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Reward-based improvements of motor performance in health and disease

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Abstract

Reward has been found to boost motor performance and improve learning in both healthy individuals and in clinical populations. The aim of this thesis was to gain a better understanding of how reward affects different specific aspects of motor performance and learning across various age and health status groups. This work provides an important step towards optimising the use of reward within clinical populations such as stroke patients.

The introductory chapter (Chapter 1) provides a comprehensive review of relevant literature, setting the stage for the investigations that follow. As motor performance and reward responsiveness tend to decline with age, Chapter 2 investigated the age-related differences in reward-based improvement in motor performance. We observed that both young and older adults showed improved performance with rewards, but the young group exhibited significantly higher reward-based enhancement in motor performance. In chapter 3, we extended these results by examining how reward impacts motor performance in stroke patients. In this study, we also investigated the impact of rehabilitation on reward sensitivity. Our findings suggest that stroke patients' motor performance significantly improved with the presence of reward. We also found that patients' performance improved after rehabilitation, but there were no changes in reward sensitivity. Chapter 4 investigated the role of the primary motor cortex within the reward-based enhancement of motor performance using repetitive transcranial magnetic stimulation. No effects on performance were observed. In Chapter 5 of this thesis, we explored how reward affects sequential movements and how manipulating task difficulty can impact reward-based improvement in sequential movement fusion. Our findings suggest that sequential movement fusion is more

effective when the task is easy, and this effect is further enhanced by the presence of a reward. The thesis concludes with Chapter 6, which synthesizes the findings, discusses their implications, and proposes directions for future research. This study not only advances our understanding of reward-based motor learning but also provides a foundation for optimizing reward utilization in clinical settings, offering hope for improved rehabilitation strategies.

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Acronyms

AE action execution.

AMT active motor threshold.

AS action selection.

ANOVA Analysis of Variance.

CI confidence interval.

CRT choice reaction time

cTBS continuous theta burst stimulation

FI fusion index

GP globus pallidus

M1 the primary motor cortex.

MRI magnetic resonance imaging.

MT movement time.

MV maximum velocity.

PD Parkinson’s disease.

PFC prefrontal cortex.

RT reaction time.

SMA supplementary motor area.

SN substantia nigra

TMS transcranial magnetic stimulation.

VTA ventral tegmental area

vmPFC ventro-medial prefrontal cortex.

Chapter 1

INTRODUCTION

1.1 Motivation of the thesis

Rewards can serve as a powerful tool to shape human behaviour. They are fundamental to why we do what we do. A tremendous amount of research has explored how rewards can influence behaviour in various fields, such as psychology, economics (Oluleye, 2011), cognitive robotics (Levesque and Lakemeyer, 2008), education and gaming (Howard-Jones and Jay, 2016). In recent years, there has been growing interest in the application of rewards in rehabilitation, particularly for individuals suffering from motor disorders like stroke. In this context, rewards could play a crucial role in motivating patients with movement disorders and facilitate the learning of correct behaviours, potentially accelerating motor recovery and enhancing rehabilitation processes (Chen, 2018; Quattrocchi, 2017; Robertson, 2013). However, there is a scarcity of studies investigating the feasibility and effectiveness of using rewards in

rehabilitation settings (Robertson, 2013). This gap in research may stem from a limited understanding of how rewards exert their effects in clinical populations. The variability among patients with injuries affecting movement, such as those seen in stroke survivors, is considerable. They present with diverse brain injury types, span various ages, and exhibit a range of cognitive and motor disabilities. Therefore, before integrating rewards into rehabilitation strategies, a deeper understanding of how they might influence motor performance is necessary. Specifically, to enhance our comprehension of reward effectiveness in rehabilitation, studies must consider how rewards affect diverse groups and different movement components. In this thesis, titled 'The Impact of Rewards on Motor Performance in Health and Disease,' we examined the influence of rewards on various movement types and components. We also explored how rewards affect motor performance across different age groups and health statuses. This comprehensive approach allows us to gain a broader vision and a more profound understanding of the effectiveness of rewards in improving patient performance. While the journey to complete understanding is long, the aim of this work is to bring us closer to that goal.

1.2 Motor control components from selection to execution

Generating movements requires the interaction of different levels of representation, encompassing the determination of appropriate motor responses (action selection) to the issuance of precise neural commands to muscles (action execution) (Diedrichsen and Kornysheva, 2015). In the next sections, I will give a concise introduction to these two essential aspects of motor control and how they change with age and in response to cerebrovascular diseases such as stroke.

1.2.1 Action Selection: What to do?

Action selection (AS), also known as response selection, is the decision-making process where an individual must choose an action from multiple possible actions in response to perceptual stimuli (Proctor and Vu, 2003). Typically, AS is studied using tasks that involve selecting a specific action from alternatives, such as choice-reaction tasks. In such tasks, participants are instructed to respond to certain stimuli as fast and accurately as possible (Burle et al., 2004b, Proctor and Vu, 2003). Another type of task used to assess AS is the Go/No-Go task. In these tasks, participants must respond to certain stimuli ("go") and withhold responses to others ("no-go") (Gomez et al., 2007). The two primary variables measured in these tasks are reaction time, the time between the presence of the stimuli and the initiation of the response, and response accuracy, which is how many times the correct choice was chosen (Proctor and Vu, 2003, Smith, 1968). AS is a complex cognitive process that includes decision-making, planning, and attention (Goghari and MacDonald III, 2009). The basal ganglia (BG) are fundamental to this process, forming a network of circuits that receive input from various cortical regions (Friend and Kravitz, 2014, Gurney et al., 2001). Its primary output is inhibitory, functioning similarly to a brake on posture and movement patterns generators in the motor system (Mink, 1996, Mink, 2018). The circuits within the BG select preferred actions and inhibit competing, undesired ones. When a preferred action is initiated, the BG output neurons linked to the corresponding motor pattern generator in the cerebral cortex reduce their activity, lifting the inhibition and effectively "releasing the brake" for that action (Mink, 1996, Mink, 2018). Conversely, BG output neurons connected to the generators of competing actions heighten their activity, applying a "brake" to prevent

interference. This dynamic results in a focused selection of the desired action and a concurrent suppression of competing ones (Cisek and Kalaska, 2010, Mink, 2018). There are multiple factors that influence the AS process (Diedrichsen and Kornysheva, 2015). One of these factors is the anticipated reward from a particular action. Our brains evaluate the possible outcomes of action and tend to favour those that offer more desirable rewards (Ridderinkhof et al., 2004). Another factor is our body's current position and capabilities, such as range of motion, muscle strength, and coordination. Our brains take this information into account when deciding which actions are most appropriate (Kim et al., 2021). Additionally, our brains consider the amount of effort and energy required for various actions, often opting for those that require less energy in order to conserve resources (Kim et al., 2021, Sheahan et al., 2016). Instructions, whether external or internally generated, also play a role in shaping action selection by setting goals, constraints, and criteria that are integrated into the decision-making process (Damanskyy, 2023, Eder and Dignath, 2017). In summary, action selection is a complex process that involves the integration of anticipated rewards, the state of our motor system, movement costs, and instructions.

AS is viewed as a hierarchical system where high-level cognitive processes like goals and intentions initiate the selection of motor action, followed by lower-level processes that specify the exact motor command required to execute the selected action (Dong and Franklin, 2014, García-Martínez and Borrajo, 2000). This pivotal step bridges cognitive intention with motor execution, which is essential in the continuum of action production (Diedrichsen and Kornysheva, 2015, Dong and Franklin, 2014).

1.2.2 Action Execution: How to do it?

Action execution (AE), on the other hand, is the process by which the selected motor action is carried out (Bizzi et al., 1991). This involves the translation of the motor command into a sequence of muscle activations that result in the desired movement (Bhattacharjee et al., 2021, Gurney et al., 2001). The complexity of AE lies in the fact that performing any given action involves coordinating multiple muscle groups across different parts of the body, which requires precise timing and sequencing of muscle activations (Diedrichsen et al., 2010, Rothwell, 2012). AE is primarily governed by the motor and premotor areas of the brain, the spinal cord, and the peripheral nervous system, with significant contributions from the basal ganglia, cerebellum, and somatosensory areas, which are instrumental in refining motor commands and ensuring precise execution (Rothwell, 2012). The process begins in the motor cortex, where a motor plan is generated. Upper motor neurons in the primary motor cortex (M1) transmit the motor plan via long axons that extend through the internal capsule, descending through the brainstem and into the spinal cord (CANEDO, 1997, Rothwell, 2012). This direct pathway, known as the corticospinal tract, is crucial for the execution of voluntary motor actions, particularly for fine movements of the limbs and digits (Armand et al., 1996, Rothwell, 2012). At various levels of the spinal cord, the axons of the corticospinal tract synapse with lower motor neurons, which extend out of the spinal cord through peripheral nerves to reach the muscles they innervate (Rothwell, 2012, Stifani, 2014). The neuromuscular junction is the site where the lower motor neurons communicate with the muscle fibres, releasing neurotransmitters that bind to receptors on the muscle tissue and trigger muscle contractions (Engel, 2008). The motor pathways are modulated by various other brain regions, including the basal ganglia, cerebellum, and sensory cortices, which provide input to the motor cortex and brainstem nuclei

(Rothwell, 2012). The cerebellum and the basal ganglia are instrumental in motor coordination, precision, and accurate timing, integrating sensory feedback to fine-tune movements and ensure smooth execution (Bostan and Strick, 2018, Rothwell, 2012). Sensory cortices process various types of feedback, such as proprioceptive data from the muscles, which informs about the position and movement of body parts, and visual input, which helps in adjusting movements based on visual information (Karadimas et al., 2020). Together, these structures adjust the force, direction, and duration of movements, thus refining the motor command before it reaches the muscles (Karadimas et al., 2020, Matyas et al., 2010). Furthermore, the somatosensory cortex, which receives and integrates sensory information, plays a crucial role in providing the necessary feedback for the ongoing adjustments of motor output, ensuring that movements are adapted to the external environment and internal conditions of the body (Matyas et al., 2010, Rothwell, 2012).

Examining AE often involves task paradigms that require the production of specific motor movements. These tasks can vary considerably, depending on the specific aspect of action execution being studied. These tasks include but are not limited to movement production tasks (Rosenbaum, 1980), force production tasks (Rancourt and Hogan, 2001), sequential movement tasks (Tanji, 2001) and dual-task paradigms (Fisk et al., 1986). The variables commonly measured in action execution studies include movement time, accuracy of the response, consistency across multiple trials, and kinematics variables (e.g., velocity, acceleration) (Jasiewicz and Simmons, 1996, Newell et al., 1979, Lee et al., 1987).

It is important to note that while AS and AE are conceptually distinct processes, they are not independent. The execution of an action provides feedback to the system that can influence future action selection (Goghari and MacDonald III, 2009). Similarly, the

process of action selection can shape the way an action is executed. The interdependency of these processes offers a dynamic system that allows for adaptation and learning (Diedrichsen and Kornysheva, 2015, Dundon et al., 2023).

1.2.3 Age-related changes in action selection

Ageing is a natural process that affects various facets of human function, including cognitive and motor functions (Seidler et al., 2010). As we age, noticeable changes occur in both the action selection and execution components of motor control. Understanding these age-related differences can provide valuable insights for developing interventions to enhance motor function in older adults.

In the context of ageing, action selection can become progressively more challenging. In one study, Woods et al. have analyzed the reaction time and selection accuracy in participants ranging from 18 to 65 years old using choice-reaction time tasks (Woods et al., 2015). They found that participants aged over 59 years were significantly slower than their younger counterparts, a decline attributed to age-related decreases in cognitive functions like attention, working memory, and cognitive flexibility (Samanez-Larkin and Knutson, 2015b, Woods et al., 2015). Moreover, older adults often exhibit a decreased ability to inhibit irrelevant or competing motor responses, leading to an increase in errors during tasks that require the selection of one action from among multiple alternatives (Levin et al., 2014, Woods et al., 2015). Such diminished capabilities in inhibiting competing motor responses among older adults may be attributed to age-related neurobiological changes in the basal ganglia and prefrontal cortex—regions critical for action selection (Esiri, 2007, Hubble, 1998).

Several studies have examined these changes and found that the basal ganglia undergo structural and neurochemical alterations with ageing. There is evidence of

reduced volume and diminished dopaminergic activity, which are associated with a decline in the processing speed and the integration of sensory and motor information necessary for initiating and controlling movements (Hubble, 1998, Seidler et al., 2010). These changes can lead to a less efficient selection process and a reduction in movement automaticity, manifesting as slowed reaction times and increased error rates in tasks requiring motor precision and control (Seidler et al., 2010). The prefrontal cortex, essential for executive functions such as decision-making, working memory, and inhibitory control, also shows marked age-related changes. Structural MRI studies have documented atrophy in the prefrontal areas, along with a decrease in white matter integrity, which may compromise the efficient communication between the prefrontal cortex and other brain regions, including the basal ganglia (Raz et al., 1998, Salat et al., 2005). Functional changes include alterations in the patterns of activation, with older adults often exhibiting reduced activation in task-relevant areas and compensatory over-activation in other regions (Cabeza, 2001, Reuter-Lorenz and Cappell, 2008). This pattern of over-activation reflects a process known as dedifferentiation, where the brain's neural networks, which typically specialize in distinct functions, become less distinct and more generalized in their activity, possibly as a compensatory mechanism to maintain cognitive function despite age-related neural decline (Cabeza, 2001, Reuter-Lorenz and Cappell, 2008). Together, these structural and functional changes in the basal ganglia and prefrontal cortex not only impair the ability to select appropriate actions but also affect the timing and execution of those actions. As a result, older adults may require more cognitive effort and time to make decisions and execute movements, particularly in complex or novel situations where multiple options are presented and the inhibition of competing responses is critical.

1.2.4 Age-related changes in action execution

Ageing also impacts action execution. Older adults typically exhibit slower movement times, reflecting a general slowing of motor responses (Lamb et al., 2016), attributed to age-related changes in muscle strength (Wagner et al., 1994), coordination (Dunsky, 2019), and proprioceptive feedback (Ribeiro and Oliveira, 2007). In addition, older adults may have difficulty producing the precise force levels needed for certain tasks and show greater variability in their motor responses (Christou, 2011). This could be due to changes in the peripheral nervous system and musculoskeletal system, as well as alterations in motor planning and control strategies (Christou, 2011, Wagner et al., 1994). Age-related changes in the musculoskeletal system include a reduction in muscle mass and strength, which is known as sarcopenia, and a decrease in bone density that can affect the leverage and force generation necessary for movement (Evans and Campbell, 1993, Larsson et al., 2019, Laurent et al., 2019). Additionally, the composition of muscle fibres shifts, with a tendency for a reduction in the number and size of fast-twitch fibres, which are crucial for rapid and forceful muscle contractions (Miljkovic et al., 2015). Joint health also declines with age, leading to increased stiffness and reduced range of motion, further compromising motor function and execution (Ralphs and Benjamin, 1994). Moreover, there are noticeable changes in motor planning and control strategies with ageing. Older adults often exhibit a conservative approach to movement, characterized by increased planning times and a preference for accuracy over speed, particularly in tasks that demand precision (Seidler et al., 2010, Stöckel et al., 2017). This shift may be compensatory, rooted in the need to avoid errors or falls due to diminished physical capabilities (Seidler et al., 2010). Neurophysiological studies suggest these changes in planning and control strategies may relate to alterations in the central nervous system. For example, there is evidence of reduced

neural plasticity and efficiency in the motor cortex and associated networks, which could account for the increased variability and reduced precision in motor responses (Guglielman, 2012, Park and Bischof, 2013). Age-related reductions in dopaminergic function can also affect motor preparation and the initiation of movement, leading to a general slowing of motor execution (Hubble, 1998, Seidler et al., 2010). The interplay between the central and peripheral nervous systems and the musculoskeletal system becomes less synchronized with age, further impacting motor control. For instance, the feedback loop between proprioceptive input and motor output may become disrupted, leading to less coordinated and more variable movements (Goble et al., 2009, Proske and Gandevia, 2012). Furthermore, older adults often exhibit reduced motor adaptability or the ability to adjust motor responses based on feedback or changes in task demands (Seidler, 2006, Panouillères et al., 2015). This could be due to age-related changes in the plasticity of the motor system and the ability to integrate sensory feedback into motor plans (Burke and Barnes, 2006, Elliott et al., 2011).

Understanding age-related differences in action selection and execution is crucial for designing effective interventions to enhance motor function in older adults, especially when ageing is accompanied by movement disorders. For instance, training programs could be developed to improve cognitive and motor abilities that are important for action selection and execution, such as attention, working memory, cognitive flexibility, muscle strength, coordination, and proprioception (Gates et al., 2020, Häkkinen, 2003, Kwok et al., 2011). Moreover, understanding these age-related differences could inform the design of environments and technologies that are more suited to the motor abilities of older adults, thereby promoting independence and quality of life (Liu et al., 2022, Mynatt and Rogers, 2001).

1.2.5 Action selection and action execution in stroke patients

Stroke often results in significant cognitive and motor impairments, affecting both action selection and action execution processes (Stewart et al., 2016, Saes et al., 2022, Yang et al., 2019). Understanding these impacts is crucial for developing effective rehabilitation strategies and improving motor function recovery in stroke patients. Stroke can disrupt the process of action selection, leading to difficulties in initiating and selecting appropriate motor actions (Stewart et al., 2016). Patients may exhibit prolonged reaction times, reflecting difficulties in decision-making and the selection of motor responses (Gerritsen et al., 2003, Sheng and Wan, 2013, Stewart et al., 2022). Damage to brain areas involved in action selection, such as the prefrontal cortex and basal ganglia, can result in deficits in the suppression of irrelevant or competing motor responses (Gurney et al., 2001, Garcea and Buxbaum, 2023). As a result, stroke patients may make more errors during choice-reaction tasks and display difficulties in tasks that require the inhibition of automatic or habitual responses (Caires et al., 2021). A stroke can also have significant impacts on the execution of movements. The effects can vary widely depending on the location and severity of the stroke. For example, when the blood supply in the motor cortex is affected, this can lead to muscle weakness (hemiparesis) or paralysis (hemiplegia) on one side of the body, impacting the ability to execute actions like reaching and grasping on the affected side (Hallett, 2001). Stroke in the motor area can also result in spasticity, a condition characterized by stiffness and tightness of the muscles, which can interfere with the normal execution of movements (Sheean, 2002). Spasticity can make it difficult for a person to perform actions smoothly and accurately and may result in jerky or uncontrolled movements (Li, 2017, Sheean, 2002). Damage to other parts of the brain, such as the cerebellum or basal ganglia, can result in ataxia (problems with balance and coordination) or slow and delayed

movements that affect the smooth execution of complex movements (Park, 2016, Teixeira et al., 2015). Finally, stroke patients often display reduced motor adaptability, or the ability to adjust motor responses based on changes in task demands or feedback (Moore et al., 2022). This could be due to alterations in the plasticity of the motor system and the ability to integrate sensory feedback into motor plans (Moore et al., 2022, Takeuchi and Izumi, 2012).

Understanding the impacts of stroke on action selection and execution is crucial for guiding rehabilitation. Rehabilitation strategies can be designed to target specific impairments in action selection and execution, such as exercises to improve decision-making and motor control, and tasks to train cognitive flexibility and sensorimotor integration (Collins et al., 2018, Stewart et al., 2022, Edwards et al., 2019). Moreover, the use of assistive technologies, such as brain-computer interfaces and robotic devices, can potentially enhance the effectiveness of rehabilitation. These technologies can provide tailored feedback and support to the patient, facilitating the relearning of motor skills and the recovery of motor function. (Chang and Kim, 2013, López-Larraz et al., 2018). Understanding the specific difficulties faced by stroke patients in action selection and execution can guide the design of these technologies to better address the needs of these patients.

1.3 Reward and motor performance:

1.3.1 Reward system

One of the primary drivers that shape our behaviour is our intrinsic tendency to seek reward and avoid punishment (Ballard et al., 2019). Reward can be defined as a positive stimulus that follows a behaviour, which increases the likelihood that the behaviour will be repeated in the future (Gottfried, 2011). The concept of reward is central to the branch of psychology known as operant conditioning, which studies how rewards and punishments influence behaviour (McLeod, 2007). Rewards are often categorised as primary and secondary rewards. Primary rewards are rewards that are inherently valuable and directly satisfy biological needs, such as food, water and sex, while secondary rewards, also known as conditioned or learned rewards, are not innately valuable but have become associated with primary rewards through learning or conditioning (Beck et al., 2010). Money is a classic example of a secondary reward (Beck et al., 2010), which is the type of reward we used in all studies in this thesis.

The operationalization of reward in research involves defining how rewards will be presented, measured, and administered to participants (Bower and Trapold, 1959, Sigmund et al., 2001). This process varies widely based on the study's goals, the population being studied, and the specific behaviors being examined. Monetary rewards, such as financial incentives, are common due to their clear and quantifiable nature (Lin et al., 2012). They are easily controllable and universally appealing but may vary in perceived value based on socio-economic status and raise ethical concerns about coercion (Lin et al., 2012). Social rewards, involving positive

feedback from others like praise and recognition, are highly motivating in social contexts (Lin et al., 2012, Sigmund et al., 2001). However, their effectiveness can vary based on individual perceptions and social anxiety (Lin et al., 2012). Tangible rewards, such as physical items like food or gifts, are concrete and immediate but may face practical distribution challenges and varying individual preferences (Silbert, 2005). Intrinsic rewards, which come from internal satisfaction from mastering a task or enjoying an activity, provide sustainable motivation aligned with personal values but are more difficult to measure and control (Schwartz and Wrzesniewski, 2016). Rewards can be delivered immediately after the desired behavior or task completion, which is generally more effective in reinforcing behavior and boosting immediate motivation (Bermudez and Schultz, 2014, Jauhar et al., 2021). Alternatively, delayed rewards can be used to study long-term motivation and planning, reflecting real-world scenarios (Bermudez and Schultz, 2014). The schedule of reward delivery can be fixed, which is predictable and easy to understand, leading to steady performance, or variable, which is unpredictable, enhancing engagement and sustained motivation (Bermudez and Schultz, 2014, Jauhar et al., 2021). The effectiveness of rewards can be influenced by individual circumstances. Personality traits such as reward sensitivity and risk aversion affect how individuals respond to rewards. Those high in reward sensitivity may respond more strongly, while risk-averse individuals may prefer fixed rewards (Martin and Potts, 2004). Socio-economic background also plays a role; individuals from lower socio-economic backgrounds may value monetary rewards more highly, while access to resources influences the perceived value of tangible rewards (White et al., 2022). Age and developmental stage are important factors as well; younger individuals may respond better to immediate and tangible rewards, while older individuals might prefer

intrinsic and delayed rewards due to shifts in motivational priorities with age (Eppinger et al., 2012). Cultural background influences reward preferences; people from collectivist cultures may value social rewards more, while those from individualist cultures might prioritise monetary and individual achievements (Hui et al., 1991).

