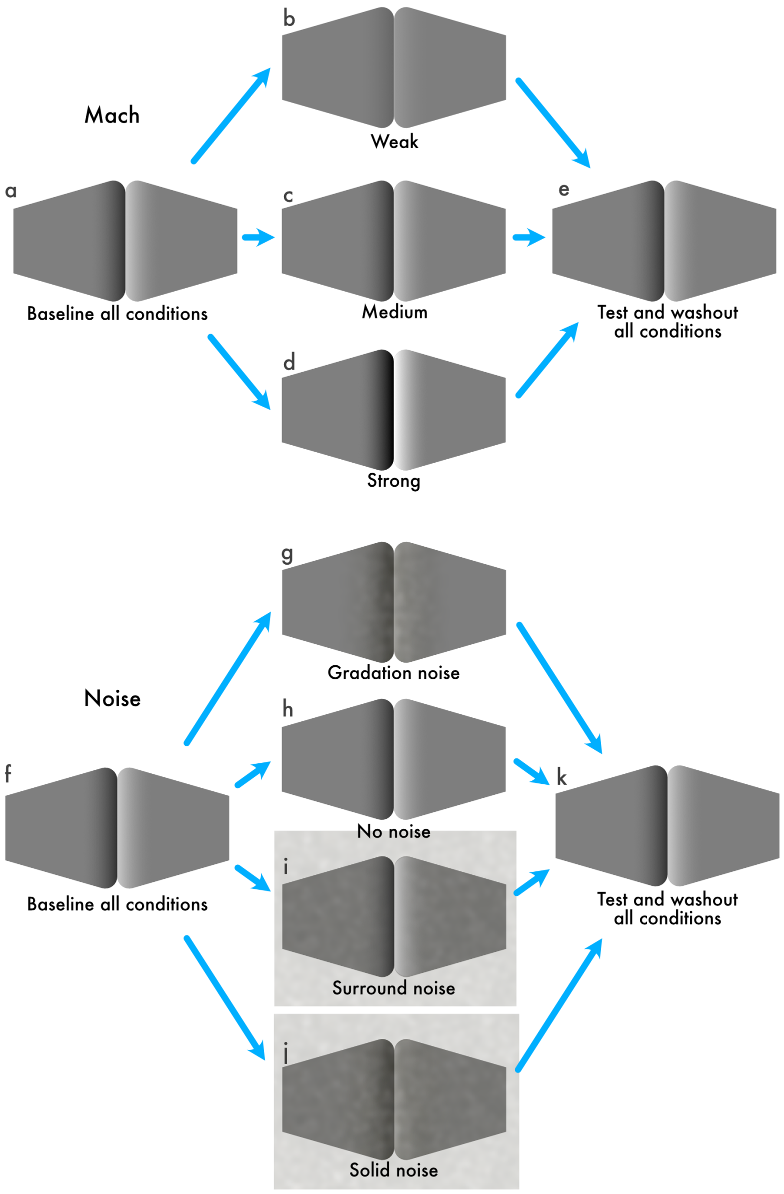


Figure 1 Examples of stimuli used from baseline to training to test and washout blocks, here demonstrated using panels of contrast 0 (where the panels are of identical lightness). Note how the Medium Mach condition (c) and No Noise condition (h) remained unchanged from the baseline and test stimuli that were used in all conditions (a,e,f,k). Descriptions of contextual cue changes: (a,e,f,k) baseline and test stimuli for all conditions used Mach bands of 0.6 opacity; (b) Mach band opacity reduced to 0.2; (c) Mach band opacity remained at 0.6; (d) Mach band

opacity increased to 1.0; (g) noise overlay of opacity 0.5 covering only the Mach bands; (h) no noise overlay, unchanged from baseline; (i) noise overlay of 0.5 opacity covering everywhere except the Mach bands; (j) solid noise overlay of 0.5 opacity covering everything.

With each bin providing a measure of illusion strength (based on proportion of incorrect responses in the 15 illusion trials per bin), we measured illusion strength throughout the baseline block, across the training block, and then again in a test block at the end. The test block was identical to the baseline block, where no noise overlays were present and Mach bands were set at 0.6 opacity. The test block was there to assess if there was any lasting change in how the stimulus was perceived when baseline conditions returned (0.6 opacity Mach bands, no noise). We included two additional washout blocks of just two bins each to see how long any potential training effects lasted.

Figure 2 Experiment structure. Inaccuracy measures were calculated for each participant for each bin of 29 trials, where a range of panel combinations were presented (29 stimuli, 15 different contrasts). Thin lines separate each bin and thick separating lines indicate where a pause occurred

There were opportunities for the participant to take a break or just pause briefly after every block or every three bins, whichever was shorter. The participant pressed the space bar to resume at a time of their choosing. Written instructions were provided on screen before the task begun, which the participant could progress through at their own pace. Two practice trials were also provided at the start. The Cornsweet stimulus in the first practice trial remained on screen until the participant performed a key response. In the second practice trial, as with the rest of the experiment, the Cornsweet stimulus remained on screen for two seconds. In the two practice trials only, progression was only achieved with a correct key press. Otherwise, no form of feedback was provided at any point during the task.

2.4 Data analysis

In all our analysis, we focused on the proportion of incorrect responses in illusion trials as our measure of illusion strength, which arises from the combining of old and new information to guide perception. To explore the unique training effects of each condition and for a deeper look at possible differences in adaptation processes between populations, we modelled the response data with a generalised linear mixed effects model (GLMM), that focused on the block-by-block changes in response inaccuracy (5 levels: baseline, training, test, washout 1, washout 2) and the conditions in each experiment which weakened or strengthened contextual cue salience (3 levels in Experiments 1, 3 and 4: MachWeak, MachMedium, MachStrong; 4 levels in Experiment 2: NoiseGradation, NoiseNone, NoiseSurround, NoiseSolid). Mixed effects models include random effects as well as fixed effects and facilitate statistical inference of uneven sample sizes, and are useful for examining repeated measurements in multi-level structured data (Yu et al., 2021). Specifically, it was useful for us to make statistical inferences about the difference between younger adults, older adults and adults with Parkinson's despite different sample sizes, and examine block-group interactions where blocks were formed of variable bin numbers.

To understand how illusion strength changed over time as a result of the experimental conditions, we devised a GLMM with group and block as fixed effects, and participant-level intercept term (ID) as a random effect to prevent inappropriate pooling of data. The data structure was a table with 22 rows per participant, with each row corresponding to one bin. For each group of participants, we added parameters to this core element (group + block + (1 | ID)) and compared models by plotting residuals, comparing AIC and BIC values, likelihood ratios, comparing adjusted R^2 values and noting the confidence intervals of the covariance parameters (Harrison et al., 2018). Using Matlab, we applied a base model using the *fitglme* function with notation:

$$\text{incorrect} \sim \text{group} + \text{block} + (\text{group:block}) + (1 \mid \text{ID})$$

The variable *incorrect* contained an inaccuracy value between 0 and 1 for the 15 illusion trials in that bin; *group* is the table column indicating the condition that trial was a part of (MachWeak, MachMedium or MachStrong) and *block* indicates which block the trial belongs to (baseline, training, test, washout 1, washout 2). *group:block* was included to assess the interaction between the two we expected, with baseline blocks being identical across groups before training block conditions diverged. Participant identifier (*ID*) was included as a random intercept to indicate the nesting of unique participants in each group with no crossover and prevented inappropriate clustering as participant IDs appeared in multiple rows (Harrison et al., 2018). This base model was applied to each experiment and compared to reduced and alternative models to assess the significance of factors of interest. Finally, all GLMMs used the maximum pseudo likelihood fit method and an identity link function.

We used this same model structure for each experiment, changing it only to examine population differences by grouping data from Experiments 1, 3 and 4 and adding one term, *population*, to reflect which experiment the participant were part of, including it as a fixed effect by itself and as part of a three-way *group* x *block* x *population* interaction. We examined main effects of group, block and group x block interactions by comparing the full model with reduced models using the likelihood ratio test (LRT). We then explored the effects of training (both during training and after) by subtracting mean baseline inaccuracy for each participant from the rest of the blocks and using 95% confidence intervals to indicate whether or not the illusion strength was significantly different from baseline.

3. Results

3.1 Experiment 1

The GLMM for younger adults in Experiment 1 incorporated *block*, *group* and a *block* x *group* interaction with Bayesian information criteria (BIC) = -3321.5, likelihood ratio = 1729.3 and $R^2 = 0.671$ (Table 1), which was significantly better than the null model (LRstat = 1990.8, ΔDF = 16, $p < .001$). For full model comparisons, see Supplementary Table 1.

incorrect ~ 1 + block*group + (1 + ID) + (1 + bl)

In line with the principle of marginality which implies interaction effects should not be tested in the absence of their inclusion as main effects (Wagenmakers et al., 2018), to assess the significance of main effects, we instead compared a reduced version of this model without the *block* x *group* interaction (*incorrect ~ 1 + block + group + (1 | ID) + (1 | bl)*) to reduced models without either *block* or *group* with LRTs (Supplementary Table 1). Resultantly, we demonstrated a significant main effect of *block* (LRstat = 41.82, ΔDF = 4, $p < .001$), and for *group* (LRstat = 51.48, ΔDF = 2, $p <.001$). As we expected, there was a significant interaction between block and group (LRstat = 948.25, ΔDF = 8, $p < .0001$), revealed by comparing the full model above to a reduced model without the interaction. Training interventions thus uniquely affected illusion strength, while baseline illusion strength, included as a random effect, may explain some of the variance in overall illusion effect across all blocks.

Being exposed to stronger Mach bands during training increased illusion strength during that block in comparison to baseline (N = 30, mean inaccuracy change = 10.1%, 95% CL [5.58 14.61]). Afterwards however, as shown in Figure 3, illusion strength decreased relative to baseline in the test block (N = 30, mean inaccuracy change= -7.85%, 95% CL [-11.53 -4.17]) and did not return to baseline even by the second washout block (N = 30, mean inaccuracy change = -5.28%, 95% CL [-9.76 -0.80]). The effect was significantly different within-subject compared to baseline, but was not significantly different across-subjects compared to unchanged Mach bands. Strong Mach Training therefore increased illusion strength acutely but weakened the illusion effect experienced by participants when returning to baseline conditions.

Being exposed to weaker Mach bands during training decreased illusion strength during that block in comparison to baseline (N = 33, mean inaccuracy change = -19.1%, 95% CL [-22.08 -16.04]), but afterwards, illusion strength increased relative to baseline in the test block (N = 33, mean inaccuracy change = 3.6%, 95% CL [0.42 6.81]) before returning to baseline levels in the first washout block (N = 33, mean inaccuracy change = 3.24%, 95% CL [-0.22 6.7]). In the within-subjects comparisons, participants demonstrated a weaker illusion effect during Weak Mach Training, which resulted in a stronger subsequent illusion effect.

Perhaps surprisingly, participants exposed to unchanged Mach bands during training experienced a decrease in illusion strength in that block in comparison to baseline (N = 29, mean inaccuracy change = -3.66%, 95% CL [-6.6 -0.73]). Afterwards, illusion strength returned to baseline in the test block (N = 29, mean inaccuracy change = -1.17%, 95% CL [-4.99 2.65]) and remained for washout blocks (N = 29, mean washout 1 change = -2.8%, 95% CL [-7.10 1.34] and mean washout 2 change = -1.18%, 95% CL [-6.07 3.7]). Being exposed to the same conditions throughout saw participants experience a dip in illusion effect which levelled out and remained unchanged in test and washout blocks.

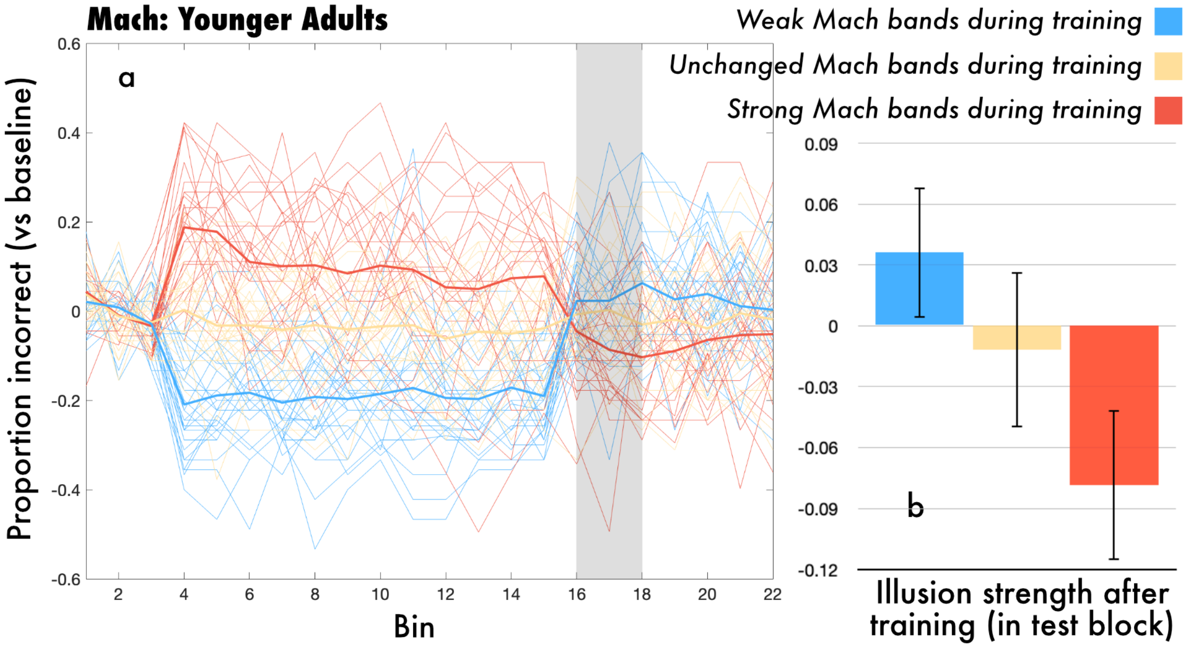


Figure 3 Illusion strength changes from baseline in Experiment 1. (a) Proportion of incorrect responses for each bin for the three conditions. Thick lines show group means, while thin lines represent individual participants. All values have had the individual mean baseline score subtracted to demonstrate illusion strength relative to baseline. (b) Bar chart showing the mean test block response inaccuracy compared to baseline (grey zone in (a)) with error bars displaying 95% confidence intervals. Strong Mach bands (100% opacity) during the training block caused more incorrect responses (greater illusion strength) during that training block, but illusion strength dropped below baseline in the test block. Conversely, illusion strength was weakened during training for participants exposed to weak Mach bands (20% opacity), but actually increased in the test block when the original 60% opacity Mach bands returned.

3.2 Experiment 2

The GLMM for younger adults in Experiment 2 incorporated *block*, *group* and a *block* x *group* interaction with Bayesian information criteria (BIC) = -3705.3, likelihood ratio = 1942.5 and R^2 = 0.622 (Supplementary Table 2), which was significantly better than the null model (LRstat = 2068.8, ΔDF = 22, p < .001). For full model comparisons, see Supplementary Table 2.

incorrect ~ group + block + (group:block) + (1 | ID) + (1 | bl:group:block)

Through comparison of one reduced model (*incorrect ~ 1 + block + group + (1 | ID)*) to reduced models without either *block* or *group* with LRTs (Supplementary Table 1), we demonstrated a significant main effect of *group* (LRstat = 23.486, ΔDF = 3, p <.001), but not for *block* (LRstat = 5.901, ΔDF = 4, p = .207). A comparison of our starting model including *block*, *group* and a *block* x *group* interaction (*incorrect ~ 1 + block*group + (1 | ID)*) with a reduced model without the interaction (*incorrect ~ 1 + group + block + (1 | ID)*) revealed a significant interaction between *block* and *group* (LRstat = 695.44, ΔDF = 12, p < .001). Training interventions uniquely affected illusion strength, while baseline illusion strength interacted with group and block in a three-way interaction as a random effect.

As shown in Figure 4, being exposed to relatively stronger Mach bands via a surround noise condition during training increased illusion strength during that block in comparison to baseline (N = 28, mean inaccuracy change = 14.1%, 95% CL [10.05 18.23]). Afterwards, illusion strength decreased relative to baseline in the test block (N = 28, mean inaccuracy change= -4.78%, 95% CL [-8.36 -1.20]) , returned towards baseline levels in the first washout block (N = 28, mean inaccuracy change = -3.61%, 95% CL [-7.69% 0.47%) and dipping back below baseline in the second washout block (N = 28, mean inaccuracy change = -3.95%, 95% CL [-7.80 -0.10]). Within this group, Strong Mach Training via a surround noise overlay therefore increased illusion strength acutely but weakened the illusion effect experienced by participants when returning to baseline conditions.

Being exposed to weaker Mach bands during training via a noise overlay targeting only the Mach bands decreased illusion strength during that block in a within-subjects comparison to baseline performance (N = 30, mean inaccuracy change = -14.6%, 95% CL [-17.69 -11.51]). Afterwards, illusion strength returned to baseline in the test block (N = 30, mean inaccuracy change = 2.84%, 95% CL [-1.02 6.71]), remaining there until the last washout block (N = 30, mean inaccuracy change = 0.77%, 95% CL [-2.93 3.44]). Participants demonstrated a weaker illusion effect during Weak Mach Training, which resulted in a stronger subsequent illusion effect.

Participants exposed to unchanged stimuli and participants exposed to solid noise overlay followed a similar pattern of illusion effect changes. Illusion strength remained unchanged in the unchanged stimuli group (N = 27, mean inaccuracy change = -1.42%, 95% CL [-4.93 2.09]) and in the solid noise group (N = 27, mean inaccuracy change = -2.75%, 95% CL [-6.22 -0.73]). Illusion strength remained unchanged through the test block (Figure 4) until the last washout block in both groups (unchanged stimuli in washout block 2: N = 27, mean inaccuracy change = 0.85%, 95% CL [-4.44 6.14]; solid noise group in washout block 2: N = 27; mean inaccuracy change = 0.0%, 95% CL [-4.68 4.65]). Being repeatedly exposed to both unchanged stimuli and stimuli with an overlay that equally affected the target and contextual elements saw no changes in illusion strength over time.

A similar pattern of results was evident in Experiment 2 compared to Experiment 1, but with a weaker and non-significant post-training effect of the manipulation that reduced Mach band salience in Experiment 2 (see blue elements of Figures 3 and 4). Further, a solid noise overlay left illusion strength unchanged in that particular group, as with the unchanged stimuli. Owing to the significant effects of Weak Mach Training and Strong Mach Training in Experiment 1, and the apparent redundancy of a solid noise overlay condition, we took forward the task from Experiment 1 forward into the subsequent experiments with older adults with and without Parkinson’s disease.

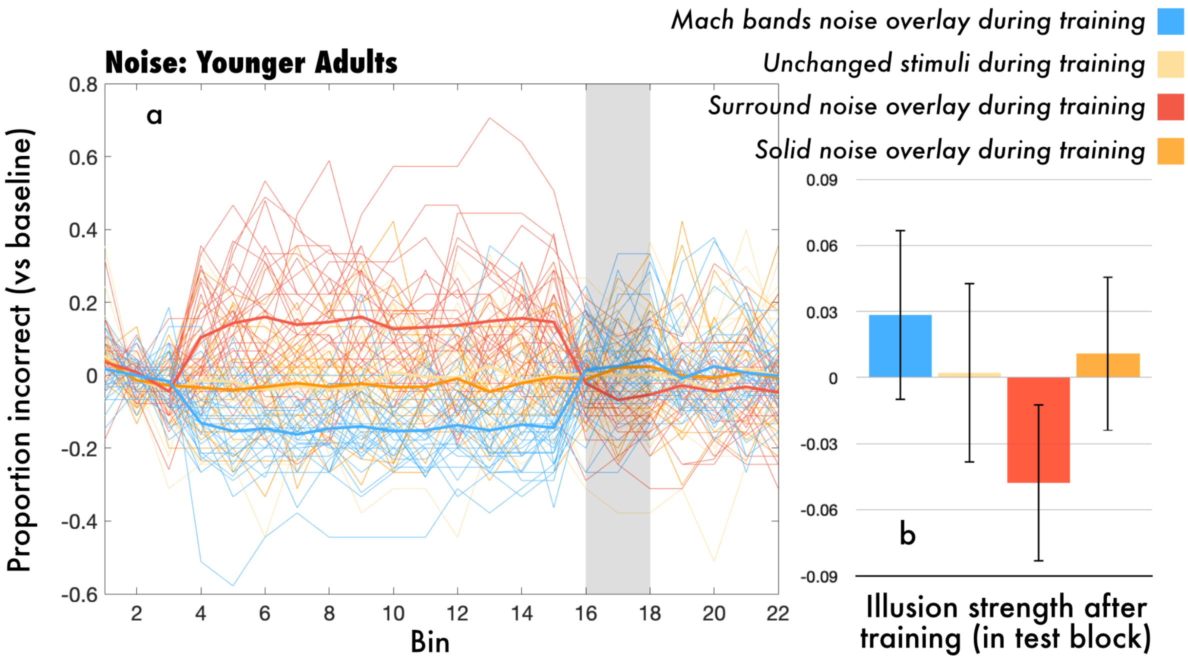


Figure 4 Illusion strength changes from baseline in Experiment 2. (a) Proportion of incorrect responses for each bin for the four conditions. Thick lines show group means, while thin lines represent individual participants. All values have had the individual mean baseline score subtracted to demonstrate illusion strength relative to baseline. (b) Bar chart showing the mean test block response inaccuracy compared to baseline (grey zone in (a)) with error bars displaying 95% confidence intervals. A noise overlay targeting Mach bands (blue) weakened illusion strength during training, and a noise overlay targeting elements surrounding but not including the Mach bands (red) increased illusion strength during training. Only the surround noise condition in this experiment saw a change in illusion strength in the test block where illusion effect was weakened, suggestive of a waning effect after repeated exposure to salient cues.

3.3 Experiment 3

The GLMM for older adults without Parkinson's in Experiment 3 incorporated *block*, *group* and a *block* x *group* interaction with Bayesian information criteria (BIC) = -3088.7, likelihood ratio = 1623.8 and $R^2 = 0.804$ (Supplementary Table 3) also with a three-way *baseline* x *group* x *block* interaction term as a random effect, which was significantly better than the null model (LRstat = 2457.1, $\Delta DF = 19$, $p < .001$). For full model comparisons, see Supplementary Table 3.

incorrect ~ group + block + (group:block) + (1 | ID) + (1 | bl:group:block) + (1 | bl) + (1 | group) + (1 | block)

Through comparison of one reduced model (*incorrect ~ 1 + block + group + (1 | ID)*) to reduced models without either *block* or *group* with LRTs (Supplementary

Table 3), we demonstrated a significant main effect of *group* (LRstat = 61.111, ΔDF = 2, p <.001), and for *block* (LRstat = 67.866, ΔDF = 4, p < .001). A comparison of our starting model including *block*, *group* and a *block* x *group* interaction (*incorrect ~ 1 + block*group + (1 | ID)*) with a reduced model without the interaction (*incorrect ~ 1 + group + block + (1 | ID)*) revealed a significant interaction effect between *block* and *group* (LRstat = 1069.3, ΔDF = 8, p < .001). Block and group altered illusion strength changes with significant interaction as a main effect, and individual variation in baseline illusion strength also impacted group and block related responses to training. Secondary outcomes indicative of motor ability and daily life activities (Key Tapping Score and ADL Score) had no effect.

Strong Mach Training increased illusion strength within-subjects in the training block (N = 29, mean inaccuracy change = 11.37%, 95% CL [5.07 17.66]) but weakened illusion effect in the subsequent test block (N = 29, mean inaccuracy change = -9.63%, 95% CL [-17.45 -1.81]) which remained below baseline until the last washout block (N = 29, mean inaccuracy change = -11.22%, 95% CL [-18.66 -3.78]), shown in Figure 5. Strong Mach Training saw participants experience increased illusion strength during training but with a subsequent reduction in illusion strength.

Weak Mach Training decreased illusion strength during training (N = 30, mean inaccuracy change = -27.38%, 95% CL [-30.45 24.30]), which returned to baseline levels in the test block (N = 30, mean inaccuracy change = -3.4%, 95% CL [-7.63 0.80]) and stayed there till the last washout block (N = 30, mean inaccuracy change = -3.76%, 95% CL [-8.02 0.50]). Participants experienced a large decrease in illusion strength during Weak Mach Training, and returned to baseline levels afterwards (and were the only group to do so in this experiment).

In this experiment, participants experienced a weakened illusion effect during a training block with unchanged stimuli also (N = 29, mean inaccuracy change = -6.4%, 95% CL [-12.02 -7.8]), which remained below baseline levels for the test block (N = 29, mean inaccuracy change = -9.97%, 95% CL [-16.42 -3.53]) until the second washout block (N = 29, mean inaccuracy change = -8.80%, 95% CL [-15.52 -4.77]). It therefore appears that in the older adults of this experiment, there was a general decline in illusion strength over time, even without manipulating the Mach bands.

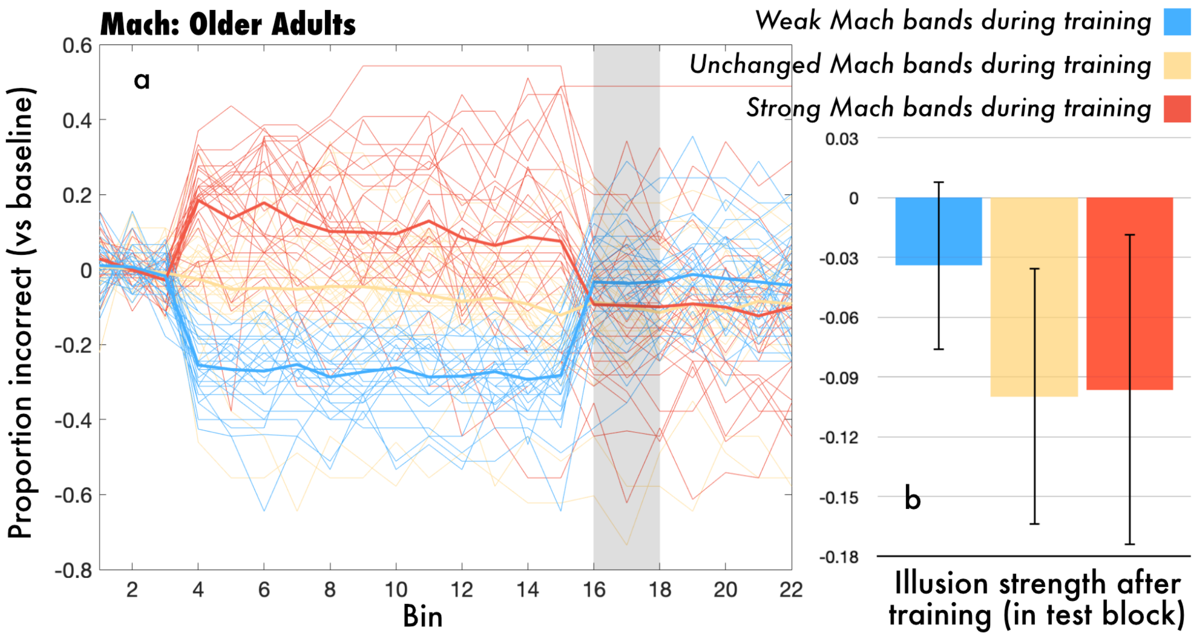


Figure 5 Illusion strength changes from baseline in Experiment 3. (a) Proportion of incorrect responses for each bin for the three conditions. Thick lines show group means, while thin lines represent individual participants. All values have had the individual mean baseline score subtracted to demonstrate illusion strength relative to baseline. (b) The bar chart shows the mean test block response inaccuracy compared to baseline (grey zone in (a)) with error bars displaying 95% confidence intervals. The test block is the first point at which participants in Weak or Strong Mach Training return to baseline conditions. Strong Mach Training sees participants experience a weaker illusion after training, but as training with unchanged stimuli achieves this too, it is likely a decline in illusion strength happens in this group anyway. In the context of a general illusion strength decline, Weak Mach Training was able to return participants to baseline levels of illusion strength, an index of contextual cue perception.

3.4 Experiment 4

The GLMM for older adults with Parkinson's in Experiment 4 incorporated *block*, *group* and a *block* x *group* interaction with Bayesian information criteria (BIC) = -1123.1, likelihood ratio = 631.32 and R^2 = 0.807 (Supplementary Table 4) also with a three-way *baseline* x *group* x *block* interaction term as a random effect, which was significantly better than the null model (LRstat = 1006.4, ΔDF = 19, p < .001). For full model comparisons, see Supplementary Table 4.

incorrect ~ group + block + (group:block) + (1 | ID) + (1 | bl:group:block) + (1 | bl) + (1 | group) + (1 | block)

Through comparison of one reduced model (*incorrect ~ 1 + block + group + (1 | ID)*) to reduced models without either *block* or *group* with LRTs (Supplementary

Table 4), we demonstrated a significant main effect of *group* (LRstat = 15.332, ΔDF = 2, p <.001), and for *block* (LRstat = 29.406, ΔDF = 4, p < .001). A comparison of our starting model including *block*, *group* and a *block* x *group* interaction (*incorrect ~ 1 + block*group + (1 | ID)*) with a reduced model without the interaction (*incorrect ~ 1 + group + block + (1 | ID)*) revealed a significant interaction effect between *block* and *group* (LRstat = 448.78, ΔDF = 8, p < .001). Various secondary characteristics such as LED Current, Time Since Diagnosis Key Tap Score, ADL and age, included as random effects, made no improvement to the model.

In Experiment 4, adults with Parkinson's similarly experienced an increase in illusion strength during Strong Mach Training (see Figure 6, N = 14, mean inaccuracy change = 14.22%, 95% CL [6.00 22.44]). Returning to baseline conditions in the test block saw illusion strength drop 11.48% (95% CL[-18.13 -4.84]) below earlier baseline levels which remained below baseline levels until the end (mean inaccuracy change in washout block 2 = -10.37%, 95% CL[-17.46 -3.29]). Strong Mach Training thus increased illusion strength during training within-subjects, but as in every experiment now, led to a decreased illusion effect in the test block.

Weak Mach Training weakened the illusion effect during training (N = 10, mean inaccuracy change = -24.25%, 95% CL[-31.02 -17.48]), and participants experienced a return to baseline illusion strength in the test block (N = 10, mean inaccuracy change = -4.23%, 95% CL[-9.34 0.87]). Illusion strength remained at baseline levels until washout block 2 (N = 10, mean inaccuracy change = -3.18, 95% CL [-9.45 3.09]). Similarly to Experiment 3, Weak Mach Training was the only training type that restored illusion strength to baseline levels.

Participants who trained with unchanged stimuli experienced a slightly lower but comparable illusion effect during training (N = 11, mean inaccuracy change = -2.39%, 95% CL[-6.65 1.87]). Reaching the test block however, illusion strength dropped significantly below baseline levels (N = 11, mean inaccuracy change = -6.57%, 95% CL[-10.23 -2.92]). Hovering just under baseline levels, illusion effect was up again slightly for washout block 1 (N=11, mean inaccuracy change = -4.68%, 95% CL[-10.39 1.04]) and washout block 2 (N = 11, mean inaccuracy change = -4.71%, 95% CL[-11.47 2.04]). Training with unchanged stimuli again suggests illusion strength declines slightly over time with repeated presentations.