When exposed to a reward or expect a reward via a reward clue, our brain releases dopamine, a neurotransmitter that is mainly associated with pleasure and reward (Schultz, 2002). From a computational perspective, dopamine signals the reward prediction error—the difference between the expected and received reward (O'Reilly et al., 2007, Schultz, 2016a). The Rescorla-Wagner/delta conditioning model captures this with a simple formula:

$$\delta = r - \hat{r}$$

Where delta (δ) represents the reward prediction error, *r* is the amount of the actual reward received, and $\hat{r}$ is the amount of the expected reward (O'Reilly et al., 2007). A positive prediction error occurs when the reward received is greater than what was expected. This activates dopamine neurons, leading to positive learning and pleasurable feelings. This, in turn, increases the likelihood of repeating that behaviour in the future. On the other hand, a negative prediction error occurs when the reward is worse or less than expected. This results in a decrease in dopamine neuronal activity, inducing unpleasant emotions such as frustration and disappointment. Consequently, it decreases the likelihood of repeating that behaviour. When the received reward meets expectations, there is no prediction error, and therefore, no significant response in the dopaminergic neurons (O'Reilly et al., 2007, Schultz, 2016a).

Neurons producing Dopamine originate mainly from the Ventral Tegmental Area (VTA) and the Substantia Nigra (SN) (Düzel et al., 2009). Both these structures play essential roles in both reward processing and reward-based enhancements in motor performance (Prakash and Wurst, 2006). The SN projects dopaminergic neurons to the striatum, constituting the nigrostriatal pathway (O'Reilly and Frank, 2006, Schultz, 1998b). The striatum also receives excitatory inputs from various cortical areas, integrating these with the dopaminergic inputs from the SN. The striatum's output influences other basal ganglia nuclei, such as the Globus Pallidus (GP), which modulate the thalamus and motor cortical areas through direct and indirect pathways (Frank and O'Reilly, 2006). When a reward is received or anticipated, a surge of dopamine is released into the striatum, which in turn inhibits the GP inhibitory effect on the thalamus. This disinhibition enhances the thalamus's excitatory influence on the motor cortex, leading to performance improvement (Figure 1.1a) (O'Reilly and Frank, 2006). In the absence of reward or following a negative outcome, reduced dopamine release leads to decreased striatal inhibition of the GP, resulting in enhanced GP inhibition on the thalamus and, subsequently, attenuated thalamic stimulation of the motor cortex (Figure 1.1b). This neural circuitry is thought to underpin reward-based enhancement in motor performance (O'Reilly and Frank, 2006, Schultz, 1998b).

On the other hand, the VTA sends dopaminergic projections to various parts of the brain, including the limbic system and the prefrontal cortex, forming the mesolimbic and mesocortical pathways, respectively (Kalivas, 1993). Activation of the mesolimbic pathway after receiving a reward leads to dopamine release in several brain structures in the limbic system that have different roles in reward processing. These areas include the amygdala, which plays a role in evaluating the magnitude and

quality of a reward (Murray, 2007); the hippocampus, which provides a reward with a context based on previous experiences (Wittmann et al., 2005); and the nucleus accumbans, which assigns emotional value to the reward stimulus, such as the feeling of pleasure (Day and Carelli, 2007).

In essence, the SN and VTA both contribute to a feedback loop where successful actions that lead to rewards result in dopamine release, which reinforces the neural pathways involved in those actions, thereby increasing the likelihood of those actions being repeated in the future (Kalivas, 1993, Prakash and Wurst, 2006). Despite strong evidence that supports the role of the above-mentioned brain areas in reward processing and reward-based enhancement in motor performance, emerging evidence suggests that other brain areas might also play a role in reward-based enhancement in motor performance, such as the primary motor cortex (M1) (Kapogiannis et al., 2008). One chapter of this thesis is dedicated to exploring the role of M1 in this context, extending our understanding of the neural substrates engaged in reward-based enhancements in motor performance.

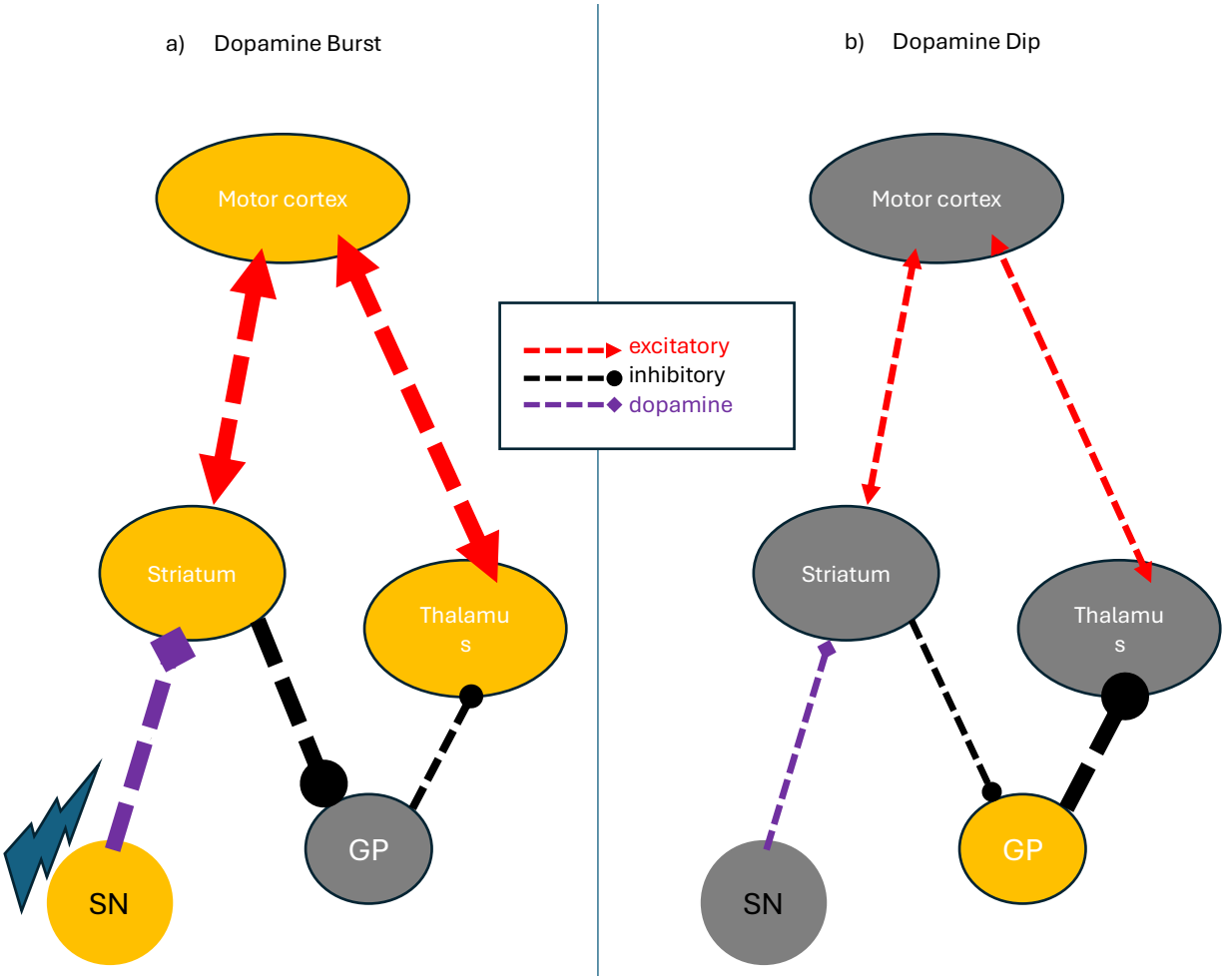


Figure 1.1: Dopaminergic pathway in the SN. a) Upon receiving or expecting a reward, Dopamine neurons in the SN excite the striatum. The burst of dopamine in the striatum (thick purple diamond arrow) excites the striatum, which inhibits the activity of the GP (thick black oval arrow). This has a 'disinhibitory' effect on the Thalamus (thin black oval arrow), which is typically inhibited by the GP. As a result, the Thalamus can more effectively excite the Motor Cortex (thick red arrow), which contributes to enhanced motor performance. b) In the absence of reward, there's less dopamine release (thin purple diamond arrow). This results in less inhibition of the GP by the striatum (thin black oval arrow), leading to a higher level of inhibition from the GP on the Thalamus (thick black oval arrow). Consequently, the Thalamus is less effective in exciting the Motor Cortex (thin red arrow) (O'Reilly and Frank, 2006).

1.3.2 Reward and Aging

Ageing can affect reward sensitivity, which is the capacity to derive pleasure and motivation from rewards (Kim et al., 2015, Eppinger et al., 2012). This change is mainly due to deterioration in the brain's reward system, particularly the dopamine system, as well as shifts in motivational priorities (Eppinger et al., 2012). This age-related reduction in reward sensitivity means that older adults may require stronger or more frequent rewards to experience the same level of pleasure or motivation as younger individuals (McGovern et al., 2014). Ageing may also involve a shift in the types of rewards that individuals find most appealing. For instance, older adults may prioritize emotional well-being over novelty or material gain, which tend to be more important to younger individuals (Carstensen and Reynolds, 2023, Roalf et al., 2011). Ageing can also affect decision-making related to risk and reward. Research suggests that older adults may be more risk-averse than younger individuals, possibly due to changes in the brain's processing of potential losses and gains (Roalf et al., 2011, Samanez-Larkin and Knutson, 2015a). This could result in a decreased sensitivity to potential rewards when there's a possibility of loss (Roalf et al., 2011). Despite these changes, older adults often develop compensatory strategies to maintain their ability to experience pleasure and stay motivated. For example, they may rely more on past experiences or use cognitive strategies to optimize their decision-making and maximize their rewards (Opitz et al., 2022, Yee et al., 2019).

1.3.3 Reward and stroke

A stroke can significantly alter various functions of the brain, depending on its size, location, and the extent of brain tissue damage (Einstad et al., 2021, Kuriakose and

Xiao, 2020). When it comes to reward sensitivity, a stroke can have an impact, although the specific effects can vary widely from person to person. Changes in reward sensitivity after a stroke are closely linked to disruptions in the brain's reward pathways, which prominently include dopaminergic circuits (Rochat et al., 2013b). Strokes that compromise the integrity of the basal ganglia can lead to significant alterations in how rewards are perceived and valued (Rochat et al., 2013a, Schultz, 2016b). Individuals who have experienced a stroke may demonstrate a blunted response to positive reinforcement, which can manifest as reduced motivation to engage in previously enjoyable activities, a condition often referred to as anhedonia (Calabrò et al., 2014). This is particularly evident in strokes affecting the striatum, a component of the basal ganglia that is critical for the anticipation and prediction of rewards (Schultz, 2016b, Calabrò et al., 2014). Moreover, strokes impacting the frontal cortex can disrupt executive functions such as decision-making and impulse control, leading to difficulties in choosing between immediate and delayed rewards, a concept known as temporal discounting (Bjork et al., 2009, Roesch and Olson, 2003). Furthermore, the impairment in reward sensitivity can extend to the cognitive domain, where stroke survivors may find it challenging to prioritize tasks based on their potential outcomes or rewards. This could be due to damage in brain areas such as the orbitofrontal cortex, which is involved in evaluating the subjective value of different choices and outcomes (Lam et al., Roesch and Olson, 2004). Post-stroke changes in reward sensitivity can also influence motor recovery. Engagement in rehabilitation exercises is often driven by perceived rewards or benefits (Verrienti et al., 2023). Thus, a diminished reward response can decrease the motivation for repetitive practice, which is essential for the recovery of motor function (Verrienti et al., 2023). Conversely, incorporating reward-based mechanisms into rehabilitation protocols may help to enhance motivation and

potentially improve outcomes by leveraging the brain's reward system to reinforce motor learning (Robertson, 2013). Strokes can also lead to cognitive deficits, including difficulties with attention, memory, and executive functions (like decision-making) (Povroznik et al., 2018, Wagner et al., 2023a). These cognitive changes can affect an individual's ability to process and respond to rewarding stimuli, potentially altering reward sensitivity (Povroznik et al., 2018, Rochat et al., 2013b). Post-stroke emotional changes, such as depression, anxiety, or apathy, are common and can also affect reward sensitivity. For example, depression is often associated with anhedonia (the inability to feel pleasure), which directly relates to the reward sensitivity (Wagner et al., 2023a). If a stroke leads to motor deficits (like weakness or paralysis) or sensory deficits, it might affect the ability to pursue or engage in previously rewarding activities, leading to changes in perceived reward sensitivity (Ramasubbu et al., 1998b). In summary, the stroke-induced changes in reward sensitivity are multifaceted, affecting emotional well-being, motivation, decision-making, and the ability to derive pleasure from rewarding experiences. These changes can have profound implications for the recovery process, underscoring the importance of evaluating and addressing reward processing deficits in stroke rehabilitation strategies.

1.3.4 Impact of reward on action selection and action execution.

Studies on action selection have shown that the presence of a reward can speed up reaction times and enhance selection accuracy, as subjects are more likely to choose the "right action" when rewarded (Manohar et al., 2015, Wächter et al., 2009). Studies on action execution have also revealed a beneficial effect of rewards, particularly on movement times and execution accuracy, where subjects execute faster and more precise movements when reaching a rewarding target, resulting in improved execution

time and accuracy (Summerside et al., 2018b, Takikawa et al., 2002b). While many studies have explored the effects of reward on either action selection or action execution, fewer have examined how reward influences both processes simultaneously in a more holistic or naturalistic context (Vassiliadis and Derosiere, 2020). This separation can impede the development of a comprehensive understanding of the relationship between reward and action. Although action selection and action execution tasks mentioned previously (sections 1.2.1 and 1.2.2) are simple and easy to administer, they do not fully reflect the complexity of real-world decision-making processes. Therefore, more research is needed that simultaneously examines the effects of reward on both action selection and execution within the same study. This way, we can gain a more comprehensive understanding of how these processes interact and are influenced by rewards in real time. Throughout this thesis, we are using a novel task developed by Codol et al. to investigate the impact of reward on action selection and execution. While this task demands specific equipment and setup that may not be accessible in all research or clinical environments, it allows us to explore how the presence of rewards impacts both action selection and execution simultaneously (Codol et al., 2020a, Codol et al., 2020c). Codol et al. have already examined the impact of reward on action selection and execution and found that reward enhances both of these processes simultaneously (Codol et al., 2020c). Their experiments demonstrated that rewards significantly shift speed-accuracy functions, enhancing motor performance during both selection and execution phases of a reaching movement. Specifically, participants exhibited improved selection accuracy without an accompanying increase in reaction times, suggesting that rewards help maintain decision-making speed while enhancing focus and reducing distractions (Codol et al., 2020c). Furthermore, the introduction of rewards was found to significantly increase the

peak velocity of movements, with the magnitude of peak velocity scaling in proportion to reward size. This increase in speed was not detrimental to the accuracy of the movements, as radial error remained stable, indicating that the efficiency of action execution was enhanced without a sacrifice in precision. These findings underscore that the simultaneous improvements in action selection and execution are predominantly characterized by increased accuracy in selection and enhanced speed in execution, illustrating the powerful influence of reward on motor performance (Codol et al., 2020c). However, given the age-related decline in motor abilities and reward sensitivity, the effects of ageing on reward-based enhancement in action selection and action execution remain unclear. This thesis includes a study addressing this gap in the literature.

Reward has also been shown to be beneficial for stroke patients. Goodman and colleagues conducted a study to investigate how monetary rewards affect ankle movement in patients suffering from hemiparetic stroke and found that those who were rewarded for their performance showed faster learning progress, smoother ankle movement, and more efficient walking (Goodman et al., 2014a). These results suggest that reward can help in accelerating motor learning and recovery after a stroke. In a more recent study, researchers examined the impact of reward and punishment on motor adaptation in stroke patients using the force field perturbation task, and showed that reward and punishment significantly enhanced motor adaptation, with the rewarded patients demonstrating increased memory retention of the new motor behaviour (Quattrocchi et al., 2017b). Nonetheless, the specific impacts of reward on action selection and action execution post-stroke are not yet understood. Understanding how rewards influence these processes can enhance our comprehension of their utility in rehabilitation. Moreover, given that motor deficiencies can negatively affect reward

sensitivity post-stroke (Ramasubbu et al., 1998b), it is pertinent to investigate whether improvements in physical capabilities can positively affect reward sensitivity. In Chapter 3 of this thesis, we have addressed these gaps by examining both the influence of rewards on action selection and execution in stroke patients and the potential role of rehabilitation in augmenting reward-based enhancements in these domains.

1.5 Experimental chapters

Chapter 2 of the thesis investigates age-related differences in the effects of reward on reaching performance. In Chapter 3, we examined how reward impacts reaching performance in stroke patients. Chapter 4 uses transcranial magnetic stimulation to investigate the role of the M1 in reward-based reaching performance. Finally, chapter 5 explores how reward and task difficulty affect sequential reaching performance.

Chapter 2

AGE-RELATED CHANGE IN THE REWARD-BASED ENHANCEMENT OF ACTION SELECTION AND EXECUTION

2.1 Abstract

Aging is associated with changes in dopaminergic function and motor performance, but less is known about how these changes affect responses to motivational cues. This study investigates the interaction between age, reward processing, and motor performance, providing insights into the potential compensatory mechanisms older adults employ in response to cognitive and sensorimotor decline. We conducted a comparative study involving two age groups: younger adults (aged 20-30 years) and older adults (aged 60-75 years). Participants performed arm-reaching movements examining action selection and action execution components of motor performance under various reward conditions. Our findings indicate that older adults show a less pronounced enhancement in motor performance in response to external rewards compared to younger adults. However, older adults maintained performance quality by prioritizing accuracy over speed, suggesting an adaptive shift in motor strategies. Additionally, older adults demonstrated a greater reliance on intrinsic motivation, which aligns with socioemotional selectivity theory. These results suggest that motivational strategies in interventions for older adults should consider enhancing intrinsic rewards to compensate for diminished sensitivity to external rewards, optimizing motor performance and having significant implications for rehabilitation and aging research.

2.2 Introduction

As we grow older, our brain undergoes both structural and functional changes that can lead to a decline in motor control (Seidler et al., 2010). Two key components of motor control, action selection and action execution, have been extensively studied and have been shown to deteriorate with age. Action selection involves the decision-

making process where the brain must choose which movement to execute in response to internal intentions or external stimuli (Proctor and Vu, 2003). This process entails evaluating different potential movements and selecting the one that is most appropriate based on the individual's current goals, environmental context, and expected outcomes (Burle et al., 2004b, Proctor and Vu, 2003). Following action selection, action execution is the process that translates the chosen action into coordinated motor output (Bizzi et al., 1991). During this phase, motor programs in the brain are activated, which are responsible for the timing and control of muscle contractions required to produce the intended movement (Bhattacharjee et al., 2021, Bizzi et al., 1991).

Both components can be negatively affected by age-related changes in cognitive and physical abilities. Regarding action selection, research has shown that older adults experience changes in their cognitive function, including a decrease in processing speed, working memory, and attentional capacity (Deary et al., 2009, Van der Linden and Collette, 2004). These changes can lead to a slower decision-making process, difficulty in selecting between competing actions, and potential challenges in adapting to new or complex motor tasks (Levin et al., 2014, Woods et al., 2015). For instance, Wood et al. investigated age-related differences in action selection by using a choice reaction time task (CRT) and found that the average CRT latencies of participants who were over 59 years old were significantly higher compared to the young group (under 24 years old) (Woods et al., 2015).

Action execution has also shown deterioration with ageing. For example, one study examined the impact of ageing on aiming movements and found that older adults (65+ years old) showed significantly longer movement times compared to younger individuals (below 30 years old) (H. Yan Jerry R. Thomas George E. Stelmach,

1998). This decline in action execution is thought to be due to several age-related factors such as delays in response generation in the motor cortex (Falkenstein et al., 2006), age-related reductions in nerve conduction velocity (Palve and Palve, 2018), muscle waste and slowed muscle contraction (Tieland et al., 2018).

It has been found that rewards can be effective in improving both the selection and execution of actions. For example, in tasks involving sequence learning, monetary rewards have been proven to decrease errors in selection and response time, leading to quicker and more accurate action selection (Klein et al., 2012b). Furthermore, reward has been shown to enhance action selection even in the presence of potential distractors in saccadic eye and reaching movements (Codol et al., 2020b, Manohar et al., 2015). It can also increase movement execution by boosting maximum velocity and reducing end-point errors during saccades (Takikawa et al., 2002a) and reaching movements (Codol et al., 2020b, Galaro et al., 2019b).

Many previous studies have focused only on action selection or action execution separately, which limits our understanding of how reward and action interact. We often engage in activities that require both action selection and execution at the same time in our daily lives. To truly understand how rewards affect real-world actions, it's essential to study how they impact both action selection and execution within the same experimental setup. Codol et al. (2020) developed a new reaching task using a robotic manipulandum to address this gap. In their study, they incorporated both a choice-reaction time component, examining the action selection, and a movement production component, examining the action execution, in young individuals. The task conatained reaching twoard targets where some trials contained more than one target and participants were instructed to select one target

based on instructions. These trials were to examine the action selection component of the reaching movement. Another set of trials within the same task contained only one target, and participants were instructed to reach toward them as fast as they could. This mixture of trial types appeared randomly and is thought to be more reflective of everyday activities. The Participants started each trial at a fixed position and reached for a target. They were rewarded for their movement speed, i.e, the faster they moved, the more money they received. Results of this study showed that reward enhanced both the selection and execution components of the reaching movement (Codol et al., 2020). However, the motivational impact of rewards appears to diminish with age. Ageing has been associated with a decrease in reward sensitivity, which is the capacity to derive pleasure and motivation from rewards (Eppinger et al., 2012, Kim et al., 2015). This reduced sensitivity may be due to age-related atrophy within dopamine-producing regions of the brain, specifically the Substantia Nigra and the Ventral Tegmental Area (Eppinger et al., 2012, Morgan, 1987, Gantz et al., 2018). Dopamine is a crucial neurotransmitter in the circuits of reward, motivation, and learning, and its decline can significantly affect these processes (Bromberg-Martin et al., 2010, Eppinger et al., 2012).

The effects of ageing on the reward-based enhancement of action selection and action execution remain unclear. Therefore, the aim of this study was to examine the impact of reward on action selection and execution in healthy older adults. Understanding these changes is crucial to understanding how ageing can affect behaviour and cognition. In addition, there has been a growing interest in using reward incentives in rehabilitation programs for clinical populations (Chen et al., 2018, Quattrocchi et al., 2017a, Robertson, 2013). Since ageing is a risk factor for many cerebrovascular diseases such as stroke (Kelly-Hayes, 2010, Yousufuddin and

Young, 2019), understanding how reward incentives affect the motor performance of elderly people would help in better implementation of reward-based rehabilitation programs.

2.3 Method

Participants

Twenty-eight young adults (aged 18-25 y, mean age 20 years, 7 male, 21 female) and 28 older adults (aged 60-81 y, mean age 71 years, 18 male, 10 female) took part in the study. Older adults were recruited from a volunteer pool at the University of Birmingham. Younger adults were all undergraduate students at the University of Birmingham. Participants were compensated £7.5 per hour plus an additional reward based on their performance. All participants were free from any medical or psychiatric conditions that could impact their ability to perform the motor task. The study was approved by the University of Birmingham Ethics Committee and was conducted in compliance with their regulations.