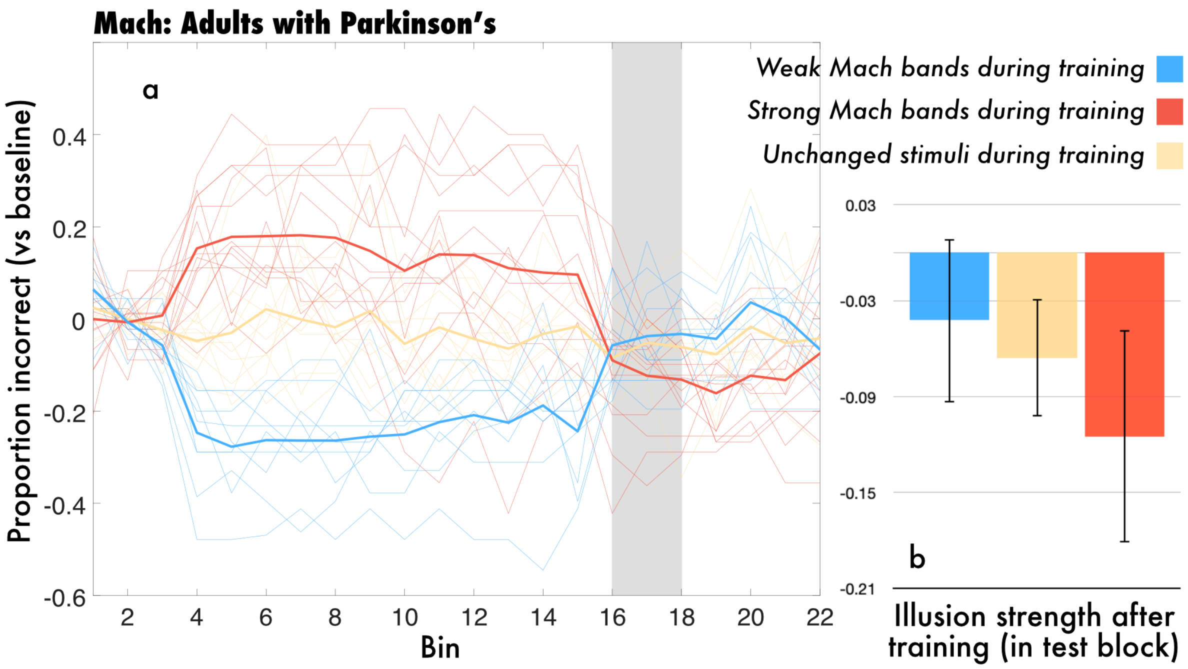


Figure 6 Illusion strength changes from baseline in Experiment 3. (a) Proportion of incorrect responses for each bin for the three conditions. Thick lines show group means, while thin lines represent individual participants. All values have had the individual mean baseline score subtracted to demonstrate illusion strength relative to baseline. (b) The bar chart shows the mean test block response inaccuracy compared to baseline (grey zone in (a)) with error bars displaying 95% confidence intervals. Strong Mach Training led to a subsequent decrease in illusion strength which lasted to the end, training with unchanged stimuli saw a slight decrease over time, significantly below baseline at test but not in the other blocks, and Weak Mach Training saw participants return to initial illusion effect levels.

3.5 Pooled analysis from Experiments 1, 3 and 4

The GLMM for all of the experiments which featured a direct Mach band manipulation were pooled together for comparison across the three population groups: younger adults, older adults with Parkinson's and older adults without Parkinson's. Baseline illusion strength (1 | *bl*) was included in all models owing to its beneficial effect on model strength in all four experiments. The best performing model for this pooled data was the GLMM *without* a population variable, neither as a main effect or when included as an interaction:

$$\text{incorrect} \sim \text{group*block} + (1 \mid \text{ID}) + (1 \mid \text{bl})$$

Population is a notable absence, where it made no significant difference to the model as main effect, revealed by comparing a base model (*incorrect* ~ 1 + *group* + *block* + *population* + (1 | *ID*) + (1 | *bl*)) to a reduced model (*incorrect* ~ 1 + *group* + *block* + (1 | *ID*) + (1 | *bl*)) with no significant effect of *population* (LRstat = 0.618, ΔDF

= 2, p = .734). To explore *population* as an interaction term, a second base model (*incorrect* ~ 1 + *group*block*population* + (1 ∣ *ID*) + (1 ∣ *bl*)) was compared to a model with *population* still included as a main effect (owing to the principle of marginality, Wagenmakers et al., 2018), but with a two-way interaction between group and block (*incorrect* ~ 1 + *group* + *block* + *population* + *group*:*block* + (1 ∣ *ID*) + (1 ∣ *bl*)). This comparison revealed the model to be best when population was not included as an interaction term (LRstat = 947.43, ΔDF = -8). For all comparisons, see Supplementary Table 5. Together, these results suggest population, while having a significant effect when looking at baseline strength only (Chapter 2), had no meaningful effect on the overall pattern of results.

4. Discussion

4.1 Training alters cue perception

Aware that a skill such as walking can be enhanced in the presence of visual cues, even with positive after-effects (Morris et al., 1996), we sought to explore changes in how contextual cues inform perception, knowing that task-relevant sensory-filtering and ongoing integration of contextual information in complex environments are harmed when basal ganglia capacity is compromised (Kearney & Brittain, 2021). Increased contextual cue salience consistently resulted in an after-effect of reduced illusion strength. Conversely, repeated exposure to Mach bands with reduced opacity did have a positive rebound effect in Experiment 1 whereby participants experienced a stronger illusion effect in the test block. This significant finding was not replicated in the following experiments. By itself, reducing salience of contextual cues is not supported here as a robust intervention to modify perceptual abilities revealed by the Cornsweet effect. However, the Weak Mach Training condition was the only condition that saw older adults (with and without Parkinson's) return to their original illusion strength in the test block; in contrast, the other conditions saw reduced illusion strength in the test block, symptomatic of a general waning of illusion strength over the course of the experiment.

In this study, we examined how participants' perception of the Cornsweet illusion adapted to increased or decreased levels of cue salience and the subsequent effects of the adapted state on the baseline level of illusion. The Cornsweet illusion task provided a simple way to continually assess the influence of context on perception, indexing how cues are being attending to. We found that the use of cues, as reflected in illusion strength, changes over time. Moreover, stronger cues increased illusion strength during the training block but reliably reduced illusion strength in the subsequent test block. No significant effect was found for population in the pooled analysis, suggesting that all participants did not vary in response to the training. This is apparent in the way that younger adults and older adults with and without Parkinson's, on average, all exhibited increased illusion strength with stronger contextual cues, weakened illusion strength with weaker contextual cues, and some degree of a rebound effect in the opposite direction.

As shown in Chapter 2, the Cornsweet illusion task involves simple visual stimuli (even if it relies on complex top-down/integration processes, see Purves et al., 1999 & Gilbert & Li, 2013). The absence of onscreen distractors may mean the task-relevant sensory filtering capacity we attribute to basal ganglia pathways is not sufficiently challenged, and thus adults with and without Parkinson's display the same pattern of illusion strength changes (Figures 5 and 6) and estimated dopamine levels had no explanatory power in our model for Experiment 4. However, we demonstrate in all experiments that participants adapt to a particular level of cue salience that impacts how cues are attended to in later conditions. The presence of such adaptation has implications for cue provision during training and forms of exercise rehabilitation, where cues can be useful to initiate an action. The adaptation effects we demonstrate suggest that excessive cue salience may prompt a reliance on artificial cues which is not necessarily helpful to improve the capacity of the nervous system to make use of often subtle or obscured information in the environment.

4.2 How can cues guide behaviour and alleviate symptoms?

According to Nonnekes and colleagues (2019), in their review of the compensatory techniques that people with Parkinson's devise to overcome motor impairments, the mechanisms by which such compensatory "tricks" work is not well understood. It has been demonstrated that a variety of sensory cues (Chawla et al., 2020; Spaulding et al., 2013), including lines on the floor (Beck et al., 2015, Morris et al., 1994, 1996), can alleviate symptoms of Parkinson's disease. What we demonstrate here is that increasing the salience of contextual cues dramatically alters perception of panel brightness, as measured in the increase in illusion strength in each of the four experiments. Thus, augmented cues may be acting to shortcut the need for complex perceptual processes (such as task-relevant filtering and contextual cue integration described in Chapter 1).

Salience is a way to consider the obviousness of a stimulus, how much it grabs the attention without looking for it, or how much it stands out compared to the rest of the environment. Jenkinson & Brown (2011) argue that salient internal and external signals can increase dopamine levels in basal ganglia pathways, introducing another angle to the explanation of why particularly salient cues can aid the movement of people with Parkinson's where base dopamine levels can be depleted. Typically, cognition, perception and action are all considered separately via isolated approaches in psychology and neuroscience (Cisek, 2019; Song et al., 2019).

However, attentional focus is an important aspect of movement: directing athletes' foci toward movement consequences in the surroundings can enhance movement and motor skill learning (Wulf et al., 2001, 2009, 2010), but directing focus toward limb movements can worsen skill performance (Bosch, 2015; Sadnicka & Kornysheva, et al., 2018).

Borrowing Marc Jeannerod's definition of intentional movement as the "means by which the organism and environment reciprocally interact" (in Malabou, 2008, p.75), it is no surprise that changing the environment affects movement and perception, shown very simply here in how contextual cue salience alters panel brightness perception. Of interest, is not just creating an environment full of salient cues that instantaneously improve skill performance. However useful it might be to tape bright orange lines on the floor en route to all one's favourite locations (or more realistically: Badarny et al., 2014; de Oliveira et al., 2021), highly salient cues may, less usefully, reduce cue sensitivity. A particular aim here was to explore how perceptual ability is altered through the modification of contextual cues.

4.3 Implications for training and rehabilitation

In the context of a general decline in illusion strength, evidenced in the groups presented with unchanged cue salience, Weak Mach Training effects are encouraging. However, this rather reinforces the findings that we adapt to the sensory conditions present, rather than proposing that subdued sensory input comprise a new approach to training and rehabilitation. If highly salient contextual cues do indeed harm the perceptual ability measured by Cornsweet illusion task, then how can lines on the floor sometimes display a lasting improvement in walking performance (Morris et al., 1996) and when might this approach be useful as opposed to those which increase processing demand (Ridgel et al., 2009, 2015; Ridgel & Ault, 2019) and intentionally decrease reliance on visual information (Sage & Almeida, 2009, 2010)?

James T. Enns describes, in *The Thinking Eye, The Seeing Brain* (2004, p.257-263), anti-gravity hills. Such hills are particular locations where it appears that something like a ball or car can roll *up* hill. The key to these locations, Enns argues, is the true horizon being hidden from view, multiple surface planes being *in* view, and a local story about the location to inform the experience. The point here, is that context is continually informing perception; there is a flowing river of signals shared between organism and environment, and so in the absence of an obvious give-away about which way is up (the horizon), other sources of information take its place. Sometimes, though, it is hard to attend to any useful sources of information. When meaningful engagement with the environment is not possible, such as for patients with near-total degeneration of the inner-ear causing a perpetual sense of falling and inability to balance, signals delivered to the tongue from a head-mounted accelerometer help the person to both meaningfully interact with the environment while wearing it, but then also for a short period after the device is removed (Bach-y-Rita, 2005; Doidge, 2008, p.1-26; Tyler et al., 2003). This sensory substitution approach was so successful that the duration of the after-effects after each session of use got longer and longer until the device was no longer needed (Doidge, 2008).

In Badarny and colleagues' (2014) study, perhaps something similar occurs: training in a virtual-reality, tiled-floor environment elicited residual as well as acute improvements in some people with Parkinson's (though with long term assessment of its effects still necessary). Some participants in that study described thinking about the virtual tiled floor after the headset was removed, providing a new attentional focus, but the intervention also could have enhanced walking enough to begin to pick up on new and useful feedback sources elsewhere. The risk of course, is that excessive use of highly salient contextual cues reduces the demand on the nervous system, on the participant, to be challenged and stretched (Lewis et al., 2000; O'Connor et al., 2017). Analogously, M.R. O'Connor in her book *Wayfinding* describes how navigation technology may help find a way quicker, but shifts the responsibility onto the technology. As such, recent tools like GPS bypass much of the needs for skilful navigation and connection with place nurtured over time, and resultantly harms spatial memory (Dahmani & Bohbot, 2020).

4.4. Conclusion

In this chapter I have shown that the influence of contextual cues on perception changes through repeated presentation, whereby Strong Mach Training led to negative residual effects in illusion strength, and Weak Mach Training led to either a stronger illusion in the test block or a return to baseline levels. Thus, while others have shown highly salient cues in training can be useful tools to improve kinematic measures (Beck et al., 2014; Morris et al., 1994, 1996), perceptual ability is not necessarily being trained in the way we might hope. Here, acute changes in the Cornsweet illusion effect – that indexes sensory integration processes – are generally followed by rebound effects in the opposite direction. Using this novel Cornsweet illusion task, we demonstrated that illusion strength can indeed be "trained", revealing the effect of cue salience on the perceptual processes that are elsewhere important in movement.

Melt

The language to communicate is not
needed beforehand. Only a willingness to
engage, to be present. Wholly present.

Our boundaries melt away, the reality
of our radical openness recognised, a
wholeness tasted. The language to communicate
is not needed beforehand. It emerges here.

We want to possess the map first.
It is called allocentric knowledge.
Like following a blue arrow on Google Maps,
we know where to go before we go, seated
on a lofty throne.

Far richer is egocentric knowledge.
It is when we only know the route
at the journey's end. Part of a whole.
Wholly present, we submit to the adventure
without seeing from above. A map not needed,
except to tell stories of where we have been.

> Fragments in this first sense is a reality of being creatures who can only apprehend with our senses in bites, in touches, in smells, in sounds, and in focused but shifting sight. We live in the reality of these pieces where the world is always too much for us to hold all at once. We creatures live in pieces, and we come to know our redemption in pieces.

Willie James Jennings, *After Whiteness*, p.34

Chapter 4

Sensory suppression training does not uniquely enhance performance in a pegboard task

1. Introduction

In the classic force-matching task, a popular measure of sensory attenuation, older adults respond in a more context-specific manner whereby the divergence in force-production between two types of matching conditions (direct and indirect) is larger than that of younger adults (Wolpe et al., 2016). We demonstrated this increase in the incorporation of a unique context into stimulus perception in Chapter 2 with the Cornsweet illusion task, and this ability that may well emerge with greater experience (Chambers et al., 2018; Idei et al., 2021), especially given an apparent absence of sensory attenuation in infants (Meyer & Hunnius, 2021). However, it has also been suggested that increased sensory attenuation – the distinct perception of an identical stimulus owing to its unique context – may emerge as compensation for worsened tactile sensitivity (Seidler et al., 2010; Wolpe et al., 2016; though see Parthasharathy et al., 2021).

Context-dependent processing, in a complex enough task, worsens in Parkinson's (Wolpe et al., 2018), but symptom severity can be improved with movement training in low light conditions (Sage & Almeida, 2009, 2010). Such exercise during low light conditions was intended to focus attention toward proprioceptive control and away from visual guidance, but could also be explained as a response to increased sensory uncertainty, much like the compensation explanation in older adults. This uncertainty explanation has already been used to explain symptoms in Parkinson's: weak predictive signals are thought to impair movement by failing to attenuate sensory input and thereby giving the person with Parkinson's an overwhelming sense of not moving (Brown et al., 2013). In such a framework, the rehabilitation possibility offered is one where sensory uncertainty could also be used to shift demand onto prior signals to enhance neural capacity (or just predictive weighting) for improved navigation of uncertain environments, not just ones filled with highly salient, certain sensory signals. In the two differing populations who are thought to display lowered sensory sensitivity in different ways, it appears that altering environment properties (reduction in peripheral tactile sensitivity and low-light conditions) alters a sensorimotor processing ability that could be important for moving through complex environments (Kearney & Brittain, 2021).

With this background, we sought to see how reducing both tactile and visual input during a pegboard task, performed across two sessions on separate days, would affect movement and retention in young healthy adults. The compensation explanation in the elderly and the uncertainty explanation in Parkinson's stem from the concept of increased reliance on memory (or priors) to navigate conditions of uncertainty as predicted by Bayesian-informed models of action and perception (Knill & Pouget, 2004; Körding & Wolpert, 2004). If these compensation and uncertainty explanations are true, and if they generalise beyond these populations, then we can hypothesise that better pegboard performance will emerge towards the end of Day 1 and on Day 2 in participants performing the pegboard tasks gloved and blindfolded, owing to the uncertain conditions demanding more from the participant's predictive capacity, which supposedly underpins optimal motor control. Further, training under uncertain conditions in training (blindfolded and gloved), should benefit performance under uncertain conditions in testing (blindfolded) and Day 2 training (blindfolded). Testing participants with and without vision offered a way to assess training effects specific to sensory context (absence or presence of vision), and we briefly discuss different perspectives by which alterations in the sensory environment might evoke neural adaptation.

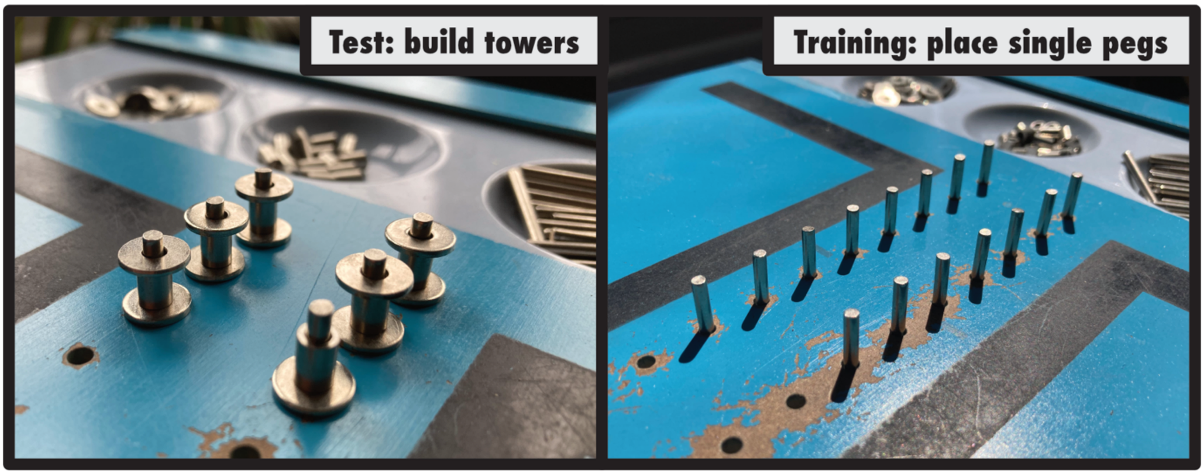


Figure 1 In test trials, participants built "towers" that consisted of 4 components: a peg, two washers and a collar. Participants built as many as they could in 30 seconds, with the number of accurately placed parts counted at the end. This task was performed at the start, middle and end of the session each day in both groups and in standard vision and blindfolded conditions. In training, participants placed single pegs, aiming for as many as they could, also in 30 second trials.

2. Methods

Twenty participants took part in this study, split evenly between and assigned randomly to one of two group. The Jamar Pegboard tasks require fine motor skill and complex movements to pick small metal pieces from bowls and reorient them onto the pegboard. The researcher demonstrated the two pegboard tasks to the participant. In the tower task, the participant built towers (Figure 1) with four components. In the peg task, participants filled the holes on the board solely with pegs. The tower task used for testing was performed blindfolded first and then with vision available, while the peg task was completed under training conditions specific to each group (Figure 2). Both groups completed tests in the same conditions, and additionally, both groups completed Day 2 under the same experimental conditions. For Day 1 training however, if the participant was in the uncertainty group, they trained on Day 1 with latex gloves on both hands and a blindfold covering both eyes. In the full-senses group for Day 1 training, no attempt was made to suppress sensory input.

Every trial that formed the training and test blocks lasted 30 seconds, and the participant tried to assemble as many towers or place as many pegs as possible. Performance was measured by the number of pieces accurately placed on the board at the end of the 30 seconds. For the towers task used for testing, this included the peg, a washer, a collar and another washer, in that order, and pieces of incomplete towers were still counted providing (1) they were accurately placed and in the right order, and (2) that there were no more than two incomplete towers at the end of the trial. We analysed performance in the vision and non-vision towers task in two separate 2(training group) x 6(time of towers task) repeated measures analyses of variance (ANOVA). Another ANOVA, 2(training group) x 6(test-difference at each time point), was used to assess the convergence of test scores in vision and non-vision conditions with the expectation that performance in blindfolded conditions (non-vision tests) could improve more in the uncertainty group, whereas performance in vision tests could improve more in the full-senses group leading to a convergence in the former and a divergence in the latter.

Finally, the researcher in each session recorded the strategy employed by each participant in the training blocks in their attempt to place as many pegs as possible. It quickly became apparent that peg-placing strategies fell into two categories: guided and unguided. In the guided strategy, participants would use one hand to find the target hole and the other hand to move the peg to the hole. And in the unguided strategy, participants would simultaneously have a peg in each hand moving the pegs towards the target holes without the guidance of the other hand.

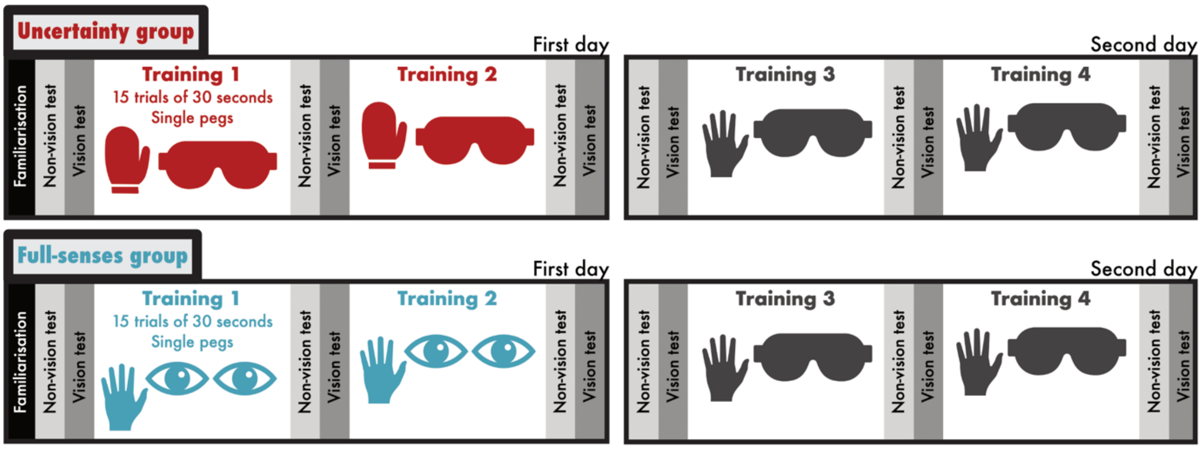


Figure 2 The experimental protocol was spread over two days, with the same towers task repeated by both groups six times interspersed throughout, but different sensory conditions for the Day 1 single peg training blocks. Day 2 was performed under the same conditions for both sets of participants.

3. Results

3.1 Analysis of training and group effects on test performance

T-tests revealed no group difference at baseline in the first vision ($t(18) = 0.534$; $p = .600$) and non-vision ($t(18) = 0.228$; $p = .822$) towers tasks. There was significant effect of time point of test in the vision tests ($F(5, 90) = 15.045$, $p < .001$, $\eta^2 = .127$) and the non-vision tests ($F(3.313, 59.635) = 17.754$, $p < .001$, with Greenhouse-Geisser sphericity correction, $\eta^2 = .202$) indicating improvement in performance, but no significant effect of group ($F(1, 18) = 0.482$, $p = .496$ for vision tests & $F(1, 18) = 0.778$, $p = .39$ for non-vision tests) nor group and time interaction ($F(5, 90) = 0.482$, $p = .496$ for vision tests & $F(3.313, 59.635) = 1.590$, $p = .197$ with Greenhouse-Geisser for non-vision tests). Further, there was no significant change in the difference between vision and non-vision tests across time ($F(5, 90) = 1.318$, $p = .263$), no main effect of group ($F(1, 18) = 0.158$, $p = .696$), and no significant interaction with group ($F(5, 90) = 1.603$, $p = .167$). In sum, the two groups performed similarly at the start of the experiment and both improved peg-placing skills across the course of the experiment evidenced in improved test performance. However, there were no between-group differences as a result of their distinct Day 1 training procedures.

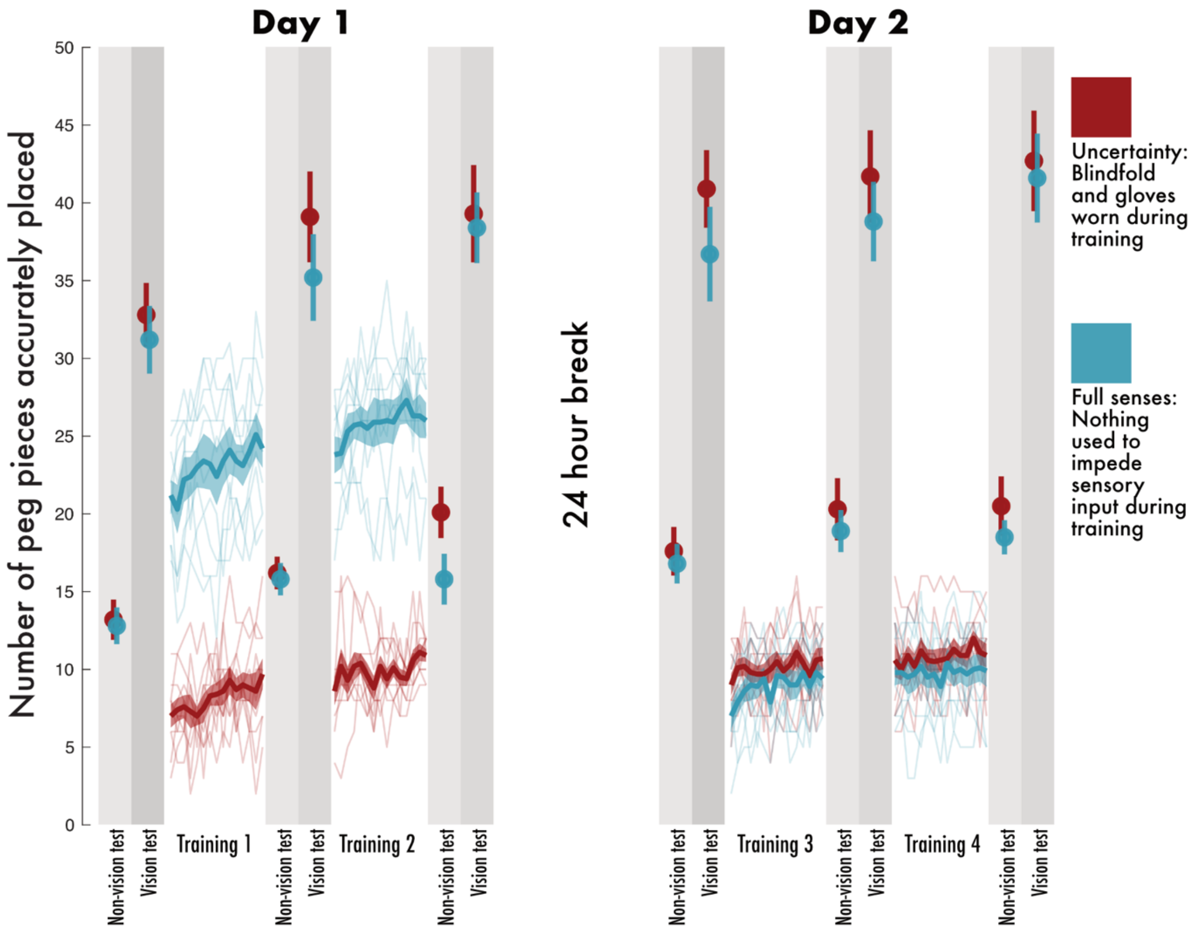


Figure 3 Number of peg pieces accurately placed in test and training trials. There were three non-vision tests and three vision tests each day (grey shading) where participants built as many towers as they could. Fifteen trials of the single peg task constituted the training blocks. Training means are indicated by thick lines with individual participants represented by thin lines. The two groups performed under different conditions in training on Day 1, but the same conditions were in place for all test trials and also Day 2 training. Standard error of the mean is indicated by vertical lines for tests and the shaded area for training.

3.2 Analysis of effect of training group on strategy employment

We observed and recorded the predominant strategy used by each participant in the single peg training on each day, and calculated the percentage usage in each training group. A chi-squared test of independence showed a significantly different strategy count on Day 1 between groups ($\chi^2(1, N = 20) = 7.5$, $p = 0.006$, odds ratio = 3.05, 95% CL[0.58 5.54] for odds ratio) but not on Day 2 ($\chi^2(1, N = 20) = 0.220$, $p = 0.639$) when conditions became the same (Figure 4). Distinct Day 1 training conditions elicited unique strategy employment, but Day 2 training, where both groups trained blindfolded and without gloves, saw a similar proportion of guided and unguided strategies for each group.

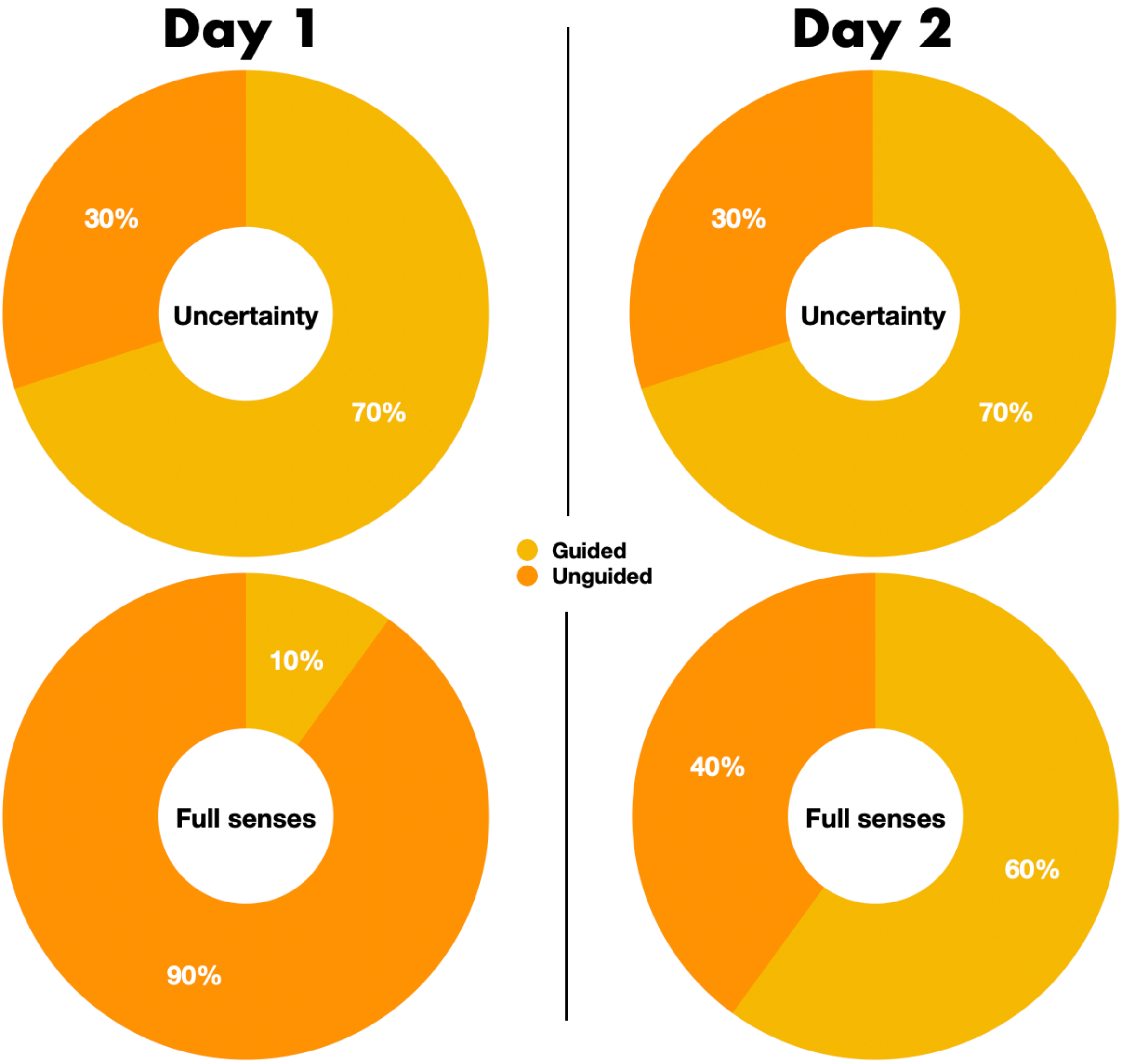


Figure 4 Two strategies emerged as participants performed the pegboard task. In what we describe as guided and unguided, participants either picked up a single peg with one hand and guided with the other hand by moving between the peg and the target location (guided), or participants picked up pegs with each hand and aimed for the target location without guidance from the other hand (unguided). Different sensory conditions appeared to drastically alter predominant strategy deployment but without lasting effect.

3.3 Post-hoc analysis: strategy and test performance

Given the significant difference in strategy based on sensory conditions, we compared pegboard test performances with strategy as the between subject factor, as part of a post-hoc analysis. Participants fit into three categories: (1) unguided strategy on both days (N = 7), (2) guided strategy on both days (N = 8) and (3) unguided then guided (N = 5); no one exhibited the other mixed strategy combination. Thus, two 3(strategy) x 6(time of towers task) ANOVAs again revealed significant main effects of time point in the vision tests (F(5, 85) = 14.863, p < .001, η^2 = *.123*) and non-vision tests (F(5, 85) = 16.065, p < .001, η^2 = *.187*), but with no evidence of main effects for strategy (F(2, 17) = 0.930, p = .414 in vision tests; F(2, 17) = 1.771, p = .200 in non-vision tests). Whilst participants approached training with unique approaches over the two days, there was no observable benefit in test performance in utilising one strategy combination over another.