Task design

The study replicated a behavioural task previously conducted by Codol et al., 2020 using a KINARM end-point robotic device (BKIN Technologies, Ontario, Canada) (Codol et al., 2020). During the task, participants held a robotic handle that could move horizontally in front of them. The view of their hands was concealed by a panel that had a mirror reflecting a screen located above it. The participants were instructed to look at the reflected screen where they could see a white cursor that indicated their hand movement. The screen had a refresh rate of 60 Hz and was at

the same level as their hidden hand, and kinematics data were recorded at a rate of 1 kHz. At the start of each trial, the robot handle brought the participants to a point 4 cm away from a fixed starting (home) position. Subsequently, a home position of 2 cm diameter appeared on the screen. The colour of the home position indicated the reward value of that trial (blue or green starting position for no-reward or reward trials respectively). At the beginning of each trial, the reward value was displayed in 2 cm high text right below the home position. These values were either 0p in no-reward trials or 50p in reward trials.

Some trials contained distractors (distractor-containing trials), while others were "distractor-free" trials, examining action selection and action execution components respectively. To begin the trial, participants were instructed to move the white cursor to the centre of the home position. Then, a 2 cm diameter target located 10 cm away from the starting position appeared. In distractor-free trials, this target had the same colour as the home position and participants were instructed to move as fast as they could toward it and stop on it. In distractor-containing trials, the first target that appears is called a distractor, and it is indicated by having a different colour than the home position. Participants were instructed to ignore the distractor and wait for the correct target (the target that has the same colour as the home target) to show up. Not following these instructions resulted in no monetary reward for that trial. All targets appeared in one of four possible target locations, positioned every 45° around the midline of the workspace, resulting in a 135° span (Figure 2.1a). We used luminance-adjusted colours to avoid any impact on detectability (https://www.hsluv.org) (Codol et al., 2020). Participants were informed that their money reward would depend on their reaction time and movement time, which would accumulate throughout the experiment. They were also informed that the end

position of their reaching was not important as long as they terminated their movement within 4 cm of the target centre.

The experiment involved the use of a uniform random distribution to determine when the first target would appear (whether it was a distractor or not). This target appeared between 500-700 milliseconds after the participant entered the home position. Correct targets in distractor-containing trials appeared between 300-600 milliseconds after the distractor target using the same random distribution. Once the movement velocity fell below the 0.03 m/s threshold, the end position was recorded, and monetary gains were displayed at the centre of the workspace. After 500 ms, the robotic arm returned the participant's hand to the original position, which was 4 cm above the home position. To start, participants performed 12 baseline trials with no distractors or rewards. After completing the baseline trials, they proceeded to complete 240 trials, which were divided into 24 blocks with 10 trials per block. The blocks alternated between reward and no-reward blocks.

Initially, we presented reward and no reward trials randomly, as done in Codol et al. (2020). However, during a pilot study with 10 older adults, we did not observe any significant impact of rewards on their motor performance. We hypothesised that this could be due to higher cognitive load in the random design as participants continuously adjust their strategies without a predictable pattern. Older adults, in particular, might find it challenging to adapt quickly to such unpredictable conditions, potentially masking any subtle effects of rewards (Seidler, 2006, Panouillères et al., 2015). To address this issue, we decided to test a block design on another 10 older participants, where reward and no reward trials were presented in blocks of 10 trials each. This design was based on the premise that a more predictable and structured environment might reduce cognitive load and allow participants to better anticipate

and respond to the rewards. The results of this pilot confirmed that the block design was more effective, as participants showed improved performance in rewarded blocks compared to no reward blocks, indicating that the block design facilitated better engagement and response to the rewards.

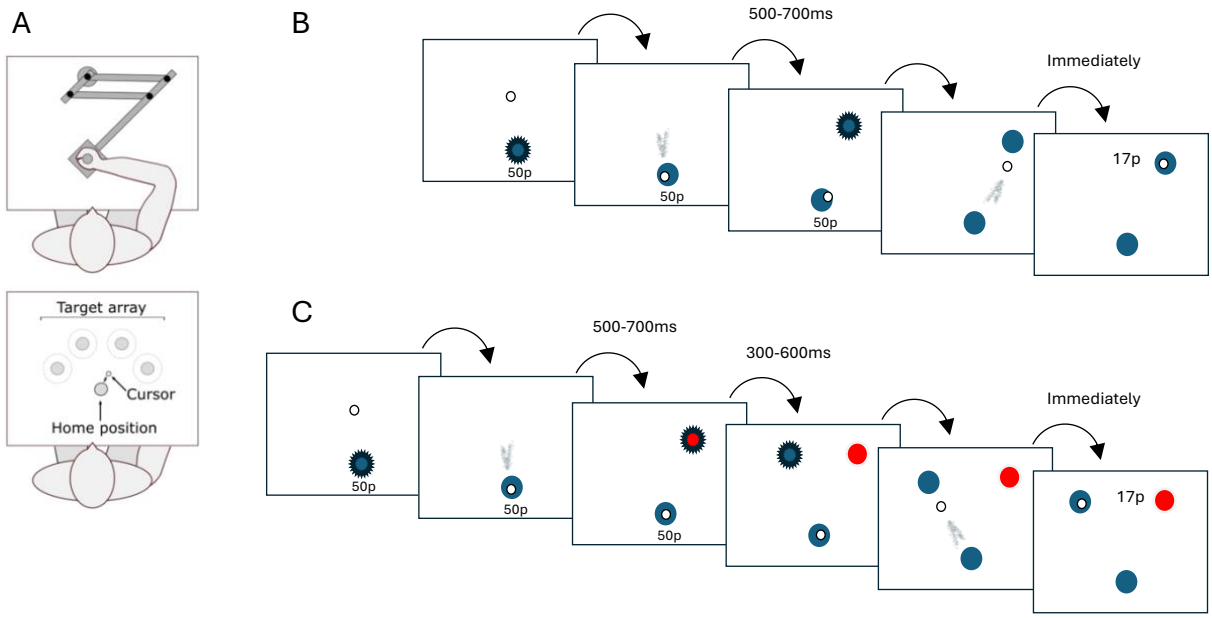


Figure 2.1: Reaching paradigm. A. Participants used a robotic manipulandum to reach a series of targets. B. Normal trial. Participants had to reach a single target and were rewarded based on their performance speed. The speed was calculated by adding the movement time and reaction time (MTRT). C. Distractor trial. Occasionally, a target with a different colour would appear first. Participants were instructed to wait for the second target, which was the correct one, and then reach for it.

We used a reward function that was designed in a closed-loop manner to consider the recent performance of all participants. This ensured that each participant received a fair amount of reward, regardless of their reaction times and movement speeds. The closed-loop design also helped to maintain a consistent level of challenge throughout the experiment (Berret et al., 2018, Reppert et al., 2018).

The reward function was defined as follows:

$$r_t = r_{max} * \max\left(1 - e^{\left(\frac{MTRT - \tau_2}{\tau_1}\right)}, 0\right)$$

where r_{max} represented the highest possible reward value that could be obtained during a trial. The *MTRT* was the sum of the "total reaction time" and the "movement time", and τ_1 and τ_2 were adjustable parameters that depended on the participant's performance. Specifically, τ_1 was calculated as the average of the 3rd and 4th fastest *MTRT*s from the last 20 trials, while τ_2 was calculated as the median of the 16th and 17th fastest *MTRT*s from the last 20 trials. At the beginning of each training block, τ_1 was set to 400 ms and τ_2 to 800 ms, and τ_1 was always less than τ_2 and both were less than 900 ms. All reward values were rounded up to the nearest penny to ensure that only whole penny values were displayed.

Data analysis

The trials were manually categorized into two categories: distracted and non-distracted (Figure 2.2). A trial was considered non-distracted if it did not have a distractor target (distractor-free trials) or if it contained a distractor but the participant moved towards the correct target. On the other hand, if a distractor target was present, and the participants moved towards it, or corrected their movement mid-way towards the correct target, then the trial was classified as distracted (Figure 2.2). The data analysis was divided into two main components: action selection and action execution. Each component was evaluated separately. The evaluation of the action selection component was conducted by measuring two key parameters in distractor-containing trials: selection accuracy and reaction time. Selection accuracy was

defined as the percentage of trials in which participants successfully initiated a reach movement towards the correct target in distractor-containing trials. Reaction time was measured by recording the duration between the correct target appearance and the moment the participant moved more than 2 cm away from the centre of the home position in distractor-containing trials where participants weren't distracted. In distracted trials, we used the time when the distractor target appeared. As for the analysis of the action execution component, we measured several parameters in non-distracted trials. These parameters included the average peak velocity during reaching, movement time, and radial error. Movement time was calculated as the time between the moment the participant moved more than 2 cm away from the centre of the starting position and when the movement velocity dropped below 0.03 m/s (endpoint of the movement). Radial error was defined as the distance between the centre of the target and the endpoint of the movement. Trials that had reaction times exceeding 1000 ms or below 200 ms, and those that were not distracted but had radial errors exceeding 3 cm were eliminated. In total, this amounted to only 1.38% of all trials.

Statistical analysis

A two-way repeated-measures analysis of variance was conducted to examine the effects of two factors - reward (reward vs. no-reward) and age group (young vs. old) and their interaction. The reward condition was the within-subject factor, while the age group was the between-subject factor.

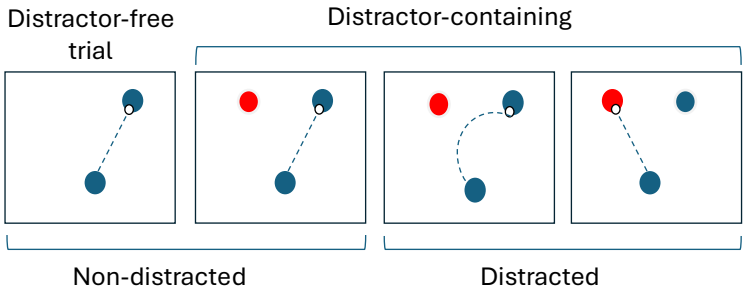


Figure 2.2: Schematic of trial types. During the reaching task, participants completed trials with and without a distractor. These trials were then manually classified as either distracted or non-distracted based on the participant's reaching behaviour. Distractor-free trials were all classified as non-distracted. In trials with a distractor, if the participant reached for the correct target (the one with the same colour as the home target), it was classified as non-distracted. However, if the participant moved toward the distractor (the one with a different colour from the home target) or initially moved towards the distractor and then corrected their path to reach the correct target, the trial was classified as distracted.

If there was a significant interaction effect, post-hoc analyses were conducted. To further investigate these effects, both paired and independent t-tests were used. Paired t-tests were used to examine the differences between the reward and no-reward conditions within each age group. In addition, independent two-sample t-tests were used to compare the impact of reward between young and old participants. To adjust for multiple comparisons in these post-hoc tests, a Bonferroni correction was applied, resulting in a revised significance level of $p < 0.0125$. To explore the observed interaction effect in more detail, a difference-in-differences (DiD) analysis was employed. Commonly used in social and economic research (Abadie, 2005), DiD analysis was employed to examine how the reward-based changes in performance differ between younger and older adults. Specifically, the difference in outcomes between reward and no-reward conditions was calculated for each participant. These differences were then compared between young and old age groups using a two-sample t-test to assess whether the impact of rewards differed significantly by age.

2.4 Results

Monetary Rewards Improve Action Execution for Both Older and Younger Adults

The two-way repeated-measures ANOVA results showed that reward improved the execution component of reaching movements in both the old and young groups (Figure 2.3, Table 2.1). Specifically, there was a main effect of reward in both maximum velocity ($F(1,27) = 75$, $p < 0.001$, $\eta^2 = 0.74$; Figure 2.3c) and movement time ($F(1,27) = 61$, $p < 0.001$, $\eta^2 = 0.69$; Figure 2.3d), suggesting that participants moved significantly faster under reward conditions compared to no-reward conditions. Whilst there was no significant main effect of age in both maximum velocity ($F(1,27) = 0.071$, $p = 0.79$, $\eta^2 = 0.0026$; Figure 2.3c) and movement time ($F(1,27) = 0.54$, $p = 0.47$, $\eta^2 = 0.02$; Figure 2.3d), there was a significant interaction in both maximum velocity ($F(1,27) = 15$, $p < 0.001$, $\eta^2 = 0.36$) and movement time ($F(1,27) = 12$, $p = 0.002$, $\eta^2 = 0.31$). This suggests that the effect of reward on movement execution varies depending on the age group. Post-hoc paired t-test revealed a significant difference in maximum velocity between reward and no-reward conditions in both young ($t(27) = -4.4$, $p < 0.001$) and old ($t(27) = 7.8$, $p < 0.001$) participants. Similarly, there was a significant difference in movement time between reward and no-reward conditions in both young ($t(27) = 3.71$, $p < 0.001$) and old ($t(27) = 3.71$, $p < 0.001$) participants. However, a two-sample t-test comparing the reward and no-reward conditions between the young and old groups did not reveal any significant differences for both maximum velocity (reward: $t(27) = 1.4$, $p = 0.16$, no-reward: $t(27) = 1.1$, $p = 0.27$) and movement time (reward: $t(27) = 2.12$, $p = 0.04$, no reward: $t(27) = 0.57$, $p = 0.57$).

More Pronounced Effect of Reward in the Younger Group

The non-significant differences found in the two-sample t-test indicate that the age of the participants did not have a direct impact on the maximum velocity and movement time of their reaching in either reward or no-reward conditions (Figure 2.3c,d). This seems to be in contrast with the significant interaction found in both maximum velocity and movement time. However, this can occur when the pattern of differences between the reward and no-reward conditions is not the same in the young and old groups. Therefore, a Difference-in-Differences (DiD) analysis was performed (comparing the difference between reward and no reward trails within each participant) and revealed that the effect of reward on maximum velocity and movement time was significantly stronger in the young group compared to the old group (maximum velocity: ($t(27) = 3.78$, $p < 0.001$; Figure 2.4a), movement time: ($t(27) = -3.5$, $p = 0.003$; Figure 2.4b)). This suggests that while both young and old adults improved their performance when a reward was present, this effect was more pronounced in younger individuals than in older ones.

Improvement in Action Execution Did Not Come at the Cost of Movement Accuracy

In terms of the radial error, older adults were significantly more accurate than younger adults (Figure 2.3, Table 2.1). There was a significant main effect of age ($F(1,27) = 16$, $p < 0.001$, $\eta^2 = 0.38$; Figure 2.3c), but no main effect of reward, ($F(1,27) = 0.0085$, $p = 0.93$, $\eta^2 = 0.001$), nor an interaction, ($F(1,27) = 0.47$, $p = 0.50$, $\eta^2 = 0.017$; Figure 2.3a). Therefore, despite the accuracy differences between older and younger adults, this indicates that the improved movement execution observed with reward did not come at the cost of movement accuracy.

Monetary Rewards Improve Reaction Time but Impairs Selection Accuracy Across Older and Younger Adults

As for the action selection component (Figure 2.3, Table 2.1), reaction times decreased significantly as a result of monetary rewards, demonstrating faster processing speeds when incentivized. This was statistically supported by a main effect of reward on reaction time ($F(1,27) = 59$, $p < 0.001$, $\eta^2 = 0.68$). Additionally, younger adults generally exhibited faster reaction times compared to older adults, as indicated by a significant main effect of age ($F(1,27) = 19$, $p < 0.001$, $\eta^2 = 0.42$; Figure 2.3a, Table 2.1). Notably, there was no interaction effect between age and reward ($F(1,27) = 0.03$, $p = 0.86$, $\eta^2 = 0.0011$), suggesting that the effect of monetary rewards on speeding up reaction times was consistent across both age groups. However, the improvement in reaction times appeared to compromise selection accuracy (Figure 2.3b, Table 2.1). The analysis revealed a significant deterioration in selection accuracy with rewards ($F(1,27) = 147$, $p < 0.001$, $\eta^2 = 0.85$), independent of age, as there was no significant main effect of age on selection accuracy ($F(1,27) = 1.1$, $p = 0.31$, $\eta^2 = 0.038$) nor any interaction effect ($F(1,27) = 0.29$, $p = 0.59$, $\eta^2 = 0.011$). This pattern indicates that the rapid response facilitated by rewards may lead to more errors in selection accuracy, affecting both younger and older adults similarly. These findings suggest that while monetary incentives effectively enhance the speed of decision-making across different ages, they may also lead to a decrease in the accuracy of those decisions, highlighting a potential trade-off between speed and accuracy in cognitive processing under incentivized conditions.

Total Reward Gained by Young and Old Groups

The average reward gained by the young group was significantly higher than that of the old group ($t(54) = 4.42$, $p < 0.001$; Figure 2.3f). This disparity in total rewards may explain the more pronounced effects of reward on performance metrics observed in the young group.

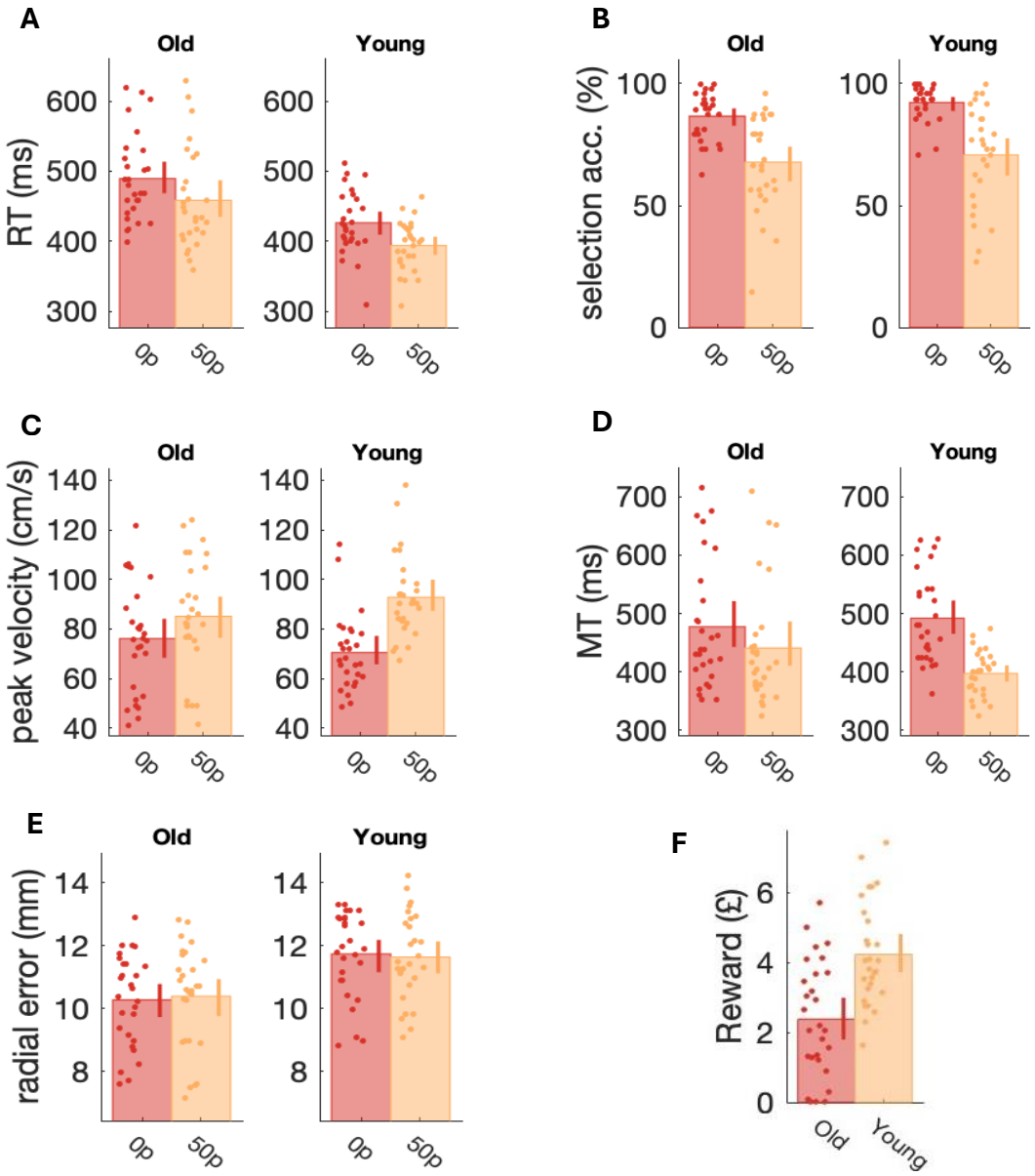


Figure 2.3: Reward-based changes in action selection and action execution in old and young groups. Action selection component: A. Reaction times. B. Selection accuracy.
Action execution component: C. Average peak velocity. D. Average movement time. E. Average radial error. F. Average total reward. The height of the bar shows the average of the group. Each dot on the graph represents an individual value, while the error bars illustrate the 95% confidence interval of the mean.

	Mean (SD)				*p* (Main effects)		*p* (Interaction)
	Old		Young		Reward	Age	
Action execution	Reward	No Reward	Reward	No Reward			
Maximum Velocity (cm/s)	85 (22.86)	76 (21.88)	93 (16.80)	70 (15.29)	< 0.001	0.79	< 0.001
Movement Time (ms)	440 (100)	480 (110)	400 (40)	490 (80)	< 0.001	0.54	0.002
Radial Error (mm)	10.4 (1.6)	10.3 (1.5)	11.6 (1.4)	11.7 (1.4)	0.93	< 0.001	0.5
Action selection							
Reaction Time (ms)	459 (70)	490 (60)	390 (40)	430 (50)	< 0.001	< 0.001	0.86
Selection accuracy (%)	68 (19)	87 (9.7)	71 (20)	92 (7.5)	< 0.001	0.31	0.59

Table 2.1: Mean and standard deviation (SD) of all variables in both reward and no-reward trials, as well as the p-values of the main effects of reward and age and their interaction. The units cm/s, ms, and mm represent centimetres per second, millisecond, and millimetres, respectively.

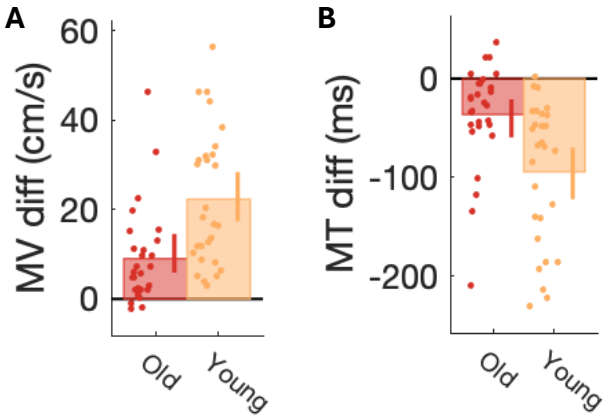


Figure 2.4: Action execution differences between reward and no-reward trials. The average performance for each participant in no-reward trials was subtracted from the average performance in reward trials in both A) maximum velocity differences (MV diff) and B) movement time differences (MT diff). Results showed that the difference in average performance between reward and no-reward trials was significantly higher in the young group compared to the old group. The height of the bar shows the average of the group. Each dot on the graph represents an individual value, while the error bars illustrate the 95% confidence interval of the mean.