3.4 Post-hoc analysis: assessing evidence for null effect of training group

Finally, in the absence of main effects for group, we performed a Bayesian repeated measures ANOVA which allows comparison to a null model, quantifying evidence for the null hypothesis (Wagenmakers et al., 2018). In the non-vision tests, the model with time of testing (tower tasks 1 to 6) as a main effect vastly outperforms the null model with a Bayes factor (BF10) of 1.773 x 109. The null model was 1.84 times more likely than the model with group as the main effect (BF10: 1.000/0.544). A two-main-effects model with both time and group ("Time + Group") was only slightly less likely than than the "Time" model though, which outperformed the model with an added interaction (BF10: 1.043 x 108/1.358 x 107 ≈ 7.68 times more likely). In the vision tests, the null model also outperformed the "Group" model ((BF10: 1.000/0.585 ≈ 1.71 times more likely), with the "Time" model performing best (BF10 = 1.612 x 108). This analysis supports the null hypothesis stating no benefit of training under uncertain conditions on tower task performance, especially as the uncertainty group appear graphically (Figure 3) to be the slightly better performing group from the start. While the Bayes factors for the "Group" models in tower tasks with and without vision is only in the anecdotal strength range (Wagenmakers et al., 2018) with fairly small sample sizes (N = 10 in each condition), our search for a robust training principle finds little hope in this iteration of an uncertainty approach.

Table 1 Model comparisons in two Bayesian repeated measures ANOVAs for tower task performance measured at six points throughout ("Time"), with each model compared to the null model.

Model Comparison: vision tests					
Models	**P(M)**	**P(M | data)**	**BF $_{M}$**	**BF $_{10}$**	**error %**
Null model (incl. subject)	0.200	3.582e -9	1.433e -8	1.000	
Time	0.200	0.578	5.468	1.612e +8	0.760
Time + Group	0.200	0.374	2.388	1.043e +8	1.116

Time + Group + Time ∗ Group	0.200	0.049	0.205	1.358e +7	1.343
Group	0.200	2.095e -9	8.379e -9	0.585	0.624
Model Comparison: non-vision tests					
Models	**P(M)**	**P(M ∣ data)**	**BF $_M$**	**BF $_{10}$**	**error %**
Null model (incl. subject)	0.200	2.925e -10	1.170e -9	1.000	
Time	0.200	0.519	4.309	1.773e +9	0.474
Time + Group	0.200	0.330	1.972	1.129e +9	2.243
Time + Group + Time ∗ Group	0.200	0.151	0.713	5.170e +8	1.196
Group	0.200	1.590e -10	6.361e -10	0.544	0.675

4. Discussion

4.1 Key Findings

In this experiment, we asked participants to accurately place as many pieces on the pegboard as possible in different combinations of task and sensory conditions. We were particularly interested in how masking some sensory input might change how participants move and learn. Removing vision unsurprisingly made the task harder: for both groups more pieces were accurately placed in the tower tasks when vision was available compared to when vision was not, and also in the Day 2 training performance compared to Day 1 for full-senses group (Figure 1). Additionally, in the single peg training task, the combination of blindfold and gloves in the uncertainty group served to worsen performance on Day 1. Training effects were present in all groups: participants got better overall with no benefit of training under uncertain conditions. There were small glimpses of group differences: at the end of Day 1, performance in the non-vision test was better on average in the uncertainty group, and at the start of Day 2, uncertainty group training performance was better on average in some, but not most, trials. However, there was no difference in Day 2 test performance between the two training groups. It appears then, that while sensory conditions altered immediate performance and gave rise to unique strategy employment, blindfolds and gloves did not dramatically benefit performance during tasks where sensory conditions were the same for both groups, neither in vision nor non-vision conditions.

4.2 Sensory uncertainty as a means to improve skill

Inspired by Parkinson's rehabilitation techniques that mask visual information to guide attention toward proprioceptive input, we wondered if the principle that underpinned this was in fact related to a Bayesian integration framework. Such a framework conceives motor control and perception as the balancing of outgoing predictive signals and incoming sensory signals based on their relative certainty – that is, how precise the signals are (Figure 5A). It has been suggested that Parkinson's symptoms can be explained with such a framework, where weak internal predictions in Parkinson's disease lead to less ability to overcome noisy environments (Figure 5B; Brown et al., 2013; Wolpe et al., 2018). This inability to extract signal from noise would explain why providing clear, precise sensory cues like tactile cues, auditory cues or lines on the floor can have an immediate benefit in alleviating symptoms like freezing and shuffling gait, and enabling more fluid movement (Quintyn & Cross, 1986). Such cueing approaches could increase the precision of sensory input, making the effects of weak prediction less noticeable. However, we wanted to know if the reverse could be used to improve precision of predictive signals over the long term. Could sensory uncertainty actually shift the demand onto the brain to come up with a solution itself, inducing longer term improvements in the capacity of the nervous system? Might uncertainty be the principle at work in the PD-SAFEx programme, whereby more reliable sensory input is reduced (Sage & Almeida, 2009, 2010), a programme that demonstrates lasting symptom improvement rather, not temporary symptom alleviation?

We show in Chapter 3 in Experiment 1 that reducing the salience of contextual cues can have a positive rebound effect in visual perception, while increased salience has a negative rebound effect. Elsewhere it has also been demonstrated that sensory uncertainty shifts reliance onto prior information, where in the absence of sensory feedback, participants relied on a priori knowledge to guide decision-making in a simple finger-tracing task with cursor deviations (Körding & Wolpert, 2004). However, in this study, we sought to investigate how masking sensory input affects a motor skill (Figure 5C). We found no significant evidence of positive training effects in the uncertainty group. The blindfold and gloves dramatically reduced training performance on Day 1 suggesting such conditions were at least sufficient to create uncertainty and make the task more challenging but still possible. However, the intended effect of removing visual input was to require the nervous system to source information from elsewhere, a search for task-relevant cues that the basal ganglia is implicated in (Bakhurin et al., 2017; Beeler & Dreyer, 2019; Kearney & Brittain, 2021). In the pegboard task however, it is possible this process is continually being undertaken in all sensory conditions that we implemented, as participants strived to get better.

The pegboard task is not as complex as, for example, a team sport, and the participants are able to perform the task from the start indicating some simplicity (Wulf & Shea, 2002) in contrast to, say, a juggling task with participants unable to juggle at the start of the study. However, while the pieces are uniform, it is nevertheless complex in the infinite ways pieces can be picked up, manipulated and placed by the participant, differing from a simulated computer task utilising a virtual and knowable world. As such, there is always some uncertainty, some element of the unknown, that means this search for information is always underway. Improvement was always possible and, much like how even though the best free-throw shooters in basketball still do not make all their free throws in their career, here, participant scores at the end of each pegboard trial varied despite an ever-present ability to to perform the skill of placing pegs. This fact, perhaps, poses the main issue to the notion of using sensory uncertainty to improve not just the precision of predictions, but capability of the nervous system. It is not just two signals at play, but vast fields of possible signals, where sensory input cannot so much be reduced as partly masked and therefore biased toward other input in an infinite world. Visual information was of course very useful and beneficial for placing more peg pieces in each 30 second trial, but participants simply adapted and both groups performed similarly in spite of their first day training conditions, with no advantage of training in more difficult conditions. The finding of similar pegboard skill improvement across training groups is consistent with the argument of Wulf & Shea (2002) who reconcile movement improvements from both making tasks more difficult and making tasks easier by considering them on a simple-complex spectrum.

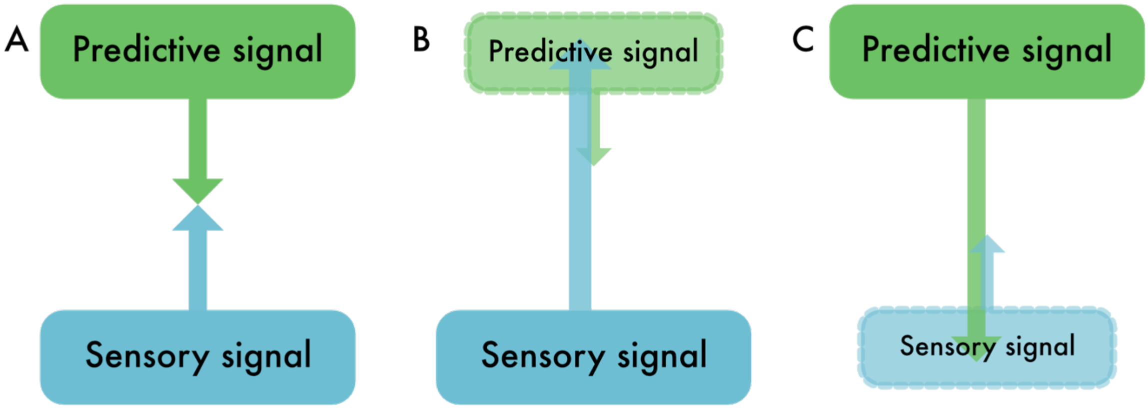


Figure 5 Schematic model of Bayesian integration approach to understanding motor control. (A) According to such a framework, signal integration is determined by relatively weighting input based on confidence, or certainty. (B) Proposed explanations of Parkinsonian symptoms using this framework suggest weak predictive signals result in an overwhelming effect of sensory input, especially of task-irrelevant signals. (C) Our approach in this experiment deliberately reduced the certainty of the sensory signals with blindfold and gloves, making the task more challenging. This could be one explanation for both motor improvements in people

with Parkinson's disease in the PD-SAFEx programme and compensatory shifts toward increased predictive weighting in healthy older age. A somewhat similar approach to sensory input reduction in Chapter 3 did show signs of a positive rebound effect, but its validity as an approach to motor improvement remained untested.

4.3 Multiple memory systems perspective

In an infinitely complex world (even inside a lab with a simple wooden pegboard), we did not so much reduce sensory input as bias it toward different sources, probably without changing the search-for-cues difficulty. The sensory masking approach could still be effective in other populations though, as the PD-SAFEx programme shows. Crucially though, the benefits of biasing sensory input may depend on there being a pre-existing over-reliance on particular sources of sensory information. People with Parkinson's tend to demonstrate a heavy reliance on vision to guide movement, which may provide clearer information in many cases, and manifests in stooping posture during walking to guide the feet visually. In the context of heavy dependence on visual guidance (Abbruzzese & Berardelli, 2003; Sacrey et al., 2009), masking visual information may be a successful approach to increasing uncertainty, where masking typically-prioritised information may then increase the demand on searching for informative cues to prompt positive training effects.

As we demonstrated in this study, sensory conditions do affect immediate performance and also the strategy employed. While strategy was not a primary outcome measure in a study where we were principally interested in movement improvement, the strategy adjustments demonstrate the flexibility of the nervous system. As Packard & Goodman (2013) point out, different environments, or contexts, elicit different memory systems, which supports the notion of altering sensory conditions to target underused or damaged systems. Similarly, the sensory substitution principles of rehabilitation outlined by Bach-y-Rita (2004, 2005) illustrate how altering sensory conditions can help participants with brain damage to meaningfully engage with their environment. It is also worth noting the success of coaching practices in sports that, rather than providing prescriptive instructions, alter qualities of the environment to coax athletes into finding their own solutions (Gray, 2020; O'Connor, 2019; Woods et al., 2020). It is not so much about making the task significantly harder, as we have done here, but perhaps about enabling deeper engagement with the sensory surround.

4.4 Sensory attenuation and the compensation explanation for increases with age

Sensory attenuation is a phenomenon whereby an identical stimulus can evoke different neural responses depending on its context and origin (Saradjian, 2015) and therefore is a useful indicator of one's ability to attend contextual cues to guide movement and perception (Kearney & Brittain, 2021). Such an ability seems important to controlling movement in complex environments, and declines of sensory attenuation measures in disease (Macerollo et al., 2015; Shergill et al., 2005, 2015; Wolpe et al., 2018) suggest higher sensory attenuation would indeed indicate a healthy central nervous system and probably better movement and perception. However, findings of increased sensory attenuation in old age (Parthasharathy et al., 2021; Wolpe et al., 2016) complicate the matter as old age is not typically associated with better motor ability (Ward & Frackowiak, 2003). Wolpe and colleagues suggest sensory attenuation increases to compensate for worsened tactile sensitivity and at least in some human populations, the selective strengthening of the basal ganglia and prefrontal pathways associated with particular sensory attenuation measures (Wolpe et al., 2016, 2018) is believed to be part of a compensatory suite of changes in response to cognitive decline. Others have suggested sensory attenuation emerges with experience (Idei et al. 2021, Chambers et al., 2018), supported by the apparent absence of sensory attenuation in infants (Meyer & Hunnius, 2021) and findings of increased sensory attenuation but unimpaired proprioception in older adults (Parthasharathy et al., 2021).

Even if advanced motor ability is not associated with older adults, increased sensory attenuation seen in older adults may indicate an advanced adaptation to noisier sensory input to maintain proficient movement in healthy ageing in spite of reported decline in tactile sensitivity. In the present study, we considered the gloves as a simulation of this noisier sensory input and thus, we expected that if the compensation explanation was true, that we might find improved performance on Day 2 induced by the uncertainty training. Accordingly, sensory attenuation has been explained by a Bayesian integration framework that highlights increased prediction signal weighting when sensory signal is noisier (Bays et al., 2006; Brown et al., 2013; Wolpe et al., 2016). We found, however, a Day 2 similarity across training groups, and therefore do not support the idea that increased sensory attenuation occurs with age as a compensation for worsened tactile sensitivity; though neither can we rule out this explanation. The compensation explanation for increased sensory attenuation requires further investigation, along with a deeper exploration of how sensory attenuation measures might accompany motor skill improvements.

The only significant difference in test performance between the two groups occurred in the third non-vision towers task at the end of Day 1 (Figure 3). The sole test-performance difference could point to practice effects of the uncertainty group training blindfolded, much like practice conditions can exhibit context-specific benefits (Godden & Baddeley 1975; Jiang et al., 2005). However, this difference subsided at the start of the next day, in spite of context-specific benefits elsewhere being reported to endure multiple days (Jiang et al., 2005). The absence of an enduring difference in this case is perhaps because of the intermittent, albeit infrequent, exposure to blindfolded training for both groups, which will have provided the full-senses group with some minimal non-vision practice.

4.5 Limitations and openings

Pilot testing in preparation for this study suggested that the wearing of latex gloves did make the task slightly more difficult; however, here, we find comparable performance between gloved and gloveless conditions demonstrated by the similarity between the first day performance of the gloved uncertainty group and the second day performance of the full-senses group. In training, we would have expected the full-senses group, as a result of both practice effects and the absence of gloves, to perform noticeably better on Day 2 compared to the uncertainty group on Day 1. We aimed to achieve a subtle difference – rejecting more difficult alternative interventions, especially as tactile change was to be compounded by absence of vision – but the intervention may well have been too subtle!

While our findings offer insight into how the absence of vision affects pegboard performance, perhaps future studies attempting to emulate minor tactile disruption might consider more difficult interventions whilst instead keeping vision available. Here, however, it was important to complete training under non-vision conditions to avoid creating an over-reliance on vision, whilst we were still able to use intermittent tower tasks to track improvements in visually guided performance. There are suggestions that gloves impede tactile sensitivity of the fingers (Novak et al., 1999; Wilson et al., 1996), contrasted with findings pointing toward no difference with or without gloves (Fry et al., 2010; Thompson & Lambert, 1995). All studies mentioned here studied surgeons who could be particularly well adapted to gloved working, and Novak et al. (1999) suggest an adaptation period of up to 120 days to get used to a new double glove ensemble. In this experiment, we hoped the gloves would subtly affect the manipulation of smaller objects and the sensitivity to a smooth, flat, wooden board.

We do, in this study, highlight limitations to the models that utilise a Bayesian framework in their ability to inform means of movement improvement in a moderately complex task. Models such as optimal control theory have been crucial in bringing sensory consequences into the equation of movement generation which have previously been absent (Versteeg & Miller, 2022). Unsurprisingly, the simple yet powerful framework does not explain the full complexity of the central nervous system. The imbalance of prediction and sensory signals offers an appealingly simple way to explain dysfunctional movement, and even to explain temporary movement improvement induced by precise sensory cues, but without, by itself, offering a way to evoke adaptation and enhancement of the brain and thus how changes in uncertainty might translate to motor skill improvement.