Learning Effect

To examine the learning effect, both movement time (Figure 5a) and gained reward (Figure 5b) were plotted on a trial-by-trial basis during the nondistracted reward trials as a function of time. The objective was to assess how performance changed from the beginning to the end of the task. This was achieved by comparing the average movement time and reward values at two distinct timepoints: early (average of the first 5 trials) and late (average of the last 5 trials).

A two-way ANOVA was conducted to examine the learning effect in both old and young groups. Regarding movement time (Figure 5a), there was a significant main effect of timepoint ($F(1, 27) = 5.5$, $p = 0.027$), indicating that movement times significantly decreased over trials for both groups. This suggests a learning effect where participants improved their performance with practice. There was also a significant main effect of age ($F(1, 27) = 39.4$, $p < 0.001$), with the young group showing significantly faster movement times compared to the old group. This highlights age-related differences in motor performance, with younger participants performing the task more quickly. However, there was a non-significant interaction effect ($F(1, 27) = 0.1$, $p = 0.75$), suggesting that the rate of improvement in movement times was similar for both groups.

Regarding improvement in gained reward across trials (Figure 5b), a similar trend to the improvement in movement time was observed. There was a significant main effect of timepoint ($F(1, 27) = 18$, $p < 0.001$), indicating that rewards significantly increased over trials for both groups. There was also a main effect of age ($F(1, 27) = 39$, $p < 0.001$), indicating a significant difference in the rewards obtained between the old and young groups. No significant interaction was found ($F(1, 27) = 0.5$, $p = 0.45$),

showing that both old and young groups exhibited similar trends in how their rewards changed over the course of the trials.

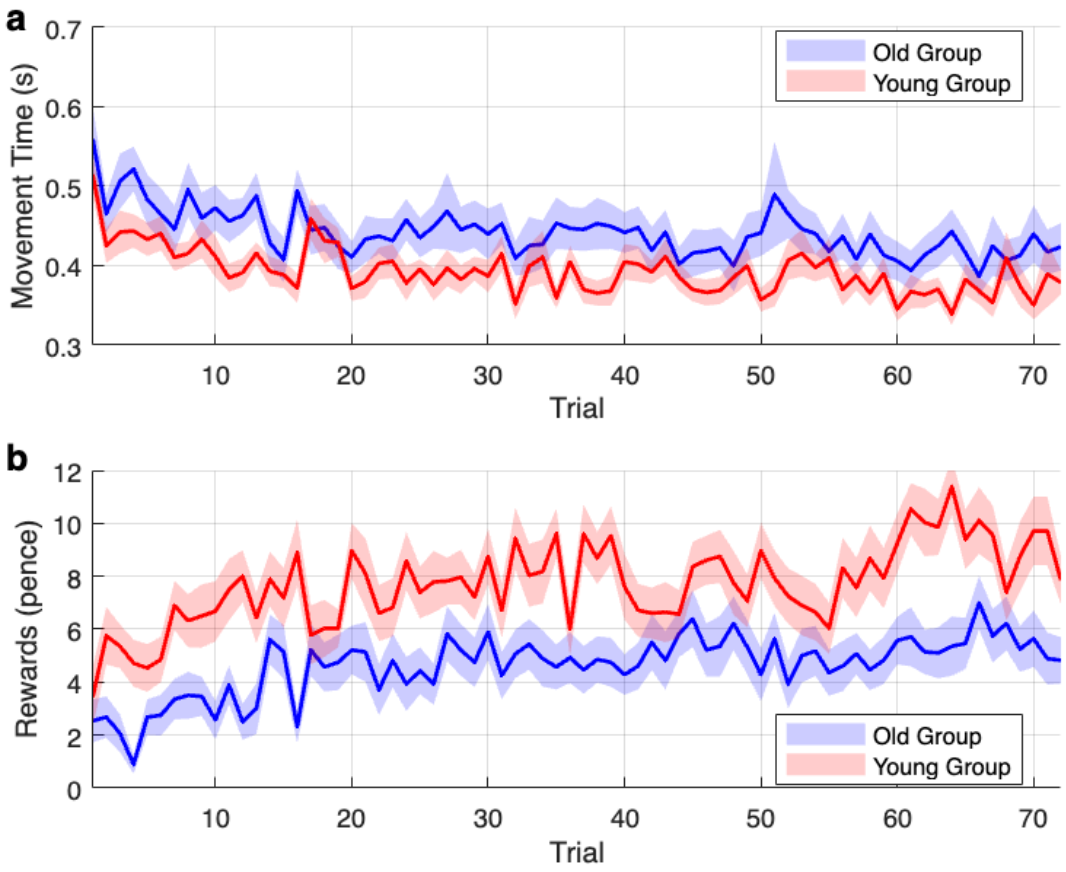


Figure 2.5. Learning Effects on Movement Time and Rewards: (a) Average movement times (seconds) and (b) average gained rewards (pence) for the old group (blue) and young group (red) across nondistracted reward trials. Shaded areas represent one standard error of the mean.

2.5 Discussion

This study aimed to investigate the impact of ageing on how reward influences action selection and execution during reaching movements. The findings contribute to a better understanding of how motivational factors and age interact to influence motor control.

Action Execution and Reward

The study showed that rewards can serve as a powerful motivator to boost motor performance in all participants, resulting in higher maximum velocity and shorter movement time. This finding aligns with previous research on how rewards impact motor performance in both young (Codol et al., 2020b, Sporn et al., 2022) and older adults (Aves et al., 2021, Tecilla et al., 2023). Although there was no significant main effect of age on these variables, the significant interaction between reward and age revealed that younger individuals showed a more pronounced effect of reward. These behavioural results support physiological studies that reported age-related decline in dopaminergic function (Eppinger et al., 2012, Morgan, 1987). Research has shown that dopamine levels and receptor density typically decline with age, which can lead to a reduction in the efficacy of dopamine neurotransmission (Hubble, 1998, Seidler et al., 2010). This decline can cause older adults to be less responsive to motivational cues, leading to a reduced sensitivity to rewards (Dhingra et al., 2020, Eppinger et al., 2012, Morgan, 1987). This could explain the findings in the current study, where the effect of rewards on execution was less pronounced in older individuals.

Moreover, older adults outperformed younger ones in no-reward trials but underperformed in reward trials. Although these differences were not statistically significant, the observed trend is noteworthy. This trend suggests that older adults may rely more on internal states or intrinsic motivation, which can be sufficient for effective motor execution in the absence of external rewards. This observation is supported by the socioemotional selectivity theory (SST), which posits that as people age and begin to perceive their time as limited, their motivational orientation starts to change (Ziaei and Fischer, 2016). They become more intrinsically motivated to

engage in an activity for its inherent satisfaction rather than for some future gains (Hess, 2014, Ziaei and Fischer, 2016, Shi et al., 2023). Some participants verbally expressed support for this idea. For instance, when told that they could earn more money if they moved faster, some explicitly said something like, "Money doesn't matter to me. I came here to help." On the other hand, younger adults may be more influenced by external rewards, which could explain their improved performance in reward conditions.

Another key finding from our study is the significantly lower radial error among older adults, which suggests that older adults prioritise accuracy over speed. This aligns with the previous findings that posit that older adults may adapt their motor strategies to maintain the quality of performance, potentially to compensate for age-related declines in sensorimotor function (Seidler et al., 2010, Helsen et al., 2016, Lee et al., 2007). The lack of a reward effect on radial error for both age groups also suggests that the motivation to perform faster does not inherently lead to a loss in accuracy, challenging the commonly accepted speed-accuracy trade-off in motor tasks (Fitts, 1954). This reward-based break in the speed-accuracy trade-off has been previously reported in studies on younger participants (Codol et al., 2020b, Manohar et al., 2015), and our study has replicated the same phenomenon in older adults.

Action Selection: Reaction Time and Age

The observation of longer reaction times in older adults corroborates previous findings that suggest a slowing of cognitive processes with age (Hardwick et al., 2022, Woods et al., 2015). However, the reduction in reaction time with rewards in both age groups indicates that motivational factors can partially mitigate such age-related slowing. This implies that the capacity to utilize external motivational cues

remains intact across the lifespan, although the extent of this utilization may differ with age.

Selection Accuracy and the Speed-Accuracy Trade-Off

A notable finding was the reward-based reduction in selection accuracy in both groups. This trade-off between speed and accuracy, particularly in a rewarded context, may arise from a more rapid decision-making process that sacrifices accuracy for speed. This is consistent with a phenomenon found in young adults known as "choking on the money", which implies that when there is a reward involved, one's ability to perform certain tasks that require cognitive skills, attention, and decision-making are often impaired (Mobbs et al., 2009, Smoulder et al., 2023). In our study, we found that this phenomenon is maintained in older adults.
Another interesting finding in this study is the possible strategy used by older adults to maintain their selection accuracy. Choosing the right action from alternatives requires inhibiting competing actions (Burle et al., 2004a), which tend to deteriorate with ageing (Levin et al., 2014, Woods et al., 2015). Our study showed that older adults have slower reaction times but still maintain the same level of selection accuracy as younger adults. This may indicate that older adults are intentionally using a compensatory strategy to maintain their accuracy. This strategy could be similar to their approach in executing tasks, where slower movements help them to maintain movement accuracy.

Implications for Motor Rehabilitation Programs

The implications of these findings are multifaceted for motor rehabilitation programs. Firstly, the inclusion of reward mechanisms may be beneficial across age groups but should be tailored according to the age-specific responsiveness to rewards. For younger individuals, externally provided rewards might be more effective, whereas older adults may benefit from interventions that emphasize intrinsic motivation or that capitalize on their propensity for greater accuracy. Secondly, the findings suggest that cognitive-motor interventions incorporating reward stimuli should account for the potential action selection speed-accuracy trade-off. Rehabilitation programs may need to carefully balance tasks that encourage selection speed to ensure that they do not inadvertently compromise accuracy. Lastly, the preserved ability of older adults to improve reaction times with reward cues, despite cognitive slowing, points towards the potential of using motivational strategies to enhance both the initiation and execution of motor tasks in older populations.

2.6 Conclusion

In conclusion, our study highlights the complexity of age-related changes in motor control and the nuanced role that reward plays in modulating these changes. While reward generally improves motor performance, the nature of its influence is distinct across age groups, necessitating tailored approaches in therapeutic settings. Understanding the specific ways in which ageing affects motor control can inform the development of more effective, personalized rehabilitation interventions that leverage the motivational power of rewards to enhance motor function.

Chapter 3

IMPACT OF REWARD ON REACHING PERFORMANCE IN CHRONIC STROKE PATIENTS

3.1 Abstract

Stroke is a leading cause of long-term disability, with many survivors experiencing persistent upper limb dysfunction. This study explores how explicit rewards influence the selection and execution of reaching movements in chronic stroke patients and assesses whether intensive upper-limb rehabilitation enhances reward sensitivity. Twenty-eight hemiparetic chronic stroke patients performed a reaching task with both paretic and non-paretic arms under various reward conditions. Our results show that rewards significantly improve movement execution, increasing speed without compromising accuracy, in both arms, with a more pronounced effect in the non-paretic arm. Additionally, intensive rehabilitation improved overall motor performance but did not alter reward sensitivity. These findings suggest that reward-based interventions can enhance motor performance in chronic stroke patients, and rehabilitation programs should consider integrating reward mechanisms to optimize outcomes.

3.2 Introduction

Stroke is one of the leading causes of long-term disability globally and often results in lifelong disability (Feigin et al., 2022). In the UK, there are around 1.3 million stroke survivors (Stroke Association, 2024), and more than 50% of them experience persistent upper limb dysfunction throughout their lives, which is associated with reduced independence and quality of life (Kwah et al., 2013, Pedlow et al., 2023). Fortunately, spontaneous recovery often occurs immediately after a stroke, leading to an improvement in upper limb functions (Cramer, 2008, Ward and Cohen, 2004). However, the rate of this recovery depends on the time elapsed since the stroke.

During the acute and subacute stages, which last from a few days to several months after the stroke, the recovery process can be quite rapid due to the high degree of neuroplasticity (the brain's ability to reorganize itself by forming new neural connections) (Cramer, 2008, Seitz and Donnan, 2015, Ward, 2005). On the other hand, in the chronic stage, which is beyond six months post-stroke, the rate of spontaneous recovery slows down, leading to persistent impairment (Seitz and Donnan, 2015, Ward and Cohen, 2004). Although neuroplastic changes can still occur during this stage, they are generally slower and require more targeted and repetitive interventions (Dimyan and Cohen, 2011, Wang et al., 2018). Therefore, it is crucial to use different rehabilitation strategies to enhance motor recovery and function in chronic stroke patients.

Various interventions have been explored and found to be beneficial (Cramer, 2019, Daly et al., 2019, Ward et al., 2019). However, the role of motivational factors in improving rehabilitation outcomes has gained considerable interest (Quattrocchi et al., 2017a, Robertson, 2013, Widmer et al., 2017). While some studies suggest that stroke survivors may have difficulties with reward processing (Oestreich et al., 2020, Rochat et al., 2013a, Wagner et al., 2023b, Widmer et al., 2019), reward incentives have proven effective in improving stroke patients' behaviour and performance. For instance, Goodman and colleagues conducted a study to investigate how monetary rewards affect ankle movement in patients suffering from hemiparetic stroke. They found that those who were rewarded for their performance showed faster learning progress, smoother ankle movement, and more efficient walking (Goodman et al., 2014b). In another study, researchers examined the impact of reward and punishment on motor adaptation in stroke patients using the force field perturbation task. They showed that reward and punishment significantly enhanced motor

adaptation, with the rewarded patients demonstrating increased memory retention of the new motor behaviour (Quattrocchi et al., 2017a). These findings suggest that rewards can be a useful tool in rehabilitation programs to accelerate upper-limb motor skill learning and recovery after a stroke. However, before implementing rewards in upper-limb rehabilitation for stroke patients, a deeper understanding of its impact on upper-limb functions, such as reaching movements, is necessary.

Daily reaching movements, like many other types of movement, involve a complex process that begins with selecting the appropriate action based on intention and desire (action selection) and then executing the selected action (action execution) (Begliomini et al., 2014, Diedrichsen and Kornysheva, 2015, Kim et al., 2021). Research has shown that both action selection and execution tend to deteriorate after a stroke. In terms of action selection, several experiments have investigated the action selection component in stroke patients by measuring choice-reaction time (CRT), which assesses the accuracy and reaction time of choosing a specific response from among several alternatives based on the task instructions (Caires et al., 2021, Miller and Low, 2001). These studies have observed that the reaction times of stroke patients are generally longer than those of healthy individuals (Caires et al., 2021, Debeljak et al., 2019, Godefroy et al., 2010). Stroke patients also experience a decline in action execution. Post-stroke pathologies like spasticity (Trompetto et al., 2014), weakness (Ng and Shepherd, 2000), and coordination deficits (Cirstea et al., 2003), can severely impact their ability to execute motor functions such as reaching and grasping (Roby-Brami et al., 2003).

Both selecting and executing actions are subject to the speed-accuracy trade-off law, which means that when actions are performed more quickly, their accuracy decreases, and the likelihood of errors increases (Fitts, 1954, Plamondon and Alimi,

1997). Interestingly, it has been found that the presence of a reward can improve both of these components in healthy individuals and can even allow them to perform actions faster without compromising accuracy (Codol et al., 2020b, Manohar et al., 2015). However, the way that rewards affect action selection and execution in the reaching movement of chronic stroke patients is not yet fully understood. Understanding how rewards influence these processes can enhance our comprehension of the impact of reward on stroke patients and the usefulness of using reward in rehabilitation. Furthermore, since motor deficiencies can negatively affect reward sensitivity post-stroke (Ramasubbu et al., 1998a), it would be beneficial to explore whether improvements in physical capabilities can positively affect reward sensitivity.

In this study, we aimed to investigate how explicit reward influenced the selection and execution of reaching movements in chronic stroke patients. As the patients recruited were participating in a 3-week intensive upper-limb rehabilitation program, we also tested patients post-rehabilitation in order to assess whether rehabilitation influenced patient's reward sensitivity.

3.3 Method:

Participants

Twenty-eight hemiparetic chronic stroke patients (aged 21-70 years, mean age 53 years, 20 male, 5 female) were recruited from the Queen Square Upper Limb rehabilitation programme (QSUL), where they were undergoing a three-week intensive upper limb rehabilitation (Ward et al., 2019). All patients were recruited during their first week (week 1) of the program. Patients who had absent movements

throughout the limb, limited active forward reach, severe spasticity, non-neural loss of range, or unstable medical conditions were excluded from the study. Out of the 28 patients, 20 (aged 21-70 years, mean age 51 years, 16 male, 4 female) were retested at the end of the rehabilitation program (at week 3). Patients were compensated with £10 per hour and an additional reward based on their performance.

Treatment programme

The QSUL clinical service is a single centre that offers 90 hours of scheduled treatment (Ward et al., 2019). The first step in the treatment process involves analysing both movement and performance while carrying out functional tasks. The next stage focuses on reducing impairment and promoting the re-education of motor control within functional tasks. Patients are encouraged to practice individualized tasks repeatedly to master them, with a focus on the quality of movement. Throughout the program, coaching is considered an essential element to embed new skills and knowledge into individual daily routines. This approach helps individuals increase their participation and confidence in their desired goals, enhancing their self-efficacy and motivation to sustain behavioural change even after the end of the treatment period (Ward et al., 2019). The overall approach involved two daily sessions of physiotherapy and occupational therapy, along with customized interventions tailored to each patient's needs. These interventions included repetitive practice using a rehabilitation assistant or robotic device, sensory retraining, dynamic and functional orthoses, neuromuscular electrical stimulation, and group work. Patients were also encouraged to work on their cardiovascular fitness during the program. The program followed a 6-hour timetable, 5 days a week, for a total of 3

weeks, which amounted to 90 hours of therapy. The program was staffed with a ratio of 1 staff member to each patient, which included 3 physiotherapists, 3 occupational therapists, and 3 rehabilitation assistants for 9 patients (Ward et al., 2019).

Task Design

The experimental setup and basic task design were similar to those described in Chapter 2, with the key differences being the inclusion of both paretic and non-paretic arms and the addition of a post-rehabilitation assessment. Stroke patients performed 120 trials instead of 240 trials as in Chapter 2. This decision was made after conducting a pilot study with 5 patients, who reported fatigue after the mid-point of the session. As a result, we decided to reduce the number of trials to half of the original amount and found that patients were able to complete the full session without any issues. The task was conducted using the bilateral robotic exoskeleton named KINARM (manufactured by BKIN Technologies Ltd, Kingston, ON, Canada), which provides complete gravitational support of the arms, forearms, and hands and allows only horizontal motion involving flexion and extension of the shoulder and elbow. The participants were seated in a KINARM chair with their arms raised and spread out in a horizontal plane (Figure 3.1A). The angle of abduction was set to around 80 degrees so that the arm, forearm, and hands were all at the same level as the shoulder. The robotic exoskeleton setup allowed for monitoring of reaching movements with both arms. The specifics of the task, including the reward structure and trial types, followed the paradigm described in Chapter 2.

Data Analysis

The data analysis followed the same procedures as described in Chapter 2, focusing on action selection and action execution components. The trials were manually sorted into two categories: distracted and non-distracted. The notable difference in this chapter is the percentage of trials eliminated due to reaction times exceeding 1000 ms, below 200 ms, or radial errors exceeding 6 cm. In this study, this amounted to 6% of all trials.

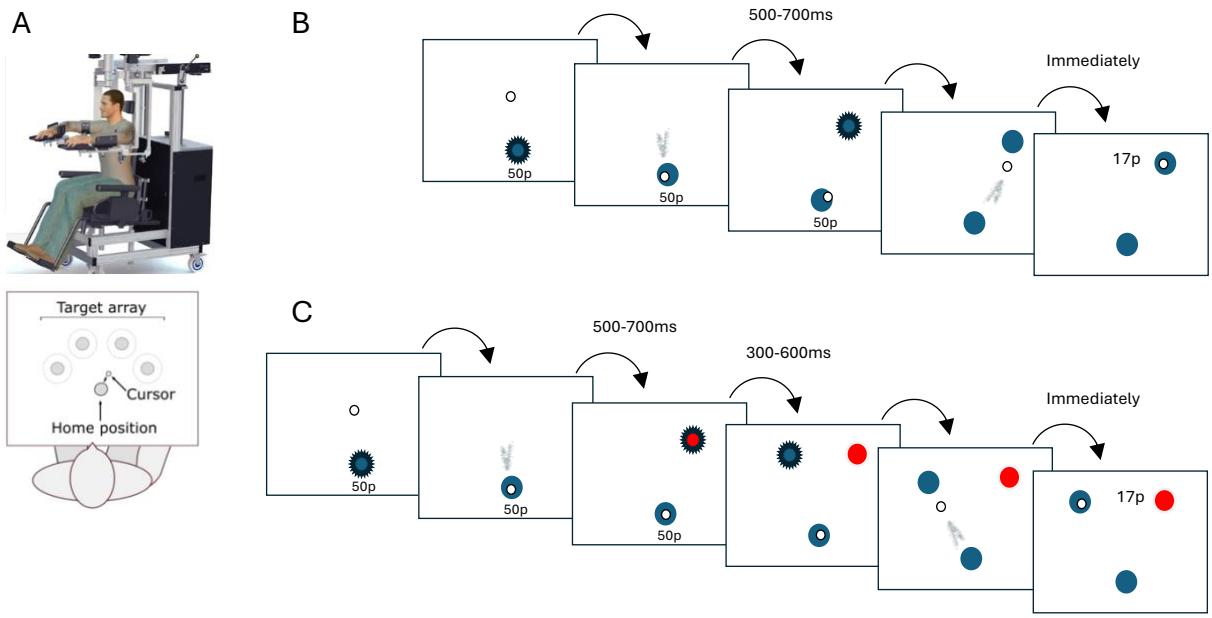


Figure 3.1: Reaching paradigm. A. Participants used a robotic exoskeletong arm to reach a series of targets. B. Normal trial. Participants had to reach a single target and were rewarded based on their performance speed. The speed was calculated by adding the movement time and reaction time (MTRT). C. Distractor trial. Occasionally, a target with a different colour would appear first. Participants were instructed to wait for the second target, which was the correct one, and then reach for it.

Clinical measures

To evaluate the motor recovery of participants' upper extremities, the Fugl-Meyer Assessment of Upper Limb (FMA-UE) was administered during the first and third

weeks of the rehabilitation program. The FMA-UE is a stroke-specific, performance-based impairment index designed to assess motor functioning, balance, sensation, and joint functioning in patients with post-stroke hemiplegia (Deakin et al., 2003). It is widely recognized as a standard measure of motor impairment following a stroke (Sanford et al., 1993). The assessment was conducted by trained physiotherapists at QSUL.

Statistical analysis

For the week 1 experiment (pre rehabilitation), we conducted a two-way repeated-measures analysis of variance (Falkenstein et al.) with two factors - reward (reward vs no-reward) and arm (paretic vs non-paretic), as well as their interaction. For the he third week (post rehabilitation), with a subset of patients, we compared the reward-based enhancement in motor performance in week 1 with that of week 3 in both the paretic and non-paretic arms separately. Thus, the factors of the two-way repeated-measure ANOVA were reward (reward vs no reward) and timepoint (week 1 vs week 3) in the paretic and non-paretic arms. If there was a significant interaction effect, we conducted post-hoc analyses using paired t-tests. To account for multiple comparisons in these post-hoc tests, we applied a Bonferroni correction, resulting in a revised significance level of $p < 0.0125$. To further examine the observed interaction effect, we conducted a Difference-in-Differences (DiD) analysis, a technique commonly used in social and economic research (Abadie, 2005). This analysis was utilized to evaluate how changes in performance due to reward varied across two dimensions: across different arms (between the paretic and non-paretic arms) and over time (between week 1 and week 3). Specifically, we calculated the difference in performance between the reward and no-reward conditions for each

participant. These differences were then analysed in two ways: firstly, comparing the differences between the paretic and non-paretic arms, and secondly, comparing the changes from week 1 to week 3, using a two-sample t-test for each comparison.

3.4 Result

Week 1 (Paretic vs. Non-Paretic Arms)

Monetary Incentives Enhance Motor Execution in Chronic Stroke Patients

The presence of monetary rewards improved the execution of reaching movements for both paretic and non-paretic arms. The two-way repeated-measures ANOVA revealed that there was a main effect for reward ($F(1,27) = 29$, $p < 0.001$, $\eta^2 = 0.54$) and arm ($F(1,27) = 12$, $p = 0.002$, $\eta^2 = 0.34$) on maximum velocity (Figure 3.2c, Table 3.1), indicating faster movements under rewarded conditions across both arms. A similar pattern emerged for movement time, with significant main effects for reward ($F(1,27) = 12$, $p = 0.002$, $\eta^2 = 0.33$) and arm ($F(1,27) = 88$, $p < 0.001$, $\eta^2 = 0.79$) (Figure 3.2d, Table 1). An interaction effect was detected in maximum velocity ($F(1,27) = 6$, $p = 0.02$, $\eta^2 = 0.2$). However, no interaction was found for movement time ($F(1,27) = 0.21$, $p = 0.65$, $\eta^2 = 0.008$). The significant interaction effect in maximum velocity suggests that the difference in maximum velocity between rewarded and non-rewarded conditions is not consistent across the two arms. To further investigate these effects, post-hoc paired t-tests were performed. These tests were used specifically to examine the effect of reward within each arm and to explore the differences between arms under different conditions. Significant differences in maximum velocity were observed between rewarded and non-rewarded conditions for both the paretic arm ($t(27) = -4.8$, $p < 0.001$) and the non-

paretic arm ($t(27) = 4.6$, $p < 0.001$). Differences were also significant between the paretic and non-paretic arms in both rewarded ($t(27) = -3.8$, $p < 0.001$) and non-rewarded conditions ($t(27) = -3.1$, $p = 0.005$), corroborating the main effects.
Given the significant interaction between reward and arm type on maximum velocity, and the significant differences revealed by paired t-tests, it was hypothesized that the increase in velocity due to rewards might differ in magnitude between arms. To explore this hypothesis, a DiD analysis was performed to compare the changes from non-rewarded to rewarded conditions across the paretic and non-paretic arms. This analysis revealed a significantly greater enhancement of the reward effect in the non-paretic arm ($t(27) = -2.35$, $p = 0.02$) (Figure 3.3).

Execution Enhancement Does Not Deteriorate Movement Precision

Investigating the precision of movements, patients demonstrated greater radial accuracy with their non-paretic arm (Figure 3.2e, Table 3.1). A significant main effect was observed for arm ($F(1,27) = 59$, $p < 0.001$, $\eta^2 = 0.71$) while neither reward ($F(1,27) = 1.5$, $p = 0.23$, $\eta^2 = 0.06$) nor the interaction between reward and arm ($F(1,27) = 0.01$, $p = 0.91$, $\eta^2 = 0.0005$) were significant. This indicates that the reward-based enhancements in movement execution did not compromise accuracy for either arm.

Reaction Time Benefits from Rewards at the Expense of Selection Accuracy

Regarding action selection, reaction times decreased in the presence of rewards (Figure 3.2b, Table 1), with significant main effects observed for reward ($F(1,27) = 24$, $p < 0.001$, $\eta^2 = 0.5$) and arm ($F(1,27) = 12$, $p = 0.002$, $\eta^2 = 0.33$). No interaction effect was detected ($F(1,27) = 4$, $p = 0.06$, $\eta^2 = 0.14$). Conversely, selection accuracy

diminished when rewards were offered for both arms (Figure 3.2a, Table 3.1). The main effect of reward on selection accuracy reached significance ($F(1,27) = 5.3$, $p = 0.02$, $\eta^2 = 0.18$) while arm ($F(1,27) = 0.11$, $p = 0.74$, $\eta^2 = 0.0047$) and interaction ($F(1,27) = 0.15$, $p = 0.70$, $\eta^2 = 0.0064$) did not. This pattern suggests a trade-off where improvements in reaction time were achieved at the expense of selection accuracy across both arms. To investigate how speed-accuracy functions are influenced by reward, an analysis was conducted as shown in Figure 3.4 (a and b). Trials for each reward value and participant were sorted based on reaction time and divided into 50 quantiles (Manohar et al., 2015). For each quantile, the average selection accuracy (percentage of non-distracted trials) over a 30% centile window was calculated. Group averages were then obtained for each quantile in both speed and accuracy dimensions, and the results are displayed in Figure 3.4. As anticipated, the reward shifted the speed-accuracy functions downward, highlighting the trade-off between speed and accuracy induced by reward incentives.

	Mean (SD)				***p* (Main effects)**		***p* (Interaction)**
	Paretic		Non-Paretic		Reward	Arm	
Action execution	No Reward	Reward	No Reward	Reward			
Maximum Velocity (cm/s)	21.52 (4.93)	23.34 (5.17)	26.75 (8.82)	30.18 (8.91)	< 0.001	0.002	0.02
Movement Time (ms)	810 (140)	780 (130)	550 (100)	520 (90)	0.002	< 0.001	0.65
Radial Error (mm)	230 (64)	226 (74)	12.5 (2.1)	12 (2.3)	0.23	< 0.001	0.91
Action selection							
Reaction Time (ms)	910 (190)	880 (160)	820 (180)	760 (160)	< 0.001	0.002	0.06
Selection accuracy (%)	69 (25.77)	64 (24.94)	71 (25.70)	65 (23.74)	0.03	0.74	0.70

Table 3.1: Reaching Performance Variables for Paretic and Non-Paretic Arms with Reward Influence in Week 1.
This table presents the average values and standard deviation (SD) for five reaching variables for both paretic and non-paretic arms in week 1, comparing conditions with and without reward. Two-way repeated-measures ANOVA p-values are reported, indicating the main effects of 'Reward' and 'Arm', as well as the interaction between these factors. The units for maximum velocity are centimeters per second (cm/s), for movement time and reaction time are milliseconds (ms), for radial error are millimeters (mm), and for selection accuracy are percentages (%).

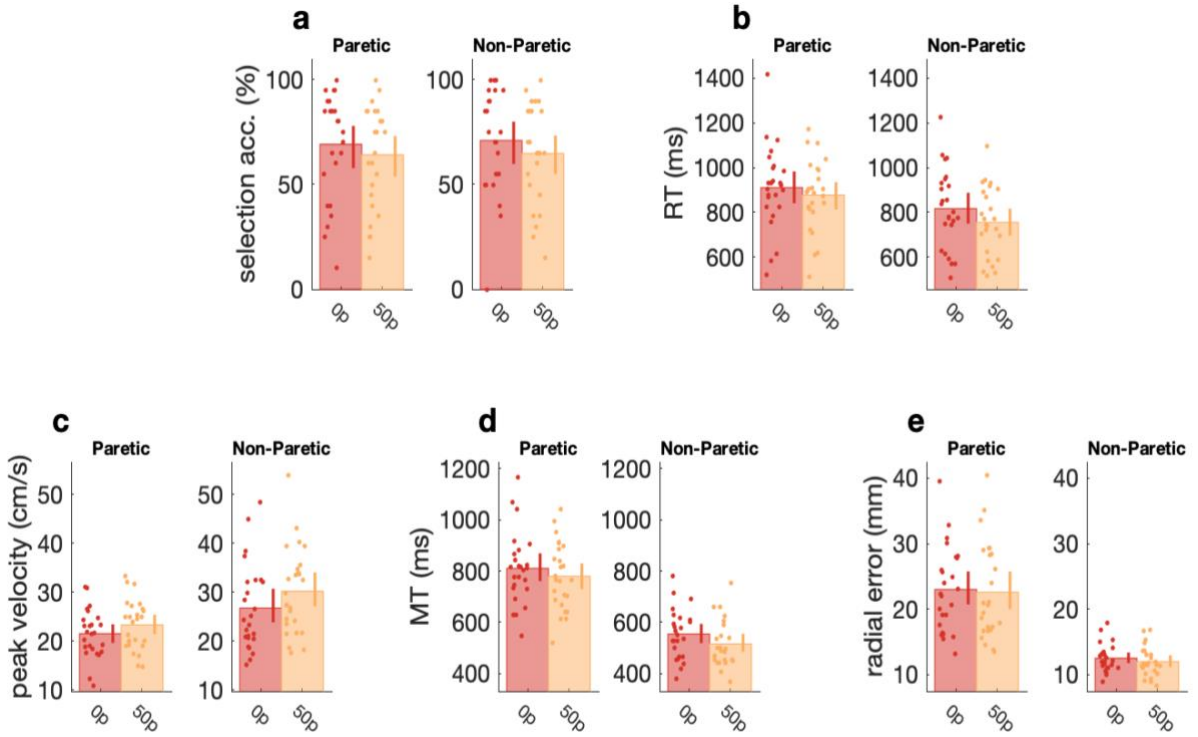


Figure 2.2: Reward-Based Changes in Action Selection and Execution for Paretic and Non-Paretic Arms in Week 1.
The effect of reward conditions on the action selection (a. Reaction times, b. Selection accuracy) and action execution (c. Average peak velocity, d. Average movement time, e. Average radial error) variables for both paretic and non-paretic arms during the initial week of the rehabilitation program. Bar heights represent group mean values in reward (50p) and no-reward (0p) conditions. Individual participant data are denoted by dots, and error bars indicate the 95% confidence intervals for the mean.

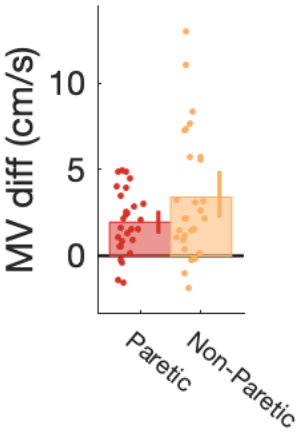


Figure 3.3: Differential Impact of Reward on Maximum Velocity by Arm
The difference in maximum velocity (MV diff) between rewarded and non-rewarded conditions for each arm. MV diff is calculated by subtracting the mean MV in no-reward conditions from the mean MV in reward conditions for each participant. The data show a statistically significant greater increase in MV diff in the non-paretic arm compared to the paretic arm. The bars represent the mean MV diff for the arm group, individual participant values are marked by dots, and error bars indicate the 95% confidence intervals for the group means.

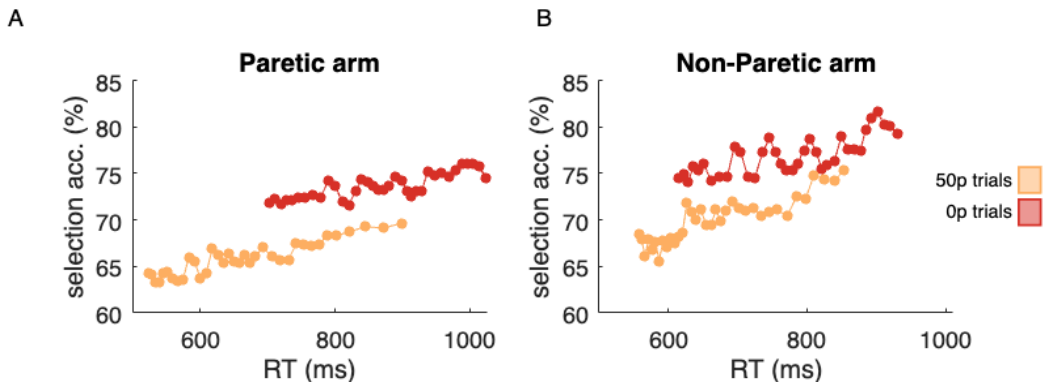


Figure 3.4. Effect of Reward on Action Selection Speed-Accuracy Trade-Off:
(A) Action selection speed-accuracy functions for the paretic arm and (B) the non-paretic arm shifted downward in reward trials. The functions are derived by sliding a 30% centile window over 50 quantile-based bins. For each bin, the counts of nondistracted and distracted trials were obtained, and the ratio (100 × nondistracted/total) was calculated. The top left corner indicates faster and more accurate performance. Selection acc. represents selection accuracy (%), and RT (ms) represents reaction time in milliseconds.

Week 1 vs Week 3 – Paretic Arm:

Rehabilitation Enhances Motor Performance While Rewards Boost Execution Speed

During the rehabilitation program, a two-way repeated-measures ANOVA was conducted to assess the effects of reward and timepoint on the movement time and maximum velocity of the paretic arm. The analysis revealed a significant main effect of reward ($F(1,19) = 9.3$, $p = 0.01$, $\eta^2 = 0.33$) and timepoint ($F(1,19) = 11$, $p = 0.005$, $\eta^2 = 0.38$) on movement time, with no significant interaction ($F(1,19) = 1.6$, $p = 0.23$, $\eta^2 = 0.076$) (Figure 3.6d, Table 2). In terms of maximum velocity (Figure 3.6c), there was a significant main effect of reward ($F(1,19) = 46$, $p < 0.001$, $\eta^2 = 0.71$), indicating faster movements in rewarded conditions, while the effect of timepoint was not significant ($F(1,19) = 0.02$, $p = 0.9$, $\eta^2 = 0.0008$). However, a notable interaction between reward and timepoint was observed ($F(1,19) = 6.5$, $p = 0.01$, $\eta^2 = 0.26$),

suggesting a time-dependent modulation of the reward effect on velocity. Post-hoc tests further examined this interaction, revealing significant differences in maximum velocity between rewarded and non-rewarded conditions at both week 1 ($t(19) = -4.6$, $p < 0.001$) and week 3 ($t(19) = -6.5$, $p < 0.001$). No significant changes were observed in maximum velocity from week 1 to week 3 in either the rewarded ($t(1,19) = -0.41$, $p = 0.69$) or non-rewarded conditions ($t(1,19) = 0.37$, $p = 0.72$). A DiD analysis was subsequently performed to compare the reward/no-reward condition differences across weeks 1 and 3. DiD revealed a significant amplification of the reward effect by week 3 ($t(19) = -2.5$, $p = 0.01$) (Figure 3.6), indicating that the impact of rewards on maximum velocity became more pronounced over time.

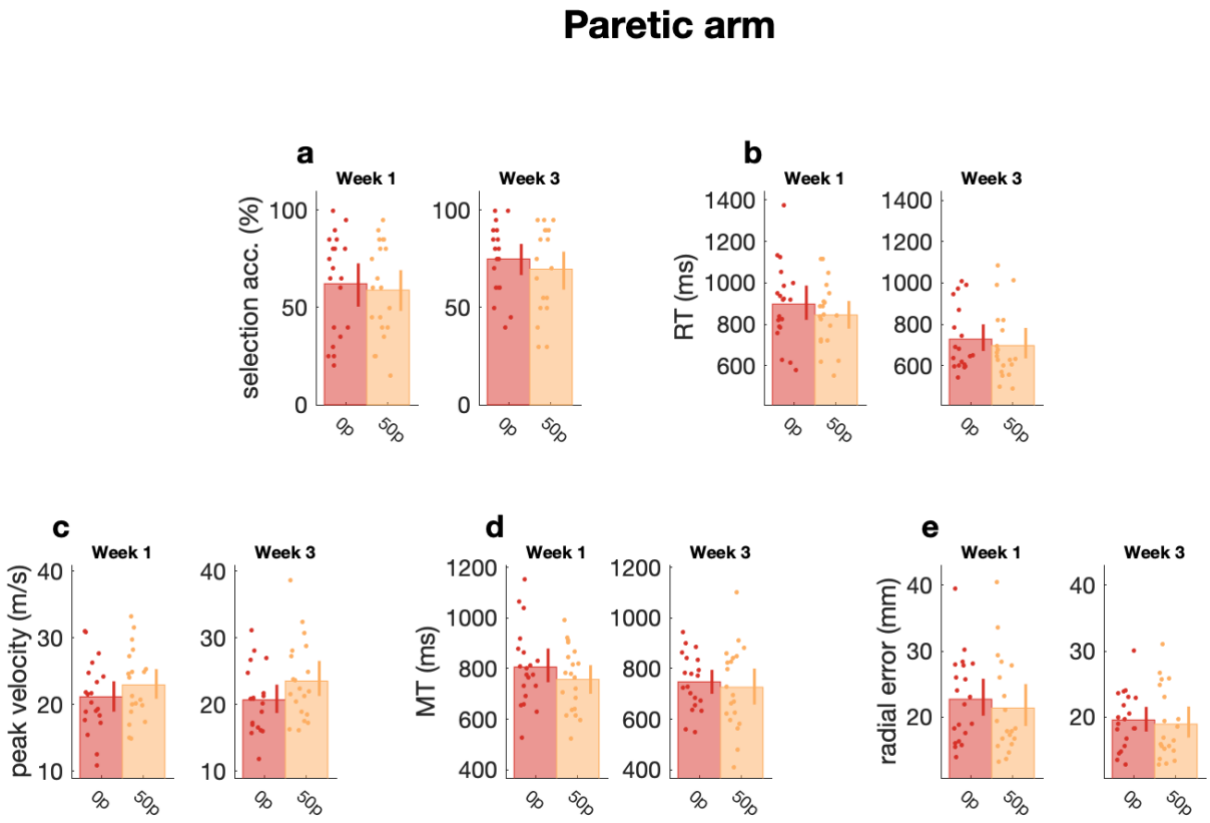
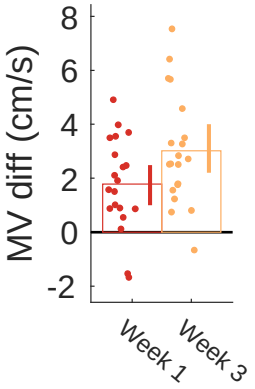


Figure 3.5: Comparative Reward-Based Changes in Action Selection and Execution for the Paretic Arm Across Week 1 and Week 3.
Influence of reward conditions on the action selection (A. Reaction times, B. Selection accuracy) and action execution (C. Average peak velocity, D. Average movement time, E. Average radial error) variables for the paretic arm at two time points: week 1 and week 3. Bar heights show the group averages, dots represent individual participant values, and error bars show the 95% confidence intervals for the mean.

Figure 3.6: Time-Dependent Reward Effect on Maximum Velocity
The Maximum Velocity differences (MV diff) are computed by subtracting the mean MV in no-reward conditions from the mean MV in reward conditions for each participant. The data indicate a statistically significant increase in the reward-based MV difference in week 3 relative to week 1. The bars represent the group mean MV difference, individual participant values are denoted by dots, and error bars correspond to the 95% confidence intervals of the group mean.



Movement Accuracy Improved with Rehabilitation and Rewards

Both reward and rehabilitation positively influenced movement accuracy (Figure 3.5e, Table 3.2). The two-way ANOVA results indicated a significant main effect of reward ($F(1,19) = 5.3$, $p = 0.03$, $\eta^2 = 0.22$). Similarly, the timepoint showed a significant main effect ($F(1,19) = 6.1$, $p = 0.02$, $\eta^2 = 0.24$). No interaction effect was found between reward and timepoint ($F(1,19) = 0.52$, $p = 0.48$, $\eta^2 = 0.026$), suggesting that both factors independently contributed to the observed improvements in movement accuracy.

Action Selection Accuracy Benefits from Rehabilitation, Unaffected by Rewards

Regarding the action selection aspect, the analysis indicated a reward-associated decrease in reaction time, with significant main effects of reward ($F(1,19) = 14$, $p < 0.001$, $\eta^2 = 0.43$) and timepoint ($F(1,19) = 5.6$, $p = 0.028$, $\eta^2 = 0.23$) but no interaction ($F(1,19) = 0.63$, $p = 0.44$, $\eta^2 = 0.032$) (Figure 3.5b). There was also a main effect of timepoint on selection accuracy ($F(1,19) = 8.4$, $p = 0.008$, $\eta^2 = 0.31$), with reward showing no significant main effect ($F(1,19) = 3.9$, $p = 0.06$, $\eta^2 = 0.17$) nor interaction ($F(1,19) = 0.16$, $p = 0.69$, $\eta^2 = 0.0086$) (Figure 3.5a).

Speed-Accuracy Trade-Off Changes Over Time

To further elucidate these findings, the speed-accuracy functions for action selection were analysed at two different time points: Week 1 and Week 3. The plots in Figure 3.7 (a and b) illustrate these functions. Participants improve their overall action selection performance, achieving faster reaction times and higher accuracy by Week 3. However, the reward-based speed-accuracy trade-off persists, with rewards consistently leading to faster but less accurate responses. This suggests that while rehabilitation improves both speed and accuracy, the inherent trade-off induced by rewards remains stable over time.

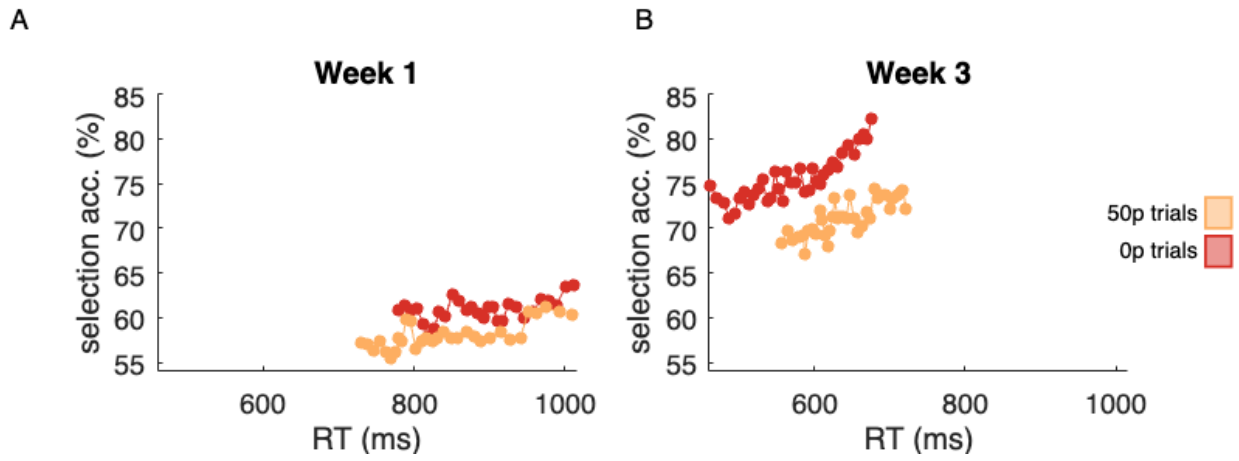
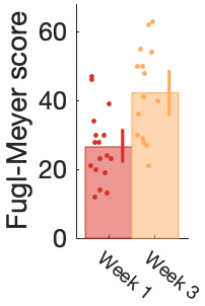


Figure 3.7. Speed-Accuracy Trade-Off in Action Selection Over Time:
(A) Speed-accuracy functions for selection in Week 1 and (B) Week 3 shift downward in reward trials. The functions are derived by sliding a 30% centile window over 50 quantile-based bins. For each bin, the counts of non-distracted and distracted trials were obtained, and the ratio (100 × non-distracted/total) was calculated. The top left corner indicates faster and more accurate performance.