Package it and sell it

“Ah, it’s the sugar making the fruit sweet”
So we separate it, package it, sell it.

“Ah, it’s the long thighs that make this athlete so fast”
So we separate look-a-likes from the crowd,
and find a way to profit.

“Ah, today was productive”
So I pick out one element I believe made it successful,
package it up, and try to repeat it.

As if I am a machine.

As if there was a single cause.

It’s not what we do, but how and why it’s done.
And the how and why take life-long journeys
to unpack.

Chapter 5

Conclusion: Context-dependent movement, task-relevant sensory filtering and approaches to Parkinson’s training

Context-dependent movement

A recurring conclusion throughout this thesis has been the importance of context in movement. The lines-on-the-floor effect, highlighted in the Introduction, reveal the role the environment can play in action. It also points to the inseparability of action and perception: neither exist without the other.

Linking research in Parkinson's disease to findings in sensory attenuation experiments, offered a way to reframe what was happening in these paradigms. The force-matching task can be made sense of in this way: the location of the hands provide context that contributes to the perception of force and guides the ongoing action of pressing. Chapter 2 reinforced this notion by using a visual illusion task where impact of contextual cues (Mach bands) were assessed via perception of panel contrast. Chapter 3 revealed a training effect through repeated exposure to a particular level of cue salience, showing the use of cues in training matters.

One unexpected finding was the lack of change in visual illusion strength in Parkinson's disease. As outlined in Chapter 1, basal ganglia dysfunction, which characterises Parkinson's, reduces the capacity to utilise useful cues to guide movement and perception. Even though the participants with Parkinson's did not change their medication to take part in the study, illusion strength was expected to correlate with estimated dopamine levels. As this was not the case, I suggested that the simplicity of the Cornsweet scene, and the obviousness of the contextual cues (Mach bands) was still comfortably within the capabilities of a depleted basal ganglia system. Thus, the dual functions of the basal ganglia highlighted in Chapter 1 – task-relevant filtering and then contextual cue integration – point to the importance of considering task set-up.

Figure 1 in Chapter 1 represents the prominent way researchers have considered motor control for the past two decades. One of the key aspects of this model is that the interaction begins with a motor command, moving outward into the world. From the motor command, an efference copy is used to predict upcoming feedback to overcome noise and delay in the system, and is then compared to actual sensory feedback. The comparison of the two signals gives rise to the final sensation. Bayesian integration is often used in optimal control and active inference accounts to model how this final sensation arises from the integration of predictive and sensory signals. The key here is that the integration of the two signals is probabilistic – the precision, certainty or clarity of the signal decides how influential it will be in the resulting conflation of these two signals, the posterior. Models usefully exclude certain complexities to present an understandable and useable image and this model of motor control has been useful. However, two of its key characteristics – a motor command as the starting point, and signal integration based on signal quality – relegates the insightful roles of context-dependence and task-relevance in movement.

Task-relevant sensory filtering

Where cognition, action and perception have traditionally been siloed, sensory attenuation research usefully points to a link between action and perception. However, the link that has been made is limited and restricted in scope. As highlighted in Chapter 1, many researchers have argued that motor activity uniformly suppresses input, while others have argued motor activity facilitates input. To reconcile these findings, I referred to the idea of task-relevance. Formulated during the pilot study described in the Introduction, 'task-relevance' differentiates between sensory inputs depending on their importance to task completion. Thus, even though motor involvement may appear similar, two tasks can elicit unique sensations from the same stimulus. This adds a layer of complexity to the sensorimotor integration explanations offered to explain sensory attenuation measures such as the force-matching task. The importance of task-relevance in sensorimotor processing is one conclusion of this thesis.

Another conclusion is that current theories of motor control do not fully account for this single extra layer of complexity. Optimal control theory (OCT) and active inference (AI) posit that signals are integrated probabilistically. This means the signals will be weighted based on the quality of the signal themselves, based on a pre-existing formula that establishes relative weighting based on signal quality (or certainty or precision). However, the notion of task-relevant sensory filtering highlights the potential for other influences on how signals might be weighted.

Rather than precision being a sensory evaluation (i.e. signal weighting based on signal quality), precision comes to depend on its relation to factors external to that signal. Here, the signal's relation to the task affects its integration (and perception), not just its quality.

So, we can imagine signals relating to the task arriving from the prefrontal cortex, signals relating to limb position coming from the limb and the parietal cortex, and signals from a stimulus triggered by that limb. These signals congregate in the basal ganglia, as the area of interest here. The weighting of each signal is not just determined by how loud each signal is shouting, but by its relevance to the other congregating signals.

This suggestion is a key departure from the OCT and AI frameworks and is a key implication of this thesis. Task-relevance is surely a simplification of what is going on in the brain, but it works here by adding a layer of complexity to rethink sensorimotor processing. Furthermore, it has been invaluable to better understand the basal ganglia and neurological rehabilitation techniques.

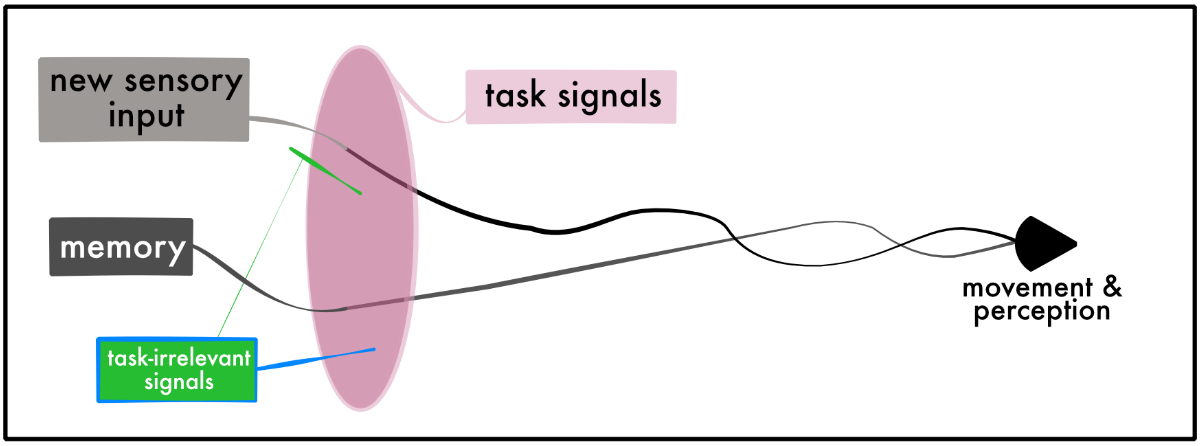


Figure 2 An alternative view of sensorimotor integration. Typically, a sensory and a motor signal, a prediction and sensory input, a prior and likelihood, are thought to be integrated based on the precision of the signal itself, its content. What I suggest here is that the influence of a signal in movement and perception is based on a signal's relation to something else. Task-relevance is one way to consider this: many signals will be shared between an organism and its environment, but the task-relevant signals will be perceived more intensely and the task-irrelevant less so, an important ability for effective movement and navigation (Kearney & Brittain, 2021). The signals that pass through this filter – based on their relation to the task and not necessarily its content – combine and can be integrated into ongoing movement and perception. This framework crucially makes sense of the disparate sensory attenuation literature pointed to in Chapter 1 and opens towards a rich discussion on approaches to effective rehabilitation.

Approaches to Parkinson's training

Approaches to training in the context of Parkinson's disease take a variety of forms. This thesis has sought to make sense of these. Chapter 1 reviewed literature relating to sensory attenuation, a phenomenon revealing aspects of sensorimotor integration processes. Using psychophysics experiments, Chapters 2 and 3 demonstrated both the influence of context in perception, and the trainability of perception through manipulating context. Then, Chapter 4 described a training protocol implemented in a more complex pegboard task. Manipulating the availability of different sensory information guided participants' strategy uptake (a form of improvisation), but skill levels remained comparable across groups. Finally, Chapter 5 linked work across different disciplines to reflect on the field of neuroscience. Drawing attention to often unnamed influences can help to avoid pitfalls in our work.

One such pitfall in rehabilitation is selecting one thing that seems to work and attempting to replicate it on a mass scale, irrespective of context. What I hope to have achieved here – for myself and the reader – is an attentiveness to the overlooked, and often ordinary, contributors to effective movement. The PD-SAFEx programme, in which participants exercise in low-light conditions, may work by demanding a shift away from sources of information that have become overly relied upon. The forced-exercise cycling protocols implemented by Ridgel and colleagues may work by challenging the participant to integrate complex sensory information into their movement. However, as Parkinson's disease symptoms reveal, emotional, sensory and cognitive context all matter. So how about the community context created in these spaces: the presence of others, the support and the responsibility?

Recent approaches such as dance classes (Bek et al., 2020) and rock climbing (Langer et al., 2021) also appear viable and effective (and probably great for many to be a part of, regardless of a particular diagnosis). Yet pinpointing one component of the training regime that promotes learning and neural restoration is not straightforward. This is in some ways the whole point. I have posited that the basal ganglia contribute to movement by filtering complex sensory environments by drawing on and combining sources from elsewhere in the brain and across the environment. Thus, the more aspects of an experience that can be connected to the movement, the more the basal ganglia enters the frame.

However, once such aspects become a standard part of initiating movement, basal ganglia involvement may diminish. Part of the function of the basal ganglia appears to the search for otherwise subtle cues, and the group of nuclei is thus active in obscure tasks like timekeeping in the absence of clear time information (see section 2.5 in Chapter 1). Similarly, the cerebellum garners more attention in sensory attenuation paradigms that use a simple sensory trigger to initiate movement (see section 3.1 in Chapter 1). Tasks requiring "self-generated movement" instead highlight basal ganglia involvement. Thus, a search is needed to involve the basal ganglia.

As the experiments in Chapter 3 demonstrate, adaptation occurs in response to sensory manipulations. A fixed approach may therefore not achieve the desired effects upon reuse. As suggested in the brief explication of neuroplasticity in Chapter 5, the notion of receiving form and giving form highlights the interplay of the roles of agent and environment. This dynamic creates an endless stream of novelty and improvisation. Future investigations could explore this further, particularly considering training approaches in living environments that grow and change with interaction, overcoming any habituation effects. Participants would then be required to find ways to be present and explore the new (but familiar).

Epilogue

Neuroscience, theology and who we are

1. Introduction

What follows is an exploration of place, environment and context to further understand the human brain. This thesis has delved into the principles of movement restoration, specifically in the context of Parkinson's disease. This has, however, prompted wider questions around what constitutes movement and how the brain is conceptualised. It has very much been an interdisciplinary approach to make sense of other researchers' neuroscientific findings, and those of the experiments I have led.

Regarding the significance of these findings for movement and for Parkinson's training, wider questions of the brain and of movement have involved inquiries into identity formation which relate to societal issues of racism and climate breakdown. These appear to evoke a consensus of condemnation with a shortage of action that goes far enough to grasp the issues at the roots. Both crises concern how we see ourselves: as humans in relation to each other and humans in relation to the rest of the world. As an endeavour to understand the biology of the human mind, neuroscience is a discipline where these issues can be seen and perpetuated. Could it also be a site for rethinking who we are and providing tools to help overcome these issues?

2. Isolated cognition

> We changed the world from the fifteenth century onwards; while Christian doctrines of creation did not account for that change, they were in fact crucial to that change. Like an essential enzyme that catalyzes change at an organic level, Christians reframed the world and bodies and in so doing reframed thought itself as an act upon the world rather than an act of the world. (p.389, Jennings, 2019)

> The deep-seated assumption that mind is an internal property of human individuals that can be studied in isolation from their involvement with one another or with the wider environment continues to reverberate within the field of psychology. (p.236, Tim Ingold, *The Perception of the Environment*).

Anderson, Richardson & Chemero (2012) posit that the cognitive sciences have often provided the forum for the examination of cognitive faculties, but treated in relative isolation. Studies about attention, for instance, fail to also be about memory and emotion. Further, cognition itself has largely been considered to be localised in the brain alone, immune from bodily and environmental processes. There are findings that suggest that the brain-body-environment interdependencies of motor control on language and bodily warmth (temperature) impinge directly on interpersonal judgment; Anderson and colleagues point out that the exercise of cognitive faculties cannot be localised to an area within the brain, or to the brain, alone.

The importance of context and environment on cognition can be argued further. In Godden & Baddeley's (1975) classic study, scuba divers demonstrated better memory for words learnt and recalled in the same location than in separate sites (underwater or on land). The lines-on-the-floor effect in Parkinson's (Morris et al., 1994, 1996; Beck et al., 2015) also demonstrates the significance of environment in movement. Despite these findings, the recent currents of research into the interrelationships of behaviour, bodily form and environment in cognition "questions some of the most deeply held beliefs in the cognitive sciences" (Anderson et al., 2012, p.718). How have beliefs in both an insulated cognition and in isolated cognitive faculties taken such deep root?

3. Two opposing world views

> The point that matters here is that they are modern versions of a powerful but not specially rational vision, derived from the atomists, of the natural worlds as somehow radically foreign to us and of ourselves as radically foreign to that world – a vision that is still influential in our thinking today. (p.35, Mary Midgley, *Science and Poetry*)

In *God of the Oppressed*, the theologian James Cone describes aspects of his life that informed him: his upbringing, his church, the cultural context and communities. He does this, he says, because most theologians will instead tell you about themselves through books they have read rather than via the social context which shapes their ideas. Cone is considered the founding father of a theological tradition known as Black Liberation Theology, which takes seriously the lived experience of black people as a starting point for framing questions about concerning divinity. Such an approach is a significant challenge to the assumption of knowledge being achieved abstractly through reason alone, a legacy of Descartes' mind-body dualism. Cone's work demonstrates that mainstream theology was itself a form of perspectival theology, stemming from often unnamed frameworks of whiteness, Western modernity and colonial power. Subsequent work in this field, such as that by Emilie Townes and Anthony Reddie consolidates the embodiment principles highlighted by Anderson et al. Knowledge is revealed to be inseparable from lived experience.

According to theologian Willie James Jennings, two opposing world views are evident when considering the scholarship of Christian intellectuals like José De Acosta who lived and worked in colonial Peru. De Acosta deemed Andeans in Peru to be idolatrous for their recognition the animate nature and possibilities for communication of plants and animals. His colonialist view of life was instead one in which:

> …the world sits silently, passively waiting to give itself up and give up what lies within it. Only in its surrender and in its role as divinely given gift can its life be honored by bringing that life to maturity through occupation, examination, manipulation, fragmentation and extraction. (p.397, Jennings, 2019)

This opposes a vision of life where the world is instead:

> …never silent, never passive, but always already actuality, speaking in and through creatures, including the human creature, and making intelligible life itself as both resource and source. Life in this regard cannot be conceived abstracted or extracted from land an animal, because that is simply not life. (p.397, Jennings, 2019)

My argument here is that neuroscience still displays the 'potentiality' world view, where humans are separate from the world, and the world's worth and life finds its meaning in the context of human consumption. As I discuss in the sections on motor control theories and neuroplasticity, a view of a passive world still shapes how we conceptualise the brain. This is important when considering questions as to why cognition is thought to be insulated from the world. However, I do not wrestle with the distortions in the cognitive sciences simply for the attainment of a more accurate conceptualisation of the brain, but instead to demonstrate that neuroscience is a site that perpetuates both the 'potentiality' and 'actuality' visions of life.

4. The role of neuroscience in societal inequality

> The vagaries of power affect the lives of each and every one of us, regardless of our awareness of this. Yet these power structures in which we are forever caught are, in themselves, human-made. While they may feel, much of the time, anonymous and institutional, they are composed of complex human relationships, and can only be transformed, unmade, and remade, by

> corporate retellings of collective stories. (p.50, Alison Webster, *You Are Mine*).

> It is remarkably hard for us to break out of this circle of increasing needs because our age is remarkably preoccupied with the vision of continually improving means rather than saving ourselves trouble by reflecting on ends. (p.36, Mary Midgley, *Science and Poetry*).