Efficacy of Rehabilitation on Upper Limb Motor Function

A paired t-test was conducted to compare the FMA-UE scores before and after the rehabilitation intervention. The assessment scores provide a quantitative measure of motor function, coordination, and dexterity, reflecting the patients' recovery progress. There was a significant improvement in the FMA-UE scores from the initial assessment in week 1 ($M = 29$, $SD = 11.5$) to the follow-up in week 3 ($M = 48$, $SD = 17.7$) ($t(19) = -5.4$, $p < 0.001$) (Figure 3.9). This marked increase in scores indicates a substantial enhancement in motor function of the upper extremities following the rehabilitation program.

Figure 3.8: Pre- and Post-Intervention Fugl-Meyer Assessment Scores for Upper Extremity Function: Fugl-Meyer Assessment scores for upper extremity function in patients at two time points: the beginning (week 1) and the end (week 3) of the three-week intensive upper-limb rehabilitation program. The height of the bar shows the average of the group. Each dot on the graph represents an individual value, while the error bars illustrate the 95% confidence interval of the mean.



	Mean (SD)				*p* (Main effects)		*p* (Interaction)
	Week 1		Week 3		Reward	Timepoint	
Action execution	No Reward	Reward	No Reward	Reward			
Maximum Velocity (cm/s)	21.29 (5.62)	23.08 (5.62)	20.50 (4.88)	23.52 (5.91)	< 0.001	0.9	0.019
Movement Time (ms)	790 (130)	750 (120)	720 (100)	710 (140)	0.019	0.006	0.23
Radial Error (mm)	24.4 (9)	23.3 (10.1)	21.2 (69)	19.6 (65)	0.015	0.05	0.67
Action selection							
Reaction Time (ms)	870 (230)	790 (160)	750 (120)	690 (130)	< 0.001	0.029	0.44
Selection accuracy (%)	62.25 (25.98)	59.00 (24.58)	75 (19)	70 (23)	0.063	0.009	0.69

Table 3.2: Reaching Performance Variables for the Paretic Arm Across Weeks 1 and 3 With and Without Reward.
Average values and SDs for five reaching variables are shown for the paretic arm in weeks 1 and 3, under reward and no-reward conditions. Two-way repeated-measures ANOVA p-values highlight the main effects of 'Reward' and 'Test' period, along with their interaction effect. The units for maximum velocity are centimeters per second (cm/s), for movement time and reaction time are milliseconds (ms), for radial error are millimeters (mm), and for selection accuracy are percentages (%).

Week 1 vs Week 3 – Non-Paretic arm

The non-paretic arm served as a control to establish baseline performance. The two-way repeated-measures ANOVA indicated a significant improvement in the execution component of reaching movements when rewards were introduced (Figure 3.9, Table 3.3). Specifically, there was a significant main effect of reward in both maximum velocity ($F(1,19) = 38$, $p < 0.001$, $\eta^2 = 0.67$) (Figure 3.9c) and movement time ($F(1,19) = 35$, $p < 0.001$, $\eta^2 = 0.65$) (Figure 3.9d). However, as the non-paretic arm was not the target of rehabilitation, no significant improvements were observed between the two time points (week 1 vs week 3), suggesting stability in baseline performance when no specific training was directed at this arm. There was no main effect of timepoint ($F(1,19) = 0.62$, $p = 0.44$, $\eta^2 = 0.031$), and no interaction ($F(1,19) = 0.17$, $p = 0.69$, $\eta^2 = 0.009$) in maximum velocity. Similarly, there was no main effect of timepoint ($F(1,19) = 0.11$, $p = 0.75$, $\eta^2 = 0.006$) nor an interaction ($F(1,19) = 1$, $p = 0.33$, $\eta^2 = 0.05$) in movement time. In terms of accuracy, the radial error analysis revealed that the execution improvements did not compromise movement accuracy, with a significant main effect of reward ($F(1,19) = 7.9$, $p = 0.01$, $\eta^2 = 0.29$) but no main effect of timepoint ($F(1,19) = 0.28$, $p = 0.60$, $\eta^2 = 0.015$) indicating that baseline accuracy was maintained. Interestingly, an interaction effect was present, $F(1,19) = 7.7$, $p = 0.01$, $\eta^2 = 0.29$, suggesting that the reward's impact on accuracy varied across the sessions, with post-hoc tests revealing significant differences under reward conditions in week 3 only ($t(1,19) = -4$, $p < 0.001$).

Intensive rehabilitation had no impact on the reaching selection component of the non-paretic arm

While rewards led to a significant decrease in reaction times ($F(1,19) = 33$, $p < 0.001$, $\eta^2 = 0.64$) indicating quicker response initiation, this change was not affected by rehabilitation ($F(1,19) = 1.1$, $p = 0.31$, $\eta^2 = 0.054$) and showed no interaction between reward and timepoint ($F(1,19) = 1.1$, $p = 0.30$, $\eta^2 = 0.056$) (Figure 3.9b). Furthermore, rewards negatively affected selection accuracy ($F(1,19) = 16$, $p < 0.001$, $\eta^2 = 0.45$), but, similarly to reaction time, selection accuracy was not influenced by rehabilitation ($F(1,19) = 0.04$, $p = 0.84$, $\eta^2 = 0.002$) nor was there an interaction between the effect of reward and timepoint ($F(1,19) = 0.38$, $p = 0.54$, $\eta^2 = 0.02$) (Figure 3.9a).

	Mean (SD)				***p* (Main effects)**		***p* (Interaction)**
	Week 1		Week 3		Reward	Timepoint	
Action execution	No Reward	Reward	No Reward	Reward			
Maximum Velocity (cm/s)	27.24 (9.20)	30.70 (9.82)	25.91 (7.63)	29.74 (9.04)	< 0.001	0.44	0.69
Movement Time (ms)	540 (110)	500 (100)	550 (100)	500 (110)	0.002	0.75	0.33
Radial Error (mm)	12.2 (2.2)	11.9 (1.9)	12.3 (1.9)	11.2 (1.8)	0.01	0.6	0.01
Action selection							
Reaction Time (ms)	710 (180)	650 (140)	670 (160)	620 (170)	< 0.001	0.3	0.3
Selection accuracy (%)	68 (22)	59 (25)	68 (26)	61 (26)	< 0.001	0.84	0.54

Table 3.3: Reaching Performance Variables for the Non-Paretic Arm Across Weeks 1 and 3 With and Without Reward.
This table displays average values and SDs for five reaching variables for the non-paretic arm in weeks 1 and 3, comparing reward and no-reward conditions. It includes two-way repeated-measures ANOVA p-values that reveal the main effects of 'Reward' and Timepoint, and the interaction between these factors.
The units for maximum velocity are centimeters per second (cm/s), for movement time and reaction time are milliseconds (ms), for radial error are millimeters (mm), and for selection accuracy are percentages (%).

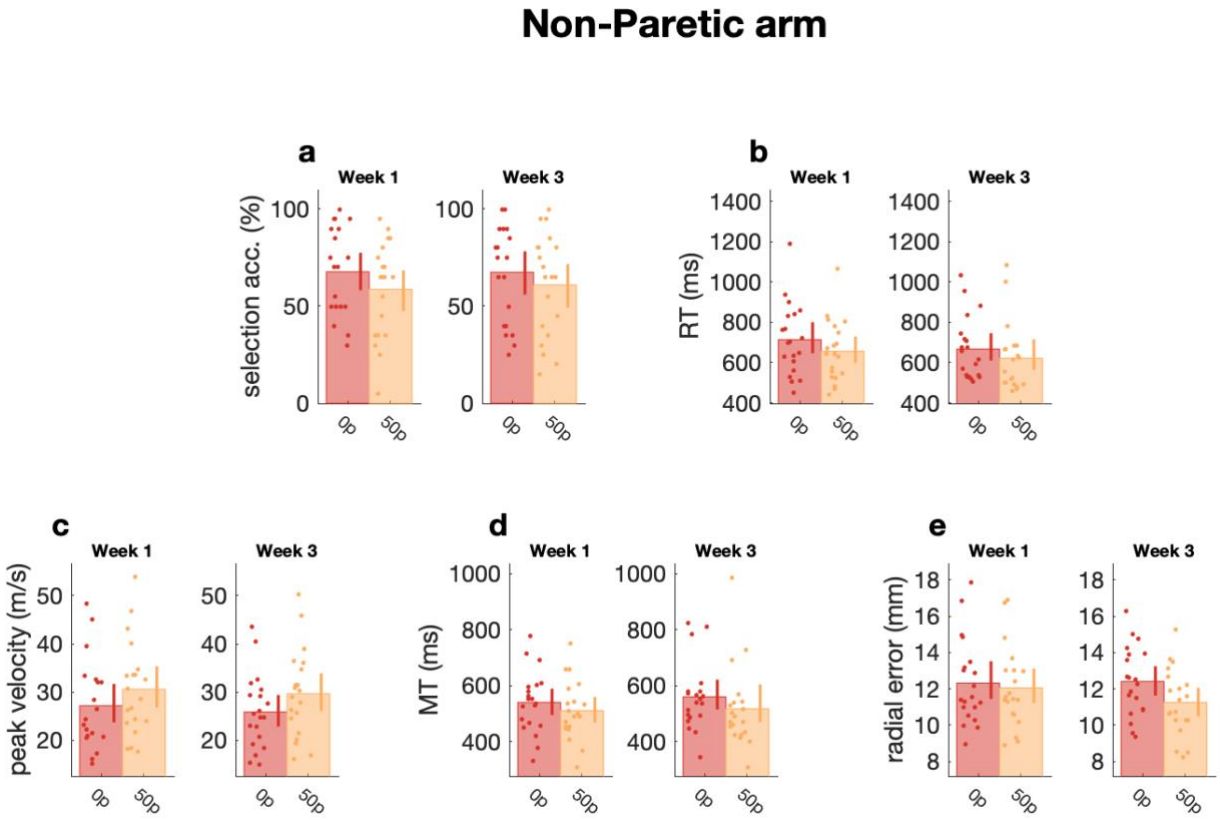


Figure 3.9: Comparative Reward-Based Changes in Action Selection and Execution for the Non-Paretic Arm Across Week 1 and Week 3
The impact of reward conditions on action selection (A. Reaction times, B. Selection accuracy) and action execution (C. Average peak velocity, D. Average movement time, E. Average radial error) variables for the non-paretic arm, comparing the beginning and end of the intervention period (week 1 vs. week 3). The group mean values are indicated by the bar heights, individual values by dots, and the 95% confidence intervals for the mean by error bars.

3.5 Discussion:

In this study, we aimed to examine how reward incentives affect different aspects of motor performance, specifically action selection and execution, in chronic stroke. Additionally, we investigated whether a 3-week intensive rehabilitation program enhanced patient's capacity for reward-based improvements.

Week 1 (Paretic vs. Non-Paretic Arms)

Monetary Incentives Improved Movement Execution in Chronic Stroke Patients without impacting movement accuracy

In the presence of reward, chronic stroke patients experienced a notable improvement in their ability to execute reaching movements across both their affected and non-affected arms. This was evident from a significant improvements in movement time and maximum velocity. These results support previous studies that have reported the positive impact of rewards on stroke patients' performance (Goodman et al., 2014b, Quattrocchi et al., 2017a, Widmer et al., 2022), and we have now extended this into reaching execution. Interestingly, this improvement in execution did not affect their reaching accuracy as there was no change in error during rewarded trials, indicating a break in the speed-accuracy trade-off. Since a break in the speed-accuracy trade-off law is considered a hallmark of skill (Diedrichsen and Kornysheva, 2015), this implies that there was a meaningful improvement in performance.

Monetary Incentives Improved Reaction Time in Chronic Stroke Patients at the cost of selection accuracy

In terms of action selection, reward led to a significant improvement in reaction time for both arms. However, this improvement came at the cost of increased errors, indicating a decrease in selection accuracy. This suggests that the cognitive and motor demands of quickly identifying the correct target and accurately moving towards it were compromised due to the pressure or desire to complete the task more quickly for a reward. This phenomenon is known as "choking on the money"

which can occur when one's ability to perform certain tasks that require cognitive skills, attention, and decision-making is impaired due to the presence of a reward (Mobbs et al., 2009, Smoulder et al., 2023).

Our previous research in this thesis showed that both younger and older adults exhibit this phenomenon, and our current study revealed that this phenomenon is present in stroke patients irrespective of the level of motor impairment. Additionally, we found that there was no significant difference in selection accuracy between the paretic and non-paretic arms, despite a difference in reaction time. This indicates that the cognitive demands of target recognition and decision-making are similar for both arms, suggesting that motor impairments in the paretic arm do not necessarily affect the cognitive process of selecting the correct target. The effect of motor impairment was solely on the execution level.

The similarities observed in reward-based changes in action selection and execution in chronic stroke patients and those seen in healthy older and younger adults suggest that stroke survivors retain comparable reward sensitivity. This may seem contradictory to studies that have reported low motivation and reduced reward processing in stroke patients (Oestreich et al., 2020, Widmer et al., 2019). However, these studies did not conclude that patients will not be influenced by reward incentives on a behavioural level. Additionally, these studies primarily focused on acute and subacute stroke patients, revealing disruptions in the ventral striatum (Widmer et al., 2019) and fronto-subcortical (Oestreich et al., 2020) circuits associated with reward processing. It is possible that by the time patients reach the chronic stage, neuroplastic changes may have already occurred, allowing partial or complete functional restoration in these regions. Such neuroplasticity may underlie the observed improvements in motor performance following reward incentives. It is

also important to note that these studies compared reward system function between stroke patients and healthy controls. While there may be differences in the extent of reward-based improvement in motor performance between chronic stroke patients and healthy individuals that reflect the differences in their reward system integrity, our study did not include a healthy control group. Therefore, we cannot definitively conclude to what extent the reward-based changes in motor performance in chronic stroke patients differ from those in healthy individuals.

Week 1 vs Week 3

The three-week intensive rehabilitation program resulted in significant improvements in motor abilities. These improvements were evidenced by the enhanced Fugl-Meyer Assessment-Upper Extremity (FMA-UE) scores for the paretic arm, which showed a significant improvement in week 3 compared to week 1.

Accompanying this positive change were significant enhancements in the initiation and execution speed of movements (reaction time and movement time), as well as in movement accuracy. It is expected for these enhancements to occur as both speed and accuracy are closely linked to improvement in motor abilities (Hesam-Shariati et al., 2019). However, it seems that the rehabilitation program did not have an additional effect on the reward-based improvements in these variables. This lack of additional gains can be attributed to the possibility that the motivating effect of the reward had already reached its peak, and further motivational potential did not lead to performance improvements beyond the general enhancements brought about by the rehabilitation. Interestingly, during the third week of the rehabilitation program, it was observed that the reward had a differential effect on the maximum velocity. Although there was no significant effect of timepoint, a significant interaction effect

was observed. This indicates that the introduction of a reward had a more pronounced effect on the maximum velocity by the end of the program. This finding suggests that improvements in motor function led to improvements in the ability to respond to motivational cues, supporting the relationship between improvement in motor functions and reward sensitivity (Ramasubbu et al., 1998a). However, it is important to note that the improvement related to rewards was limited to maximum velocity, and it is difficult to conclude that the intensive rehabilitation program broadly impacts reward-based motor performance improvement.

The observed discrepancy between the substantial improvements in FMA scores and the more subtle changes in specific task performance metrics, such as maximum velocity and movement time, from week 1 to week 3 highlights the difference between broad functional assessments and specific kinematic measures. The FMA provides a comprehensive evaluation of motor function, encompassing a wide range of abilities, including joint range of motion, muscle strength, coordination, and voluntary control (Deakin et al., 2003). Therefore, improvements in FMA scores may reflect gains across multiple aspects of motor recovery, some of which might not be directly or immediately reflected in the speed and efficiency of specific task-related movements. For instance, a patient might exhibit increased muscle strength and coordination, as detected by the FMA, allowing them to perform a wider range of movements and activities. However, these gains might not immediately translate into faster movement speeds or reduced movement times during a specific reaching task.

An additional noteworthy result was the overall improvement in selection accuracy observed in week 3 compared to week 1. This improvement may stem from the focused attention required to perform movements correctly during upper-limb rehabilitation. Such sustained attention can, over time, improve the patient's ability to concentrate and maintain attention, which is essential for minimizing distractions during tasks. This interpretation aligns with the findings of An and Kim, who trained 30 stroke patients in activities of daily living for 30 minutes five days a week over five weeks and observed improvements in their attention and executive functions (An and Kim, 2021). The rehabilitation-driven enhancement in selection accuracy observed in this study appears to mirror the positive impact of rehabilitation on attention and cognitive functions reported by An and Kim. The absence of a rehabilitation effect on the non-paretic arm was anticipated, as this arm was not the focus of the rehabilitation efforts. Results from the non-paretic arm also rule out a training effect and confirm that the observed changes in the examined variables for the paretic arm were attributable to the rehabilitation intervention.

Limitation

Lack of Control Group

One limitation of this study is the absence of a control group consisting of age-matched healthy individuals. Including such a control group would allow for assessing whether the stroke patients' responses to the rewards are typical or differ from those of individuals without neurological impairments, thereby strengthening the conclusions about the specific impacts of stroke on reward processing and motor performance. While age-matched healthy individuals were tested using a similar task design in the previous chapter, it is important to note that the Kinarm devices used in

the two studies were different. The first chapter employed the end-point Kinarm, whereas this study utilized the Exoskeleton Kinarm. These devices differ significantly in how they support the arm, including variations in holding position and gravitational support, which can substantially affect task performance. Due to these differences in the mechanical and functional properties of the devices, a direct comparison of the results between healthy individuals and stroke patients across these chapters was deemed inappropriate.

Age variability

Another limitation is the inclusion of different age groups. Age significantly influences neuroplasticity (Park and Bischof, 2013) and motor performance (Ward and Frackowiak, 2003). In addition, older adults may exhibit slower motor recovery rates (Yoo et al., 2020) and differ in their responses to motivational stimuli compared to younger adults (Dhingra et al., 2020), which was demonstrated in the previous chapter of this thesis. However, due to the same resource limitations that impacted control group recruitment, our study did not stratify patients by age or include a sufficient age range to analyse these potentially differential effects. Future research may consider stratifying stroke survivors based on age and using age as a covariate in analyses. This approach will provide insights into how different age groups respond to reward incentives during rehabilitation. Understanding age-related differences in recovery and motivation can lead to personalized, age-adapted rehabilitation strategies that optimize motor function improvements for individual stroke survivors.

3.6 Conclusion

This work suggests that reward can improve the speed and accuracy of motor execution in stroke survivors without compromising movement precision, indicating a preserved sensitivity to rewards in the chronic stage of stroke recovery. The rehabilitation program itself also contributed to significant improvements in motor abilities but without a clear impact on reward-sensitivity. Expanding on these findings, the next step in this line of research would be to investigate the impact of reward incentives on rehabilitation outcomes. This would involve incorporating reward stimuli into rehabilitation programs and assessing their effectiveness in improving motor function, engagement and overall recovery in stroke survivors. By doing so, we can further explore the potential benefits of a reward-based approach and optimize rehabilitation strategies to enhance the quality of life for stroke survivors.

Chapter 4

EXPLORING THE ROLE OF THE PRIMARY MOTOR CORTEX IN REWARD-BASED ENHANCEMENTS OF MOTOR CONTROL USING CONTINUOUS THETA BURST STIMULATION

4.1 Abstract

While rewards are known to enhance motor performance, the neural mechanisms underlying these effects remain unclear. This study investigates the role of the primary motor cortex (M1) in reward-based motor control enhancements using continuous theta burst stimulation (cTBS) to modulate M1 activity. Twenty-seven participants performed a reward-based reaching task under M1 cTBS and sham conditions. Our findings replicate the reward-based improvements in movement execution, characterized by increased speed without loss of accuracy. However, contrary to expectations, M1 cTBS did not significantly affect either the selection or execution components of the task or the reward-based enhancements. These results suggest that the observed reward effects are not solely mediated by M1, highlighting the need for further research to identify the neural substrates involved in reward-based motor performance enhancements.

4.2 Introduction:

There is clear evidence that explicit reward improves both action selection and execution in healthy subjects (Chen et al., 2017). In a sequence learning task, for example, monetary reward reduces selection errors as well as response time, implying faster and more accurate action selection (Klein et al., 2012b, Derosiere et al., 2017). Reward also improves action selection in the face of potential distractors in saccadic eye movements (Manohar et al., 2015) and reaching movements (Codol et al., 2020b). It also has shown to invigorate movement execution by enhancing maximum velocity and reducing end-point error during saccades (Takikawa et al., 2002c) and reaching movements (Summerside et al., 2018a, Galaro et al., 2019a,

Codol et al., 2020b). Despite multiple previous reports confirming these reward-driven improvements (Griffiths and Beierholm, 2017, Reppert et al., 2018), there is still a lack of understanding about the neural substrates underlying these effects. We aim to study how the primary motor cortex (M1) contributes to reward-based improvement in motor performance using transcranial magnetic stimulation (TMS). Through the study of animal and human lesions, it has been found that certain brain structures are involved in reward processing. These structures include the orbitofrontal (Baylis and Gaffan, 1991, Hikosaka and Watanabe, 2000), medial prefrontal regions (Xue et al., 2009, Pastor and Medina, 2021), amygdala (Murray, 1991, Nakamura et al., 1992), striatum (Schultz, 1998a), pallidum (Smith et al., 2009), and midbrain dopaminergic nuclei (Mirenowicz and Schultz, 1994, Romo and Schultz, 1990). These regions are interconnected and form a complex integrated network (Wise, 2002, Romo and Schultz, 1990, Ikemoto, 2010, Wickens et al., 2003). It is commonly believed that rewards impact behaviour by affecting the activity of these structures and that motor areas are solely responsible for execution (Pessiglione et al., 2007, Schultz et al., 2000, Wickens et al., 2003). Nonetheless, recent research suggests that the M1 may have a more extensive role in reward processing than previously thought (Thabit et al., 2011, Galaro et al., 2019b, Ramkumar et al., 2016, An et al., 2019). Various studies suggest that M1 may combine and process information related to rewards with selecting and executing movements. TMS research has demonstrated that alterations in M1 excitability can occur in reaction to reward prediction (Kapogiannis et al., 2008) and the desire to attain a gratifying stimulus (Gupta and Aron, 2011). In a more recent study, Galaro et al., found that M1 excitability mediates the effect of reward and reflects its subjective value (Galaro et al., 2019b). Several other studies

recorded neural activity from the M1 of monkeys performing reaching and grasping tasks, where some trials were cued as rewarding, others as non-rewarding, and found that firing rates of M1 neurons were generally higher during rewarding trials, suggesting that neural activity levels in M1 encode reward information during action execution (An et al., 2019, Ramkumar et al., 2016).

Regarding action selection, multiple sources of evidence suggest that M1 may encode action values when making motor decisions. Research using TMS has demonstrated that the magnitude of motor evoked potentials (MEPs) measured during decision-making is influenced by the value of the potential actions to be selected (Klein-Flügge and Bestmann, 2012, Derosiere et al., 2017, Klein et al., 2012a). However, many other researchers argued that it is unclear whether these changes in neural firing rate and excitability during action selection and execution in M1 reflect the M1 intrinsic reward processing activity or if these activities reflect motivational modulation from other brain reward-related structures (Roesch and Olson, 2003, Roesch and Olson, 2004, Thabit et al., 2011, Gupta and Aron, 2011). To investigate the role of M1 in the reward-based improvements of action selection and execution, continuous theta-burst TMS (cTBS) will be used to alter M1 excitability prior to participants performing a reward-based reaching task. cTBS has previously been shown to decrease cortical excitability in M1 and alter neural activity for 20 minutes after stimulation (Huang et al., 2005, Goldsworthy et al., 2012). Recently, we used cTBS on the supplementary motor area (Saes et al.) and ventromedial prefrontal cortex (vmPFC) to disrupt neural activity in these two regions before participants performed a reward-based action selection and execution reaching task. We found that both the selection and execution of reaching movements significantly improved with the presence of reward. However, cTBS on

these two areas had no effect on the reward-based changes in action selection and execution (Codol et al., 2020a). This led us to the prediction that other brain areas, such as M1, might be driving the observed reward-based enhancements in action selection and execution.

4.3 Method:

Participants

31 individuals were initially recruited for the experiment. Of these, three participants did not return for the second session, and one participant was unable to complete the stimulation process during the first session. Therefore, 27 participants participated in the experiment, with a mean age of 20 and a range of 18-25 years. Out of these participants, 20 were female. They were compensated £7.5 per hour and received performance-based monetary rewards during the reaching task. All participants were right-handed and did not have a family history of epilepsy, motor, psychological, or neurological conditions, or any medical condition that would prevent them from using cTBS. The study was approved by the University of Birmingham Ethics Committee and was conducted in compliance with their regulations.

Task Design

The task design in this study followed the basic paradigm described in Chapter 2. The key difference was the addition of continuous theta burst stimulation (cTBS) to modulate M1 activity. The specifics of the task, including the reward structure and trial types, remained consistent with the details provided in Chapter 2.

Procedure

The experiment occurred in two sessions, with at least a 5-day interval between them. The participants were randomly assigned to receive either sham or M1 cTBS, and the order of stimulation was counterbalanced. During the first session, participants underwent screening to ensure that they didn't have any medical or psychological conditions that would prevent them from participating in the study. Next, they were given a leaflet to read about the TMS technique and had the opportunity to ask the experimenter any questions they had. After that, they were exposed to TMS on their forearm to familiarize themselves with the sensation. We used a figure-of-eight, 80mm diameter coil (Magstim Co Ltd, Whitland, UK) to deliver the stimulation. The TMS coil was placed tangentially over the left hemisphere, with the handle pointing back and away from the midline at about 45°, in the optimal position (hot spot) for eliciting MEPs in the contralateral first dorsal interosseous (FDI) muscle. For sham cTBS, the stimulating coil was placed orthogonally over the FDI muscle hot spot. To ensure precise TMS coil placement, we used Brainsight's frameless neuronavigational system (Brainsight, Rouge Research) to register participants' heads to a default Talairach template in the Brainsight software. Resting motor threshold (RMT) was determined by finding the minimum single-pulse intensity on M1 that caused MEPs of at least 50 μV in 5 out of 10 trials. To record MEPs evoked by TMS, surface electromyographic electrodes were placed on the FDI muscle. The muscle activity signals were then recorded and amplified using the Biopac system (BIOPAC Systems, Inc., Santa Barbara, CA).

cTBS procedure

We applied the cTBS technique using one cycle that lasted for 40 seconds at 70% of the RMT or 48% intensity, whichever was the lowest. We chose to use the RMT instead of the active motor threshold (AMT) to ensure that there was no influence from prior voluntary motor activity on the after-effects of cTBS (Haeckert et al., 2021, Gentner et al., 2008, Goldsworthy et al., 2012). We applied a total of 200 burst trains at a frequency of 5 Hz, with 3 pulses per burst and a pulse frequency of 50 Hz, which resulted in a total of 600 pulses (Huang et al., 2005, Galea et al., 2010).

Data analysis

The data analysis followed the same procedures as described in Chapter 2, focusing on action selection and action execution components. The trials were manually divided into two categories: distracted and non-distracted. The notable difference in this chapter is the percentage of trials eliminated due to reaction times exceeding 1000 ms, below 200 ms, or radial errors exceeding 3 cm. In this study, this amounted to 0.86% of all trials.

Statistical analysis

We used a 2 × 2 repeated measures analysis of variance (Falkenstein et al.) with two factors: reward value (0p versus 50p) and cTBS group (sham, M1). We adjusted for sphericity using the Greenhouse-Geisser method as needed for repeated-measures ANOVA. For post hoc analysis, we used a two-tailed t-test with Bonferroni correction. We considered effects significant if $p < 0.05$.

4.4 Results

Reward enhanced execution but impaired selection

In contrast to Codol et al. (2020), reward improved the execution component but not the selection component of reaching movements (Figure 4.1). Specifically, reward led to faster reaction times ($F(1,26) = 32.5$, $p < 0.001$, $\eta 2 = 0.55$) (Figure 4.1a), but also caused a decrease in selection accuracy ($F(1,26) = 52.4$, $p < 0.001$, $\eta 2 = 0.67$) (Figure 4.1b), indicating that selection speed was increased at the expense of selection accuracy.

In terms of execution, reward increased peak velocity ($F(1,26) = 67.5$, $p < 0.001$, $\eta 2 = 0.72$) (Figure 4.1c) and decreased movement time ($F(1,26) = 60$, $p < 0.001$, $\eta 2 = 0.7$) (Figure 4.1d). However, the radial error remained similar across both rewarded and non-rewarded trials ($F(1,26) = 0.2$, $p = 0.66$, $\eta 2 = 0.007$) (Figure 4.1e), indicating that reward improved the speed of execution whilst maintaining accuracy.

M1 cTBS had no effect on performance

There was no significant impact of cTBS on the reward-driven effects. In terms of selection, there were no main or interaction effects observed for cTBS on reaction times (cTBS: $F(1,26)= 0.07$, $p = 0.78$, $\eta 2 = 0.002$; interaction: $F(1,26) = 0.17$, $p = 0.68$, $\eta 2 = 0.006$) (Figure 4.1a) or selection accuracy (main effect of cTBS: $F(1,26) = 0.37$, $p = 0.54$, $\eta 2 = 0.014$; interaction: $F(1,26) = 0.25$, $p = 0.62$, $\eta 2 = 0.009$) (Figure 4.1b).

Similarly, cTBS had no effect on execution. There were no main or interaction effects observed for cTBS on peak velocity (cTBS: $F(1,26)= 0.01$, $p = 0.9$, $\eta 2 = 0.004$;

interaction: F(1,26)= 0.1, p = 0.75, $\eta 2$ = 0.003) (Figure 4.1c), movement times (cTBS: F(1,26) = 0.17, p = 0.67, $\eta 2$ = 0.006; interaction: F(1,26) = 0.17, p = 0.68, $\eta 2$ = 0.006) (Figure 4.1d) or radial error (cTBS: F(1,26) = 3.7, p = 0.65, $\eta 2$ = 0.125; interaction: F(1,26) = 0.025, p = 0.87, $\eta 2$ = 0.009) (Figure 4.1e). Therefore, cTBS over M1 had no general effect on selection and execution performance, nor on the effects of reward.

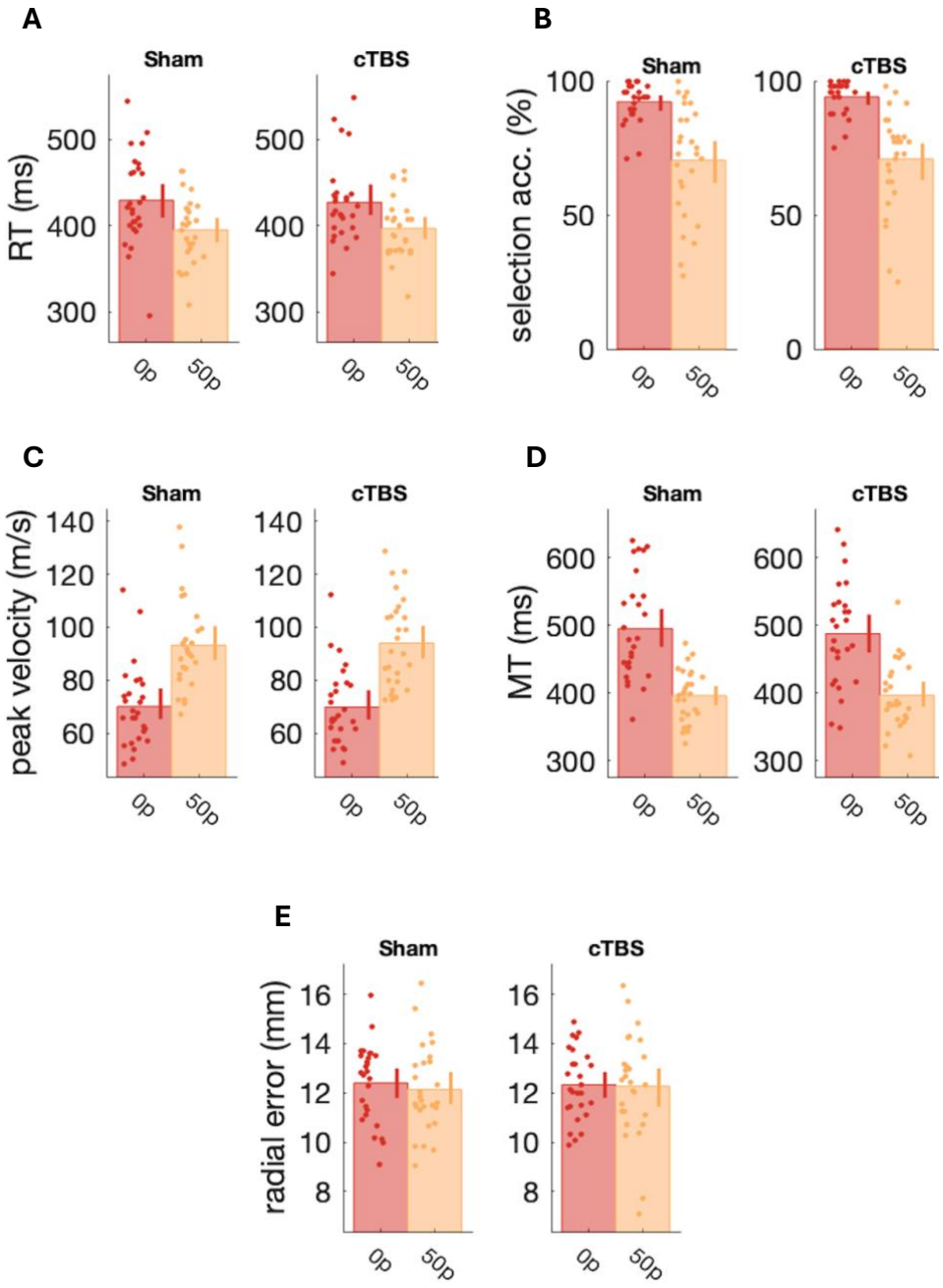


Figure 4.1: Effect of reward and cTBS on action selection and execution.
Action selection variables: A. Reaction times, B. Selection accuracy.
Action execution variables: C. Average peak velocity, D. Average movement time and E. Average radial error. The height of the bar shows the average of the group. Each dot on the graph represents an individual value, while the error bars illustrate the 95% confidence interval of the mean.

4.5.Discussion

Our study employed cTBS to disrupt M1 activity, aiming to investigate its role in the reward-driven enhancements of selection and execution performance during a reaching task. The reward effects on action execution, as originally reported by Codol et al. (2020), were consistently replicated among our participants. However, unlike multiple previous studies (Codol et al., 2020b, Manohar et al., 2015), we found that the introduction of reward led to a decrease in selection accuracy. Furthermore, we found that M1 cTBS did not induce any notable changes in these behavioural effects.

Such a reward-based decrement in selection accuracy, although contradictory to previous results (Codol et al., 2020b, Manohar et al., 2015), aligns with previously reported phenomena known as "choking under pressure" or "choking on the money" (Mobbs et al., 2009). Several behavioural studies have shown that when faced with high reward contingencies, performance on certain tasks, notably those requiring attention, decision-making, and cognitive skills, is impaired (Ariely et al., 2009, Mobbs et al., 2009). This phenomenon is hypothesized to occur because the anticipation of a reward triggers increased activity in the brain's reward circuitry, particularly in areas such as the nucleus accumbens, prefrontal cortex, and amygdala. These regions are crucial for processing reward expectations and motivational states but can also interfere with cognitive control processes (O'Reilly and Frank, 2006, Schultz, 1998b). Increased reward-circuitry activity can lead to heightened arousal and stress levels, which in turn disrupt attention and executive function, crucial components for tasks requiring cognitive effort (Beilock and Carr, 2001). Specifically, the prefrontal cortex, which plays a key role in maintaining

cognitive control and managing complex decision-making processes, may become overloaded under high-stress conditions, leading to diminished performance (Arnsten, 2009). This overload can manifest as a reduction in working memory capacity and impaired attentional focus, both of which are essential for accurate action selection (Smoulder et al., 2023, Mobbs et al., 2009). In our study, the reward-induced decrement in selection accuracy suggests that participants were exhibiting the "choking on the money" phenomenon during the action selection process, which is a cognitively demanding process. Moreover, our findings suggest that participants associated the reward more strongly with speed than with selection accuracy, as evidenced by improvements in reaction time at the expense of selection accuracy. The discrepancy between this study and our previous results is not entirely clear. Despite similar instructions being used in the current study and Codol et al., 2020 study, even minor variations in how the instructions are given may cause participants to interpret them differently, thus affecting their performance. It's possible that in the current study, there was an unintentional emphasis on speed over accuracy, causing participants to prioritize speed to maximize their rewards. However, this explanation is speculative and may not fully explain the observed differences. Other factors, such as variations in participant groups, their personal interpretation of the task, or specific strategies used to optimize rewards, could also be contributing factors.

Regarding the impact of cTBS, the goal was to modulate M1 activity to investigate its role in reward-based enhancement in motor control. We assumed that we would observe an inhibitory effect of cTBS on reaching performance, based on previous reports regarding the impact of cTBS on index finger movement performance (Wilkinson et al., 2010, Iezzi et al., 2010), and the impact of cTBS on functionally connected brain areas to the stimulated area (Valchev et al., 2015, Jung and

Lambon Ralph, 2021). We also hypothesized that inhibiting M1 activity may not only inhibit performance in general but also diminish the positive impact of reward. This would suggest reward processing activities within M1 (An et al., 2019, Ramkumar et al., 2016). Alternatively, cTBS may cause a general decrease in selection and execution performance but not affect reward-based improvements. This would support the idea that reward processing was occurring in other neural structures (Roesch and Olson, 2003, Roesch and Olson, 2004, Thabit et al., 2011, Gupta and Aron, 2011). However, we observed no change in performance across the two sessions, preventing us from drawing definitive conclusions about the impact of M1 modulation on reward-based enhancement in reaching. Several factors may explain the lack of observed impact of cTBS on motor performance. One possible factor is the variability in response to cTBS. While many studies have shown that cTBS has an inhibitory effect (Huang et al., 2005, Goldsworthy et al., 2012), other studies have reported high variability in response to cTBS. For example, McCalley et al. (2021) found that only one-third of the participants showed an inhibitory response to cTBS, while two-thirds of the participants showed either no response or an excitatory response (McCalley et al., 2021). This variability could potentially explain the lack of observed impact of cTBS on performance. Another possibility may be attributed to the specificity of the muscle targeted by the stimulation. In this study, cTBS was applied to the FDI muscle, following established protocols (Huang et al., 2005, Galea et al., 2010). The FDI muscle, primarily involved in index finger movements, likely plays a limited role in the broader dynamics of whole-arm movements that characterize forward-arm reaching tasks. Consequently, the stimulation of FDI might not have been sufficient to influence the performance of arm reaching, which predominantly involves larger muscle groups like those in the upper arm and

forearm. For future investigations, it would be prudent to apply cTBS to muscle groups that are more directly involved in the execution of the task at hand. This approach could enhance the relevance and impact of neuromodulation on the behavioural output. Additionally, adapting the cTBS protocol for tasks that are more reliant on the activity of the FDI muscle, such as simple index finger tasks that have a reward-based component (Wilkinson et al., 2010, Iezzi et al., 2010) could provide more definitive insights into the effects of cTBS. Moreover, implementing a pre-experimental screening to assess individual responsiveness to cTBS could be beneficial. This screening would involve measuring MEPs before and after cTBS application to identify participants who exhibit a clear inhibitory response in the targeted muscle. This stratification would help ensure that the data collected reflect the influence of cTBS on participants who are responsive to this form of stimulation, thereby potentially increasing the robustness and interpretability of the findings. Another potential area of future studies worth investigating is exploring alternative neuromodulation techniques such as low-frequency repetitive TMS (rTMS) (typically 1 Hz) and cathodal transcranial direct current stimulation (tDCS) (Siebner et al., 2004). Both techniques can modulate cortical excitability, which may influence reward-based changes in motor enhancement (Yadollahpour and Yuan, 2018). Future studies may consider using these two techniques on M1 to reveal its role in reward-based enhancement in motor performance.

4.6 Conclusion

Without any observable effect on performance, we cannot draw any conclusions about the impact of M1 modulation on reward-based changes in action selection and execution. Our findings suggest that cTBS over M1 had no observable impact on

reaching performance. Future studies could potentially explore the role of M1 in reward-based enhancement in motor control by utilizing the same cTBS protocol but with a simpler reward-based movement task that is dependent on finger movement, which might be more likely to show an impact. Additionally, we recommend stratification based on cTBS response to account for inter-subject variability. This approach may provide greater insight into the role of M1 in the reward-based enhancement in motor control.

CHAPTER 5

THE IMPACT OF TASK DIFFICULTY ON REWARD-BASED FUSION OF SEQUENTIAL REACHING MOVEMENTS

5.1 Abstract

Fusion of sequential movements is essential for efficient motor performance, particularly in rehabilitation contexts. This study examines how task difficulty, modulated via target size, influences reward-based fusion in sequential reaching movements. One hundred participants performed a sequential reaching task on a touchscreen device with either large or small targets, under reward and no-reward conditions. Our results show that rewards improve movement time and maximum velocity, particularly with larger targets, but do not significantly affect movement fusion. Task difficulty was the primary factor influencing fusion, with larger targets promoting significantly higher fusion indexes than smaller targets. These findings suggest that task difficulty plays a crucial role in optimizing motor performance and that reward-based improvements may not be sufficient to enhance movement fusion. Future interventions should focus on task design to promote efficient motor learning and performance retention.

5.2 Introduction

In our daily-life activities we perform many sequential actions such as driving, typing or playing a musical instrument. When a particular sequential task is new to an individual it is often performed as a series of discrete sub-movements (Fowler, 1980, Jin et al., 2014, Shah et al., 2013, Willingham, 1998). With practice, these sub-movements are blended together to form continuous action, a phenomenon known as fusion (Sosnik et al., 2015, Sosnik et al., 2007, Sosnik et al., 2004a). The term fusion, also known as coarticulation in some literature, is a process of optimizing discrete motor components into a single kinematically unique motor primitive, allowing us to perform sequential tasks more efficiently (Sosnik et al., 2007, Sosnik et al., 2004a).

Numerous studies have investigated how fusion is formed in different sequential movement tasks such as piano playing (Winges and Furuya, 2015), fingerspelling (Jerde et al., 2003), typing (Soechting and Flanders, 1992, Soechting and Flanders, 1997), and reaching (Sporn et al., 2022, Todorov and Jordan, 1998). All of them have found that the formation of fusion makes the motor performance more efficient, resulting in the movement being performed with greater speed and smoothness. In addition, this mechanism allows for the effortless execution of skilled sequential actions. Sosnik et al. demonstrated that when a sequence of discrete movements is fused, the motion becomes ballistic, preventing individuals from stopping until the sequence is complete (Sosnik et al., 2015, Sosnik et al., 2007). This indicates that fusion changes the way the brain plans a movement, and when different motor elements combine, they are represented as a single motor primitive (Sosnik et al., 2015, Sosnik et al., 2004a, Willingham, 1998).

Stroke patients often experience long-term disability, with upper limb weakness and spasticity being the most common issues, leading to disjointed jerky movements (Sheean, 2002, Tyson et al., 2006). The jerky movements of stroke patients suggest that they are likely experiencing a breakdown in movement fusion. Several studies found that stroke patients exhibit disjointed sub-movements initially, but these gradually blend with adjacent actions during the recovery period, leading to more coherent movements (Dipietro et al., 2007, Gulde et al., 2017, Rohrer et al., 2002, Rohrer et al., 2004). Nonetheless, there is a notable gap in research focusing on the role of movement fusion in stroke rehabilitation. Therefore, investigating potential facilitators of movement fusion would be helpful to promote the return of movement smoothness and improve the efficacy of interventions.

Reward seeking has been shown to be effective in altering human and animal behaviour (Arias-Carrión and Pöppel, 2007, Berridge and Kringelbach, 2008, Sigmund et al., 2001). The impact of reward on different aspects of motor learning and memory has been investigated by many researchers. Reward has been shown to enhance implicit motor learning (Wächter et al., 2009), motor memory retention (Abe et al., 2011), and action selection and execution (Codol et al., 2019). In addition, Sporn et al. found that reward facilitated the emergence of fusion, and this gained effect became reward independent – even in the absence of a reward, participants continued to fuse their movements (Sporn et al., 2022). These studies showed that a monetary reward could improve fusion in neurologically impaired patients with arm function issues, such as stroke patients, and increase their movement efficiency in a rehabilitation setting.