Recent critiques of neuroscience by Victoria Pitts-Taylor and Oliver Rollins' highlight the risks of perpetuating cycles of inequality by disregarding the social, environmental and cultural complexities that interact with the neurobiological factors we give most attention to (Pitts-Taylor, 2016; Rollins, 2021a). Historically, the shortcomings of neuroscience are perhaps easier to pinpoint. Francis Gall's reduction of cognitive faculties into specific, clearly demarcated areas of the brain reflects both aspects of the argument by Anderson and colleagues' (2012): the division of different cognitive faculties, and the reduction of cognition to the brain alone. With race being an issue of identity, and racism being fuelled through geographical enclosures and the reduction of human identity to that which can wholly be carried on skin-bounded selves (Jennings, 2010, p.226), neuroscience plays a bigger role in the struggle for justice than simply needing to account for race as a demographic factor (Rollins, 2021a, p.108-110).

As long as neuroscience predominantly subscribes to a view of the world as largely silent, passive, waiting to be used and extracted, we will continue to tell stories of human identity enclosed neatly inside the body – even inside the skull – and thus continue to perpetuate cycles of inequality. For instance, Rollins (2021a) examines the neuroscientific inquiries into what makes some individuals violent and others not. In attempting to establish the neurobiological basis for violence, within a vision of a more just and safe society, Rollins argues that the current framework that explains violence primarily focuses on the individual and their brain. Part of the problem is not "empirical ineptness, but a clue that certain social meanings, complexities and lives are being meticulously overlooked and erased from these biosocial equations of life" (p.155). Inspired by Wittgenstein's 'forms of life' concept and Crenshaw's concept of intersectionality, Bryson writes that people are not bodies but instead are lives (p.219, 2021). Such an argument demands a far more complex explanation than just "their brain made them do it". Irrespective of the depth and detail of study into matters concerning neurons, synapses and neurotransmitters, this demand rather asks us to consider the connectedness of the brain to the landscapes in which it is situated.

Similarly, Victoria Pitts-Taylor's (2016) critique of inquiries into how poverty affects the brain highlights not only the potential for targeted investment, but also the risk of divestment in programmes that address poverty itself. She describes one programme which provides "brain training" for participants, one that targets particular parts of the brain previously linked to the experience of poverty. Such an approach has a dual outcome: it aims to improve the life chances of participants, but also solidifies a particular phenotype of poverty, which dulls our attention to both the effects of poverty beyond the brain and the forces fuelling poverty and inequality. Neurobiology is an interesting part of these equations, but it is not the whole equation. Also overlooked is the relational aspect of similar interventions: the presence and attention of another person delivering an intervention (O'Connor & Nagel, 2017), and the reality of a brain that is not just "trained" with the puzzle-type tasks we associate with cognition and mind. A single model will not achieve all epistemic ends (Potochnik, 2022); the failure to recognise the obscuring of environmental, social and cultural complexities is symptomatic of a neuroscience that attempts to consider the mind and the brain in isolation, rather than embedded in a relational world.

In clinical neurological research, representation is important. It offers routes which improve access to treatments in marginalised communities and better tailor healthcare activity (Ojukwu et al., 2021). It is important to note the often unscrutinised WEIRDness (western, educated, industrialised, rich and democratic) of research populations (Henrich et al., 2010), which may go unquestioned because of the invisible normativity of whiteness as the reference point (Dyer, 2017, p.3; hooks, 2009, p.93, Reddie, 2009). Two further arguments must be made here.

First, there already exists a general consensus pushing for better inclusion of groups both under-represented in neurological research, and over-represented in health statistics. As Rollins (2021a) notes, organisations such as the National Institute for Health have abandoned a "one size fits all" model and require racial and ethnicity information in more representational samples. This does not result, however, in the destructive dynamics of race being discussed beyond it simply being a demographic variable to control for (Rollins, 2021a, p.108-110, 2021b).

Secondly, emphasising the addition of under-represented groups into the same clinical trials within the same paradigm of healthcare negates a double opportunity: firstly to both reimagine our approaches to health, and secondly to question the role of racialised existence and hyper-separated states of humans from the natural world in modern diseases, as we continue to treat the brain as the sole source of brain disorders (Fried, 2022; Hari, 2020; see also Ahsan, 2022).

5. Theories of motor control and sensory attenuation

The great philosophical question goes: if a tree falls in a forest and no one is

> around to hear, does it make a sound? But this is a troubling question, exalting one kind of being above all others. What then of the ears of snakes, or wood frogs, or mice, or bugs? Do they not count? What then of grass, of stone of earth? Does their witness not matter? If a man flies in Jamaica, and only the poor will admit to seeing it, has he still flown? […] Always – always – there are witnesses. (Kei Miller, *Augustown*)

One of my main arguments so far is that sensory attenuation can be understood as context-dependent processing, not necessarily the cancellation of sensory input by motor commands. Predictive models of motor control that underpin the cancellation accounts do not readily explain the variety of effective rehabilitation approaches. The lines-on-the-floor effect also revealed a deeper involvement of the environment in movement, one not captured by motor control theories which begin the story of movement with an outward (or downward) projection of predictive signals. These accounts paint a picture of an optional, rather than unceasing, interaction with the environment. They play down the role of context in eliciting a predictive signal in the first place, and thus resonate more with a ‘potentiality’ world view than an ‘actuality’ perspective.

Classic nerve conduction experiments reduced movement to reflex (Bennett, 1999), so recent motor control theories have successfully imagined a more complex interaction of agent and environment, but they still sit inside an imagination limited by the ‘potentiality’ world view. Falandays (2021) draws on Eastern philosophies to challenge the predominantly Western ‘substance ontology’, where everything can be considered as *things* in isolation, as opposed to processes with ‘fuzzy’ boundaries between entities. Falandays proposes that nothing exists without interaction, and the brain is in perpetual exchange with its environment as a complex open system far-from-equilibrium. Falandays’ and Raja et al.’s, (2021) critiques of Karl Friston’s free-energy principle – the prominent theory of the brain and movement (and everything, see Sun & Firestone, 2020) – focus on the sharp and arbitrary delineation between agent and environment. Such delineation draws on this same atomistic tradition in the sciences that Mary Midgley points out to us: the belief that we can best study things in isolation.

A favourite anecdote: even the best basketball players in the world do not make one hundred percent of their free-throws. Why not? A free-throw is taken from behind the same line that is the same distance from a rim that is the same size and same height off the ground. The ball is the same size, weight and is inflated to the same air pressure; each aspect is controlled as tightly as possible by professional leagues in the interests of sporting integrity. An alternative question might be to ask how would anyone be able to make one hundred percent of their free throws? Certain variables can be highlighted from one attempt to the next; the crowd noise could be different, muscle fatigue could have increased, game context (task information) could be new, attention might be drawn toward another aspect in an infinitely complex scene: the ball, the floor, heart rate, perspiration, interaction with the referee, a painful right wrist… The longest stretches of made free-throws are perhaps achieved by the skilful navigation of these variables, an attentiveness to the world symptomatic of a self who recognises their inseparable part of it, and of course lots of practice.

As highlighted in Chapter 1 and demonstrated in subsequent chapters, altering characteristics of the environment can shape movement in the present but also evoke beneficial adaptations and improvements. PD-SAFEx (Sage & Almeida, 2009, 2010) and forced-exercise cycling programmes (Ridgel et al., 2009, 2015; Ridgel & Ault, 2019) succeed in long-term symptom alleviation by focusing on tasks and qualities of the sensory environment, and not a reductive attempt to manipulate limb trajectory in isolation. If the nature of place is important in prompting positive neural adaptation, the question also arises: what role does the nature of place and environment have on worsening neural capacity in the first place? This question has not been thoroughly explored in the case of Parkinson's disease. There have been some investigations: tentative links between Parkinson's and pesticides and similar pollutants have been articulated (Ball et al., 2019; Hong et al., 2014; Jayaraj et al., 2016; Meredith & Totterdell, 2010), with varied prevalence according to geographic region (Gordon et al., 2012; Rusiecki et al., 2008; Wermuth et al., 2002). Additionally nutritional risk factors and buffers have been reviewed (Bianchi et al., 2022). Yet there is need to both tie these findings together and not leave out of the discussion how risk factors have become prevalent and sometimes unavoidable. We are not so good, it seems, at looking at cause in more than one place at a time. As Fried (2022) argues, medical scientists are prone to mistaking mental illnesses for the diagnostic criteria they are classified by, and we study isolated parts of an illness in the brain rather than the illness as a complex system of interacting biological and social processes.

6. The intriguing case of neuroplasticity

> This 'whole person' of whom we have been talking is not, then, a solitary self-sufficient unit. It belongs essentially within a larger whole, indeed within an interlocking pattern by a great range of such wholes. These wider systems are not an alien interference with its identity. They are its home, its native climate. The soil from which is grows, the atmosphere… (p.14, Mary Midgeley, *Science and Poetry*)

Neuroplasticity – the ability of the brain to change and adapt to the environment – is increasingly recognised as a key characteristic of the brain (Füchs & Flugge, 2014). The brain is far from fixed, but is rather adaptive and responsive to a range of environmental conditions: it is able to grow new neurons (neurogenesis), and alter connectivity between neuronal populations depending on situational demands and nourishing factors such exercise, sleep and proper nutrition (Shaffer, 2016). According to Papadopoulos (2011), plasticity is the possibility of recombining brain-body matter which draws focus to the relations between brain, body and environment. The brain may no longer be understood as a "self-contained, decontextualized entity" (p.432). Plasticity as a concept thus presents an image of a brain connected to the conditions of the world.

Neuroplasticity was first described in neuroscience by Santiago Ramón y Cajal and William James in the late 1800s (Berlucchi & Buchtel, 2009). However, it has only in the last several decades become widely accepted and discussed by neuroscientists. There has been a fierce debate about the existence of neuronal plasticity (the non-pathological change in neuronal structure in adult brains). There are many who have rejected the coherence of plasticity. As one psychologist questioned, "Why does the protoplasm stretch towards one neighbouring neuron when the organism happens to be in one situation, towards another neuron when the organism is in another situation? General silence on the part of the neurologists" (Berlucchi & Buchtel, 2009, p.315). Situation and context were overlooked as playing any meaningful role in the neuron's behaviour. The confusion around the seemingly erratic characteristics of neuronal response led to further questions as to who or what agent controlled such changes, as it was understood that situational factors could not possibly play active roles.

More recently it has been recognised that neurons do not respond uniformly to one type of stimulation, where response is also mediated by factors such as expectation, instruction and time of day (Sanes & Lichtman, 1999). Plasticity reveals living systems situated in contexts that explain how experiences come to be variegated. This powerful idea, described by Malabou (2008) as the ability to give form and receive form, has the potential to resist reductionism and determinism attributed to the neurosciences (Pitts-Taylor, 2016, p.122-123). Even though we are more than just our brains, plasticity conveys how we exist in the world: are we insulated and distant with optional interactions, or never existing without interaction and learning? Yet the prevalence of plasticity has only recently been confirmed in the adult brain (Eriksson et al., 1998). There is also a risk that plasticity comes to be misconstrued as a demand for a docile flexibility and a desire for endless self-enhancement (Malabou, 2008; Papadopoulos, 2011). That this concept did not find traction until recently is symptomatic of a neuroscience built on the 'potentiality' world view, but the notion of plasticity challenges how we see the world, and also how we see ourselves.

7. Conclusion

There is plenty of recognition within neuroscience of a more embodied and embedded cognition to challenge notions of an isolated cognition. Borrowing first from Black Liberation Theology, I linked Cone's contextual theology work to neuroscience research that recognises an embedded and plastic brain. What Cone's work did was highlight the perspective and context of mainstream theology that was otherwise considered 'correct', positionless and immune from social context. I thus subsequently borrowed from Jennings' work that points to the legacies of colonialism and mission Christianity as part of the context that uninvitingly shapes our world view.

Neuroscience exhibits strands of work that resonate with both the 'potentiality' and the 'actuality' perspectives. Using critiques from Pitts-Taylor and Rollins, I argued that the work we do in neuroscience plays out and intersects with societal issues. Research programmes affect societal inequalities, and the theories we form have traction in debates concerning identity. Neuroplasticity offers an interesting and potentially fruitful account of the human brain. Neuroplasticity is also a story to tell ourselves that nurtures loving and not exploitative attitudes, but its history reveals the skepticism and ignorance such stories can face. What other stories are we telling in neuroscience, where do they come from and what difference are they making?

Fin

Supplementary material

Supplementary Information 1 The Activities of Daily Living questionnaire in the experiments described in Chapters 2 and 3. For each statement below, participants selected "Never done", "Stopped doing" or "Still do", having been given the instruction: "For each activity below, please choose the response that best indicates your engagement with the activity".

1) Visit other people's houses
2) Receive visitors at your house
3) Go to religious building(s) for rituals or social activities connected with religion
4) Take part in social gatherings
5) Take part in cultural events such as concerts, shows, exhibitions, theatre plays or movies at the cinema
6) Drive a car
7) Take short trips out of town
8) Take longer trips out of town or out of the country
9) Do voluntary work
10) Do paid work
11) Sit on boards or committees of associations, clubs, schools, unions, cooperatives, or community centres, or engage in political activities
12) Take part in refresher courses or any type of university course
13) Participate in community centres or groups specifically for the elderly

Supplementary Table 1 Model comparisons for Experiment 1 in Chapter 3.

	DF	**AIC**	**BIC**	**LogLikelihood**	**Deviance**	**LRTstat**	**Change in DF**	**p-value**
Full model: incorrect ~ 1 + block*group + (1 ǀ ID) + (1 ǀ bl)	18	-3422.5	-3321.5	1729.3	-3458.5	-	-	-
Full model vs **null** (incorrect ~ 1)	2	-1463.7	-1452.5	733.87	-1467.7	1990.8	16	0
Full model vs **reduced model 1** incorrect ~ 1 + group + (1 ǀ ID) + (1 ǀ bl)	6	-2456.8	-2422.8	1234.2	-2468.5	990.07	12	0

Reduced model 3 (incorrect ~ 1 + block + group + (1 | ID) + (1 | bl)) vs **reduced model 1** (incorrect ~ 1 + group + (1 | ID) + (1 | bl))	6	as above	as above	as above	as above	41.82	4	<.001
Full model vs **reduced model 2** incorrect ~ 1 + block + (1 | ID) + (1 | bl)	8	-2442.8	-2397.9	1229.4	-2458.8	999.73	10	0
Reduced model 3 (incorrect ~ 1 + block + group + (1 | ID) + (1 | bl)) vs **reduced model 2** (incorrect ~ 1 + block + (1 | ID) + (1 | bl))	8	as above	as above	as above	as above	51.481	2	<.001
Full model vs **reduced model 3** incorrect ~ 1 + block + group + (1 | ID) + (1 | bl)	10	-2490.3	-2434.1	1255.1	-2510.3	948.25	8	0
Full model vs **reduced model 4** incorrect ~ 1 + block*group + (1 | ID)	17	-3387.4	-3291.9	1710.7	-3421.4	37.172	1	<.001
Full model vs **reduced model 5** incorrect ~ 1 + block*group + (1 | bl)	17	-3162.1	-3066.6	1598	-3196.1	262.47	1	0
Full model vs **alternative model 1** incorrect ~ 1 + block*group + (1 | ID) + (1 | bl) + (1 | RT)	19	-3420.5	-3313.9	1729.3	-3488.5	0.00000019179	-1	NaN

Supplementary Table 2 Model comparisons for Experiment 2 in Chapter 3.

	DF	**AIC**	**BIC**	**LogLikelihood**	**Deviance**	**LRTstat**	**Change in DF**	**p-value**
Full model: incorrect ~ group + block + (group:block) + (1 | ID) + (1 | bl:group:block)	23	-3838.9	-3705.3	1942.5	-3884.9	-	-	-

Full model vs **null** (incorrect ~ 1)	2	-1787	-1775.3	895.48	-1791	2068.8	22	0
Starting model (incorrect ~ 1 + group*block + 1 | ID) vs **reduced model 3** incorrect ~ 1 + group + block + (1 | ID)	10	-3766.3	-3638.5	1905.2	-3114.9	695.44	12	0
Reduced model 3 (incorrect ~ 1 + group + block + (1 | ID)) vs **reduced model 1** (incorrect ~ 1 + group + (1 | ID) + (1 | bl))	6	-3097	-3062.1	1554.5	-3109	5.901	4	0.207
Reduced model 3 (incorrect ~ 1 + group + block + (1 | ID)) vs **reduced model 2** (incorrect ~ 1 + block + (1 | ID))	7	-3077.4	-3036.7	1545.7	-3091.4	23.486	3	<.001
Starting model (incorrect ~ 1 + group*block + 1 | ID) vs **alternative model 1** incorrect ~ 1 + block*group + (1 | ID) + (1 | bl)	23	-3813.8	-3680.1	1929.9	-3859.8	49.433	1	<.001
Alternative model 2 (incorrect ~ 1 + group*block + (1 | ID) + (1 | RT)) vs starting model (incorrect ~ 1 + group*block + 1 | ID)	23	-3766.3	-3638.5	1905.2	-3810.3	0.0000004031	1	NaN
Alternative model 3 (incorrect ~ 1 + group*block + (1 | ID) + (1 | age)) vs starting model (incorrect ~ 1 + group*block + 1 | ID)	23	-3764.7	-3631.1	1905.4	-3810.7	0.3786	1	0.53835

Alternative model 1 (incorrect ~ 1 + block*group + (1 | ID) + (1 | bl)) vs **alternative model 6** incorrect ~ group + block + (group:block) + (1 | ID) + (1 | bl:group:block)	23	-3838.9	-3705.3	1942.5	-3884.9	25.147	0	0

Supplementary Table 3 Model comparisons for Experiment 3 in Chapter 3.

	DF	AIC	BIC	LogLikelihood	Deviance	LRTstat	Change in DF	p-value
Full model: incorrect ~ group + block + (group:block) + (1 | ID) + (1 | bl:group:block) + (1 | bl) + (1 | group) + (1 | block)	21	-3205.7	-3088.7	1623.8	-3247.7	-	-	-
Full model vs **null** (incorrect ~ 1)	2	-768.52	-757.39	386.26	-772.52	2475.1	19	0
Starting model (incorrect ~ 1 + group*block + (1 | ID)) vs **reduced model 3** incorrect ~ 1 + group + block + (1 | ID)	9	-1909.9	-1859.7	963.93	-1927.9	1069.3	8	0
Reduced model 3 (incorrect ~ 1 + group + block + (1 | ID)) vs **reduced model 1** (incorrect ~ 1 + group + (1 | ID) + (1 | bl))	5	-1850	-1822.1	929.99	-1860	67.866	4	<.001
Reduced model 3 (incorrect ~ 1 + group + block + (1 | ID)) vs **reduced model 2** (incorrect ~ 1 + block + (1 | ID))	7	-1852.7	-1813.8	933.37	-1866.7	61.111	2	<.001
Starting model (incorrect ~ 1 + group*block + (1 | ID)) vs full model	17	-2963.2	-2868.5	1498.6	-2997.2	250.47	4	0

Starting model (incorrect ~ 1 + group*block + 1 | ID) vs **alternative model 1** incorrect ~ 1 + block*group + (1 | ID) + (1 | bl)	18	-2977.5	-2877.3	1506.8	-3013.5	16.341	1	<.001
Alternative model 2 (incorrect ~ 1 + group*block + (1 | ID) + (1 | age)) vs starting model (incorrect ~ 1 + group*block + 1 | ID)	18	-2961.2	-2861	1498.6	-2997.2	<.001	-1	NaN
Alternative model 3 (incorrect ~ 1 + group*block + (1 | ID) + (1 | keyTap)) vs starting model (incorrect ~ 1 + group*block + 1 | ID)	18	-2961.2	-2861	1498.6	-2997.2	<.001	-1	NaN
Alternative model 4 (incorrect ~ 1 + group*block + (1 | ID) + (1 | ADL)) vs starting model (incorrect ~ 1 + group*block + 1 | ID)	18	-2961.2	-2861	1498.6	-2997.2	<.001	-1	NaN
Alternative model 5 (incorrect ~ 1 + group*block + (1 | ID) + (1 | RT)) vs starting model (incorrect ~ 1 + group*block + 1 | ID)	18	-2961.2	-2861	1498.6	-2997.2	<.001	-1	NaN
Alternative model 1 (incorrect ~ 1 + block*group + (1 | ID) + (1 | bl)) vs **alternative model 9** incorrect ~ group + block + (group:block) + (1 | ID) + (1 | bl:group:block) + (1 | bl) + (1 | group) + (1 | block)	21	-3205.7	-3088.7	1623.8	-3247.7	234.13	3	0

Supplementary Table 4 Model comparisons for Experiment 4 in Chapter 3.

	DF	**AIC**	**BIC**	**LogLikelihood**	**Deviance**	**LRTstat**	**Change in DF**	**p-value**
Full model: incorrect ~ group + block + (group:block) + (1 | ID) + (1 | bl:group:block) + (1 | bl) + (1 | group) + (1 | block)	21	-1220.6	-1123.1	631.32	-1262.6	-	-	-
Full model vs **null** (incorrect ~ 1)	2	-252.23	-242.94	128.12	-256.23	1006.4	19	0
Starting model (incorrect ~ 1 + group*block + (1 | ID)) vs **reduced model 3** incorrect ~ 1 + group + block + (1 | ID)	9	-727.42	-685.6	372.71	-745.42	448.78	8	0
Reduced model 3 (incorrect ~ 1 + group + block + (1 | ID)) vs **reduced model 1** (incorrect ~ 1 + group + (1 | ID) + (1 | bl))	5	-727.42	-685.6	372.71	-716.01	29.406	4	<.001
Reduced model 3 (incorrect ~ 1 + group + block + (1 | ID)) vs **reduced model 2** (incorrect ~ 1 + block + (1 | ID))	7	-716.09	-683.56	365.04	-730.09	15.332	2	<.001
Starting model (incorrect ~ 1 + group*block + (1 | ID)) vs full model	17	-1160.2	-1081.2	597.1	-1194.2	68.447	4	<.001
Starting model (incorrect ~ 1 + group*block + 1 | ID) vs **alternative model 1** incorrect ~ 1 + block*group + (1 | ID) + (1 | bl)	18	-1165.7	-1082	600.83	-1201.7	7.4584	1	0.006
Alternative model 2 (incorrect ~ 1 + group*block + (1 | ID) + (1 | timeSinceDiagnosis)) vs starting model (incorrect ~ 1 + group*block + 1 | ID)	18	-1158.2	-1074.6	597.1	-1194.2	0.012	1	0.913
Alternative model 3 (incorrect ~ 1 + group*block + (1 | ID) + (1 | keyTap)) vs starting model (incorrect ~ 1 + group*block + 1 | ID)	18	-1158.2	-1074.6	597.1	-1194.2	<.001	-1	NaN

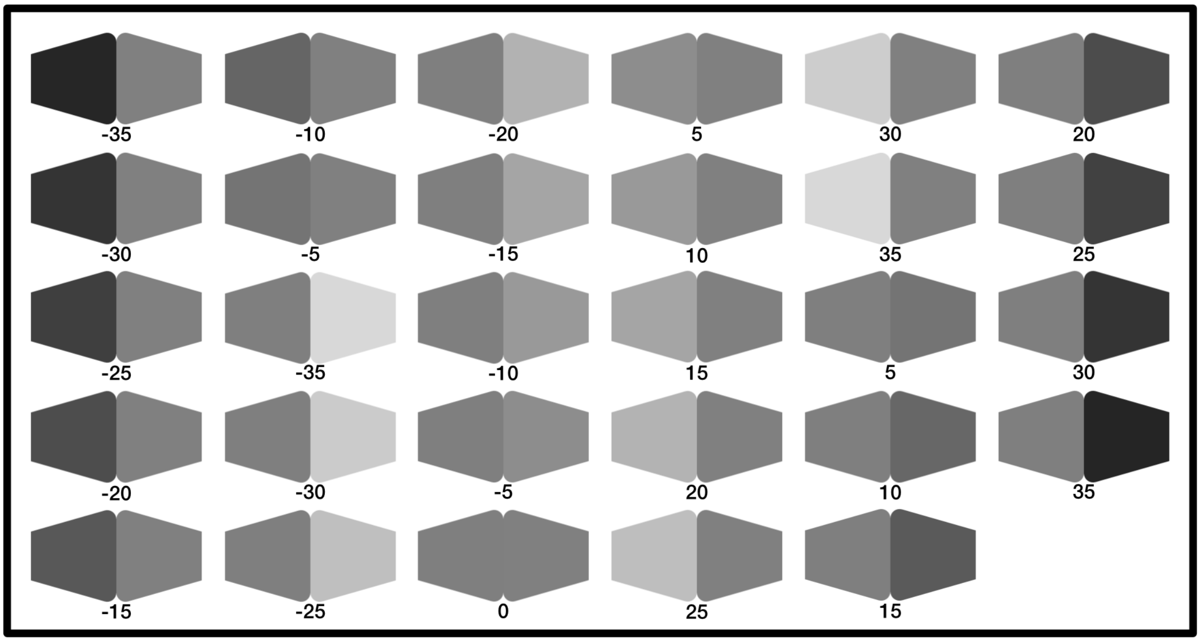
Alternative model 4 (incorrect ~ 1 + group*block + (1 ǀ ID) + (1 ǀ ADL)) vs starting model (incorrect ~ 1 + group*block + 1 ǀ ID)	18	-1158.2	-1074.6	597.1	-1194.2	<.001	-1	NaN
Alternative model 5 (incorrect ~ 1 + group*block + (1 ǀ ID) + (1 ǀ RT)) vs starting model (incorrect ~ 1 + group*block + 1 ǀ ID)	18	-1158.2	-1074.6	597.1	-1194.2	<.001	-1	NaN
Alternative model 6 (incorrect ~ 1 + group*block + (1 ǀ ID) + (1 ǀ LEDcurrent)) vs starting model (incorrect ~ 1 + group*block + 1 ǀ ID)	18	-1160.3	-1076.7	598.15	-1196.3	2.106	1	0.147
Alternative model 10 (incorrect ~ 1 + group*block + (1 ǀ ID) + (1 ǀ RT)) vs starting model (incorrect ~ 1 + group*block + 1 ǀ ID)	18	-1159.4	-1075.8	597.7	-1195.4	1.192	1	0.275
Alternative model 1 (incorrect ~ 1 + block*group + (1 ǀ ID) + (1 ǀ bl)) vs **alternative model 7** incorrect ~ group + block + (group:block) + (1 ǀ ID) + (1 ǀ bl:group:block) + (1 ǀ bl) + (1 ǀ group) + (1 ǀ block)	21	-1220.6	-1123.1	63.32	-1262.6	60.989	3	<.001

Supplementary Table 5 Model comparisons for pooled data from experiments 1, 3 and 4 in Chapter 3.

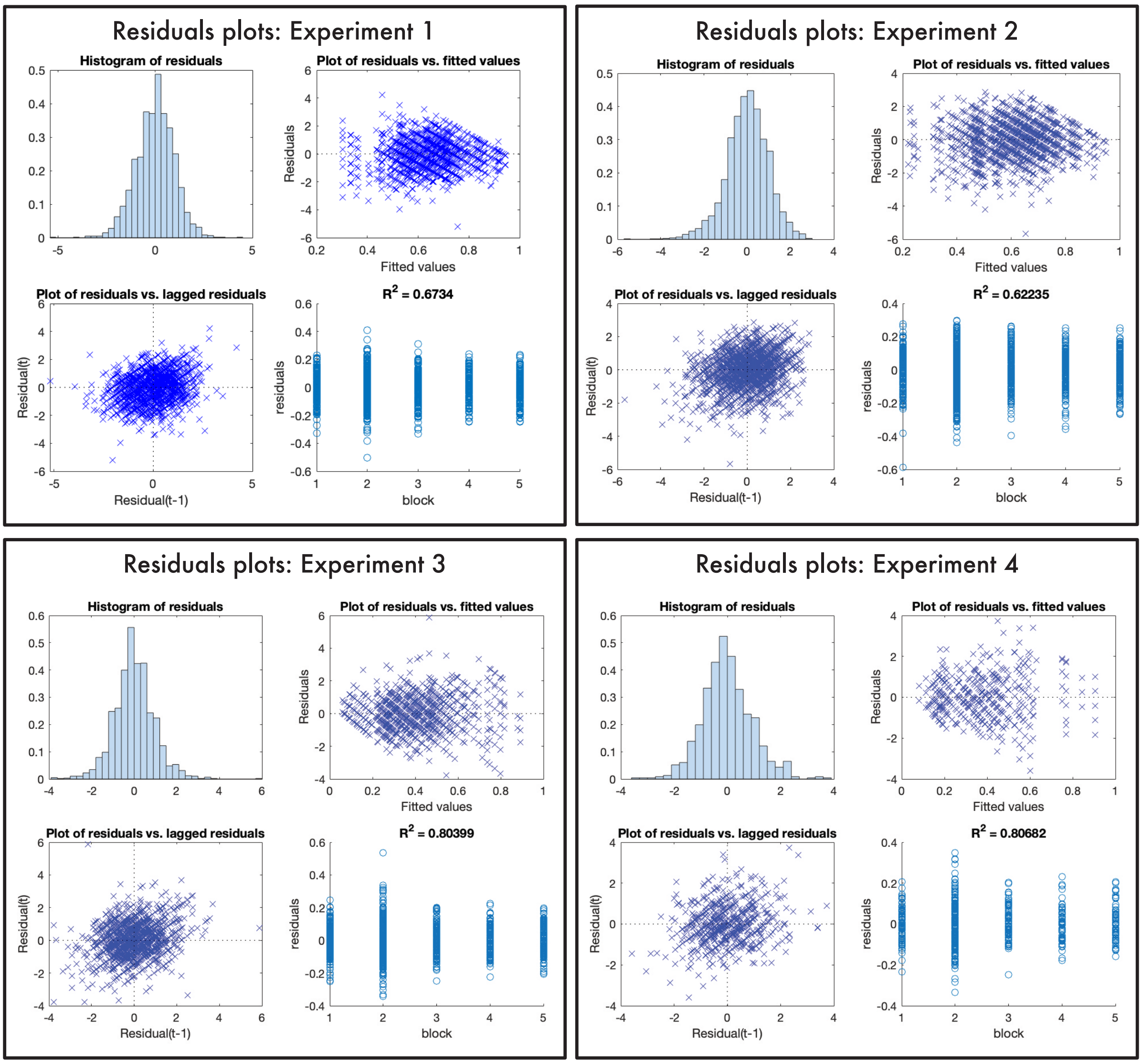
	DF	**AIC**	**BIC**	**LogLikelihood**	**LRTstat**	**Change in DF**	**p-value**
Full model: incorrect ~ 1 + block*group + (1 ǀ ID) + (1 ǀ bl)	18	-7529.2	-7412.9	3782.6	-	-	-
Full model vs **null** (incorrect ~ 1)	2	-2383.9	-2371	1194	5177.3	16	0

Starting model (incorrect ~ 1 + group*block*population + (1 | ID) + (1 | bl) vs **reduced model 1** incorrect ~ 1 + group + block + population + group:block + (1 | ID) + (1 | bl) [to assess if interaction benefits from population as a third term]	20	-7526.3	-7397.1	3783.2	947.43	-8	NaN
New starting model with no interaction to assess main effects (incorrect ~ 1 + group + block + population + (1 | ID) + (1 | bl)) vs **reduced model 2** (incorrect ~ 1 + group + population + (1 | ID) + (1 | bl)) [to assess block main effect]	8	-5023.3	-4971.6	2519.7	88.582	4	<.001
New starting model with no interaction to assess main effects (incorrect ~ 1 + group + block + population + (1 | ID) + (1 | bl)) vs **reduced model 3** (incorrect ~ 1 + block + population + (1 | ID) + (1 | bl)) [to assess group main effect]	10	-4944.9	-4880.2	2482.4	163.04	2	<.001
New starting model with no interaction to assess main effects (incorrect ~ 1 + group + block + population + (1 | ID) + (1 | bl)) vs **reduced model 4** (incorrect ~ 1 + group + block + (1 | ID) + (1 | bl)) [to assess population main effect]	10	-5107.3	-5042.7	2563.6	0.61832	2	.73406
Reduced model 4 (incorrect ~ 1 + group + block + (1 | ID) + (1 | bl)) vs **alternative model 1** (incorrect ~ 1 + block*group + (1 | ID) + (1 | bl)) [to assess block:group interaction]	18	-7529.2	-7412.9	3782.6	2438	8	<.001

Supplementary Figure 1 Stimuli used in Chapters 2 and 3, but with the Mach bands hidden to more clearly show underlying panel contrast.



Supplementary Figure 2 Closer inspection of models described in Chapter 3.



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