However, it has been established that these reward-based benefits are temporary and disappear once the reward is removed (Codol et al., 2020b, Manohar et al., 2015, Summerside et al., 2018b). Yet, these findings are based on simple tasks that only involve a single action, such as reaching for a static target. On the other hand, in more complex sequential or continuous tasks, the positive effects of rewards tend to last longer and persist beyond the removal of the reward (Sporn et al., 2022). This difference in sustainability is thought to be due to distinct underlying movement mechanisms with differing energy efficiency profiles. For discrete reaching, reward initially speeds up isolated sub-movements through heightened muscle co-contraction and stiffness (Codol et al., 2020b), but this process incurs high metabolic costs that cannot be sustained without reward due to its energetic inefficiency (Codol et al., 2020b, Ueyama and Miyashita, 2011). On the other hand, during sequential reaching, performance gains from reward become independent of further incentives, as fusion enhances movement time while increasing efficiency (Sporn et al., 2022). Given the

vulnerability of clinical populations to energy expenditure, it is crucial to identify strategies that promote the energetically favorable process of fusion to optimize motor skill learning and retention in rehabilitation. Despite this, there has been little exploration into how to facilitate fusion. Sporn et al. found increased early spatial variability driven by reward correlated with greater later fusion (Sporn et al., 2022). This indicates that trial-by-trial variability during movement may be how sensorimotor systems learn (Dhawale et al., 2017). This suggests that encouraging environmental exploration through relaxed accuracy demands could increase behavioural variability, thereby improving subsequent fusion and performance. Sosnik et al. also found that less stringent accuracy requirements could accelerate fused movement formation, while stricter accuracy requirements could limit fusion (Sosnik et al., 2015, Sosnik et al., 2007). Therefore, adjusting task difficulty could offer a means of reducing the accuracy requirements and promoting environmental exploration. Fitts's law states that human movement time is determined by the index of difficulty (ID), which is based on the distance between the target and the hand, as well as the size of the target (Fitts, 1954). In other words, shorter distances and larger targets result in faster and more accurate movements. Therefore, by systematically changing the size of the target, we could influence the formation of fusion in sequential reaching. However, the effects of target size on fusion are not yet fully understood. The current study aims to investigate how task difficulty, modulated via target size, influences reward-based fusion during upper limb sequential reaching. Varying target sizes will provide insight into how stricter accuracy demands impact fusion development. According to the literature, it is hypothesised that reward will enhance performance across all target sizes through different mechanisms. For larger target sizes, reward will decrease movement time by promoting fusion, leading to long-lasting and energetically efficient performance gains.

For smaller target sizes, the reward will result in faster discrete movements by increasing the maximum velocity of individual sub-movements. However, fusion will be inhibited, leading to the use of energetically inefficient strategies, such as increased arm stiffness. This will result in transient decreases in movement time for each discrete movement when the reward is removed.

5.3 Method

Participants

100 participants (61 males, age range: 18-40, Mage: 27 years, 89 right-handed) were recruited via Prolific (www.prolific.ac) to take part in an online sequential reaching task. All participants were novices to the task and were free of motor, visual and cognitive impairment. Following task completion, participants were compensated £5 and additional money could be earned based on performance during reward trials. Ethical approval was obtained through the University of Birmingham's Departmental Ethics Board (ERN_09_528AP30A).

Materials

The online task was created using Java programming language and was hosted on the Gorilla Experiment Builder server (https://gorilla.sc). Participants were recruited through Prolific (www.prolific.ac) and were able to use any smartphone with a touchscreen to complete the task. Once the participant clicked on the task link, they were directed to the task page on the Gorilla website. They were then presented with the information sheet, consent form, and demographic questions, including information about their age, gender, handedness, and phone brand/model. After that, they proceeded to the learning phase of the task where they familiarized themselves

with the task (see below). The data was downloaded directly from the Gorilla server. Code for the task can be found here here: https://osf.io/9qk2n/.

Design

Experimental design

Participants were randomly assigned to one of four groups, each consisting of 25 participants. The groups were: Large Reward (RL) with 12 males (age range 18-37, mean age 23 years); Large No Reward (LNR) with 18 males (age range 17-37, mean age 24 years); Small Reward (SR) with 17 males (age range 18-39, mean age 24 years); and Small No Reward (SNR) with 16 males (age range 18-38, mean age 24 years). The study utilized a 2x2 factorial design with two factors: target size (small vs. large) and feedback (reward vs. no reward).

Task design

The task was based on the research conducted by Sporn et al. (2022), with some modifications made to the target sizes. Four circular targets were placed around a central "via target". During the task, the target size remained constant, with 5% and 12.5% of the screen being covered by small and large targets, respectively (Figure 5.1a). Since phone sizes varied among participants, the x and y position of each target was calculated as a percentage of the screen from the top and left of the viewport. Targets 2 and 3 were positioned at an obtuse angle of 126 degrees from the via target to ensure fusion was possible (Figure 5.1c).

Procedure

The experiment comprised of five blocks namely learning, baseline, training, post-reward and post-no-reward, which was similar to that of Sporn et al. (2022) (Figure 5.1a). The participants were instructed to hold their phone with their non-dominant hand and complete the trials as quickly and accurately as possible using the dominant hand's index finger.

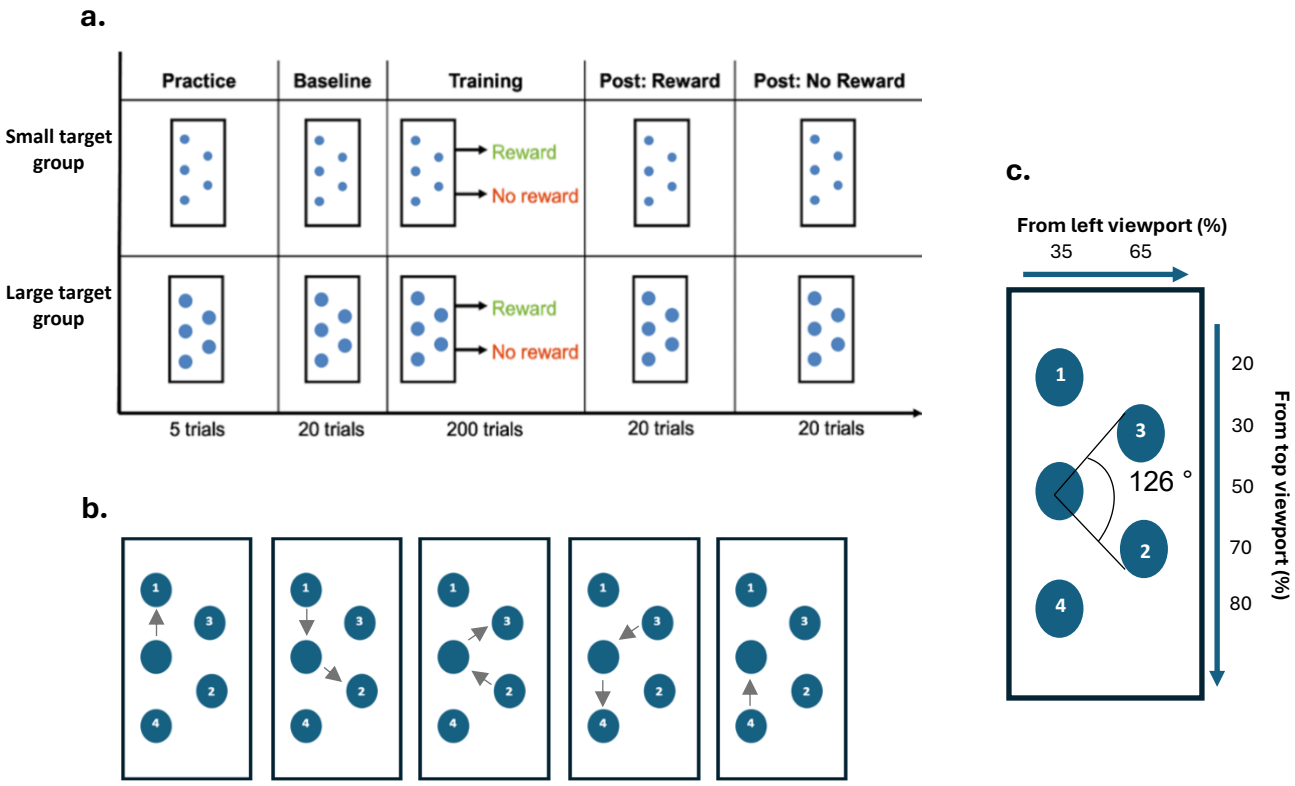


Figure 5.1: Experimental setup. a) Study design. The study involved 5 practice trials to learn the sequence, followed by 20 baseline trials with no reward. Participants then completed 200 training trials either with a reward or without a reward, depending on the group they were assigned to. This was then followed by two blocks of 20 post-assessment trials (post-reward and post-no-reward, counterbalanced across participants). b) The sequence consisted of 8 sequential movements starting from a central "via target". c) Target positions are shown as percentages from the top/left edge of the display area.

Learning

To prepare participants for the main experiment, an initial learning phase was included. During this phase, participants were required to familiarize themselves with the

movement sequence. When ready to start a trial, participants had to press and hold the central target for 1.5 seconds. They would then slide their finger from the central target to hit four surrounding targets in a specific numbered order. After each movement, the finger returned to the central target before moving on to the next target in the sequence. This resulted in eight consecutive reaching movements per trial (Figure 5.1b). To demonstrate that they had memorized the sequence, participants were required to successfully complete five consecutive trials without errors. Only then could they proceed to the next part of the experiment. This ensured participants had learned the sequence so that any improvements seen later could be attributed to enhanced execution, rather than continued memory gains. Trials during the learning phase were not rewarded.

Baseline

The baseline block consisted of 20 trials to evaluate pre-training differences between the groups. The trials were conducted in the same manner as previously described, but without the numbered cues indicating the order of target hits. Participants were asked to complete each trial as quickly and accurately as possible, but the trials were not rewarded. No feedback related to performance was provided during these baseline trials in order to obtain an unbiased measure of each participant's starting ability prior to training.

Training

The training block consisted of 200 trials conducted in the same manner as the baseline trials. Participants in both large and small target groups were randomly assigned to either the reward or no-reward group. Those in the reward group were

informed that they could earn monetary rewards ranging from 0 to 5 pence based on their movement time, with faster performances yielding greater rewards. After each trial, this group was provided feedback on their performance in the form of the money earned. Participants in the no-reward group were told they would not receive any financial incentives but should still aim to complete each trial as quickly and accurately as possible. Unlike the reward group, the no-reward group did not receive any feedback about their performance after trials. The only information provided to them was to proceed to the next trial (Figure 5.2).

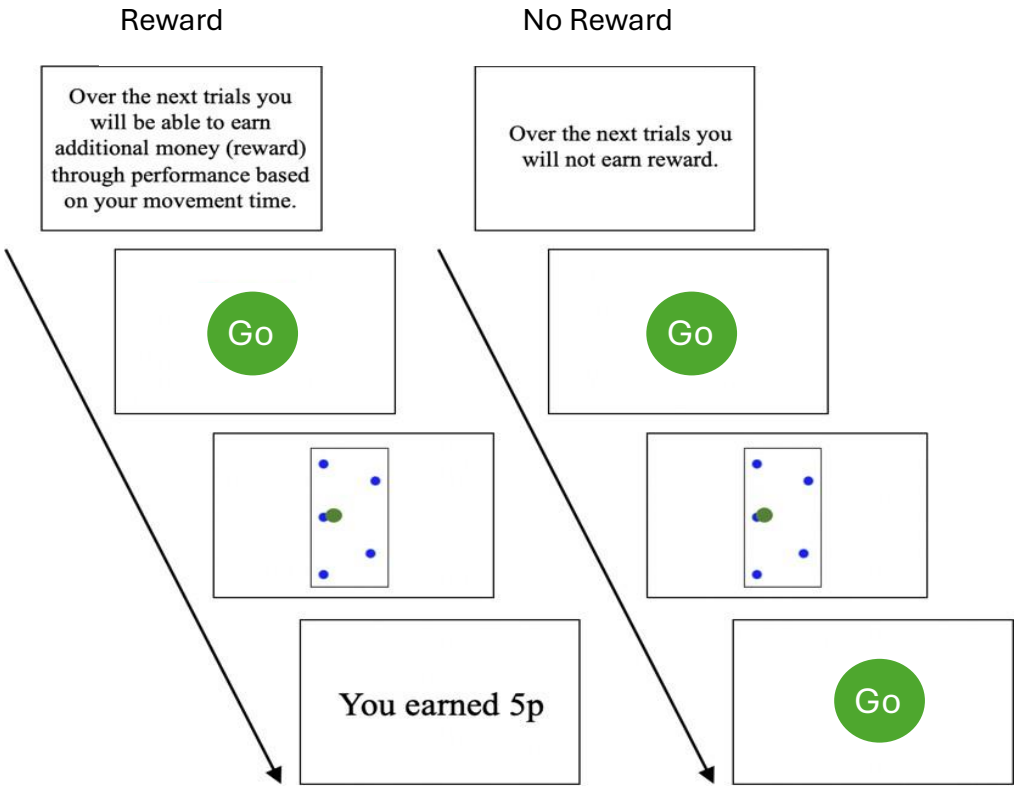


Figure 5.2: Details of reward and no-reward training trials. In the training phase, participants were presented with a sequence of instruction screens, task cues, and feedback on each trial. For the reward group, participants were informed of the amount of reward earned, which ranged from 0-5p. For the no-reward group, no feedback was given.

Post-Assessments

Participants completed two post-assessments: post-reward (all participants were rewarded) and post-no-reward (all participants were not rewarded). Each block had 20 trials, the same as training.

Measurement

Movement Time (MT)

Movement time was taken by calculating the total movement duration of each trial, which is the time between exiting the start circle and reaching the last target.

Maximum Velocity (MV)

To calculate the maximum velocity, we used the derivative of positional data to create velocity profiles for each trial. The velocity profiles were then smoothed with a Gaussian kernel ($\sigma = 3$) and divided into 8 segments, representing individual movements towards targets using target entry and exit data (see Figure 5.3a). Next, we identified the maximum velocity for each movement and calculated the average of these eight values. This provided us with a single value for maximum velocity per trial.

Fusion Index (FI)

The FI provided a measure of how successive movements were fused from one target to the next, forming smoother reaching actions within each trial. Initially, participants produced eight distinct velocity profiles for each individual movement (Figure 5.3a). However, as training progressed, sub-movements began to merge, evident by the reduction from eight to five velocity peaks (Figure 5.3b). This indicated a higher degree

of fusion between elements of the movement sequence, reflecting more efficient motor planning and control.

Fusion was measured by the fusion index (FI) developed by Sporn et al. (2022):

$$Fusion\ Index = 1 - \frac{\frac{(V_{max1} + V_{max2})}{2} - V_{min}}{\frac{(V_{max1} + V_{max2})}{2}} \quad \text{Equation 1}$$

where V_{max1} and V_{max2} are the maximum velocity of two consecutive reaching movements, and V_{min} is the minimum velocity of the via point between these movements. FI compares the average maximum velocities of two sequential reaches with the minimum velocity around the via target. The smaller the difference between these two measures, the higher the resulting index, which indicates a higher amount of fusion. The maximum FI score of each consecutive reaching is 1, which indicates a fully fused movement, and the minimum FI score is 0, indicating no fusion at all. When reaching between consecutive targets, fusion is more likely to occur when the angular direction between the movements is obtuse (larger than 90 degrees) (Sosnik et al., 2004b). In the current task, there were three target pairs that satisfy this condition, and, therefore, the maximum FI for each trial was 3.

Reward Calculation

The monetary reward values were determined using a closed-loop design that dynamically adjusted the rewards based on each participant's MT. Specifically, the MTs from the previous 20 trials were sorted from fastest to slowest. The participant's MT on the current trial was then given a rank within this array of past performances. This rank determined the reward amount allocated according to table 5.1, with a higher MT

rank earning higher rewards. This ensured that participants earned similar amounts and were continuously challenged to increase their speed throughout the task.

Table 5.2. Monetary Rewards (Pence) Awarded According to Participant's Ranking of Current Movement Time Among Previous 20 Trials

Reward	Rank
5p	>= 90%
4p	>= 80% and < 90%
3p	>= 60% and < 80%
2p	>= 40% and < 60%
1p	>= 20% and < 40%
0p	< 20%

Error

When a participant missed a target, reached the wrong target, or lift their finger before the completion of the trial, an error massage was displayed asking the participant to repeat the trial. Error was calculated as the proportion of repeated trials to the whole number of trials.

Statistics

Matlab (Mathworks, Natwick, MA, USA) was used to perform the analysis. Values for all participants in each measured variable were pooled, and values above 3 standard deviations away from the mean were considered outliers. If a participant had an outlier in any of the measured variables, the whole trial's data was removed and not included in the analysis. Ninety-eight participants had one or more outliers. The average of removed trials among these participants was eight trials. An inspection of histograms and one-sample Kolmogorov-Smirnov tests showed that all measures were not normally distributed. Since there are no non-parametric alternatives, and ANOVAs are relatively robust to violations of normality (Schmider et al., 2010), ANOVAs were used in all measure during training and post-assessments. A 3-way mixed ANOVA (2 × 2 × 2) was carried out where the main effects and interactions of reward (reward, no

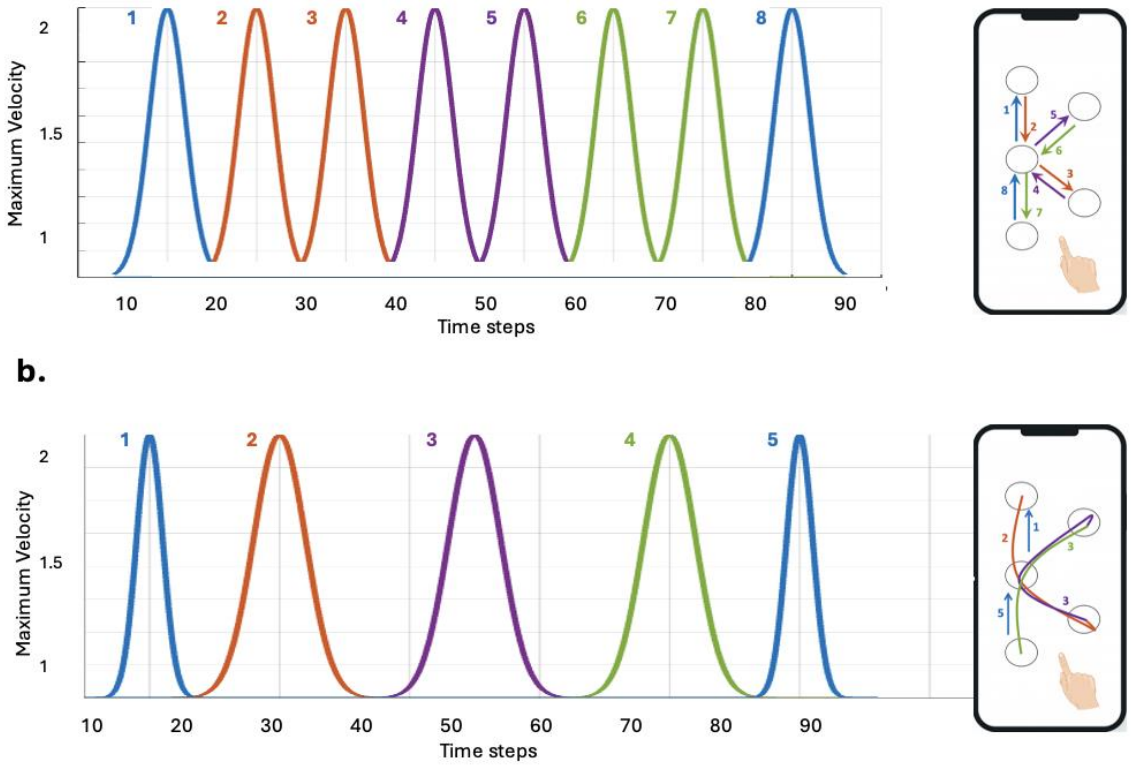


Figure 5.3: Measurement of fusion. a) Velocity profiles and predicted paths for the eight individual sequential movements. b) Velocity profiles and predicted paths when movements were fused. c) Velocity profiles and straight line trajectories between targets pre-fusion. d) Velocity profiles and curved trajectory post-fusion. Higher FI values were reflected by a reduced difference between the first two peaks and an increased minimum velocity (Vmin) around the via target.

reward), target size (large, small) and timepoint were evaluated during training (early vs late) and post-assessment (post-reward vs post-no reward) in MT, MV and FI. Here, reward and target size are between-subjects factors and timepoint is a within-subjects factor. The effect of timepoint was examined by calculating the average of the first and last 20 trials of the training block for each measure. Significant interactions were followed up with Mann-Whitney U tests on the differences across timepoint and post assessment phase. An analysis of variability in each group was based on CI standard deviations of early training, which were compared using Mann-Whitney U tests.

5.4 Results

Screen Size

Screen sizes were measured in inches, with the distribution ranging from 5 inches to 6.53 inches diagonally. Since device sizes were not controlled, comparing phone screen sizes in different groups was necessary to ensure this was not a factor during the experiment. A 2 (size: large vs. small) x 2 (reward: reward vs. no-reward) ANOVA was conducted. There was no statistically significant main effect of size ($F(1, 96) = 0.0006$, $p = 0.98$) or reward ($F(1, 96) = 0.005$, $p = 0.82$) nor an interaction between the effects of size and reward on screen area ($F(1, 96) = 1.64$, $p = 0.2$) therefore, screen size was not accounted for during statistical analysis.

Reward and large target size decreased movement time

All groups showed a significant decrease in MT over the course of training, and groups with access to reward and a large target size displayed significantly faster MTs (Figure 5.4; Table 5.2). There was an instantaneous main effect of target size on MT at baseline, ($F(1, 96) = 4.21$, $p<.045$). In the training phase, mixed ANOVA

showed a significant effect of reward upon MT ($F(1, 96) = 9$, $p = 0.003$, $\eta^2 = .9$). There was also a significant effect of timepoint (early vs late), ($F(1, 96) = 57.47$, $p < 0.001$, $\eta^2 = .99$), and of target size on MT, ($F(1, 96) = 10.63$, $p = 0.002$, $\eta^2 = .905$). However, there were no significant interactions between reward, timepoint and target size, ($F(1, 96) = 1.3$, $p = 0.25$, $\eta^2 = .57$).

In the post-assessment phase, all groups showed decrease in movement time in the post reward phase compared to post no reward phase (Figure 5.4, Table 5.2). There was a significant effect of phase (post-reward vs post-no reward), ($F(1, 96) = 38.47$, $p < 0.001$, $\eta^2 = .97$) and target size, ($F(1, 96) = 12.78$, $p < 0.001$, $\eta^2 = .92$) but no significant effect of reward, ($F(1, 96) = 12.78$, $p = 0.094$, $\eta^2 = .74$). There was no interaction between reward, phase and target size ($F(1, 96) = 0.54$, $p = 0.46$, $\eta^2 = .35$).. The lack of a significant main effect for reward in the post-assessment phase indicates that when rewards were removed, their immediate positive effects on MT did not persist.

Table 5.2: Mean and standard deviation (SD) of movement time values in training and post assessment phases

	Mean (SD)			
	Large		Small	
Movement Time (s)	Reward	No Reward	Reward	No Reward
Early Training	1.8 (0.76)	2.1 (1)	2.2 (0.63)	2.7 (1)
Late training	1.31 (0.4)	1.8(1)	1.82(0.55)	2.25 (0.67)
Post Reward	1.17 (0.38)	1.42 (1.1)	1.66 (0.39)	1.79 (0.49)
Post No Reward	1.3 (0.44)	1.62 (0.9)	1.85 (0.41)	1.97 (0.51)

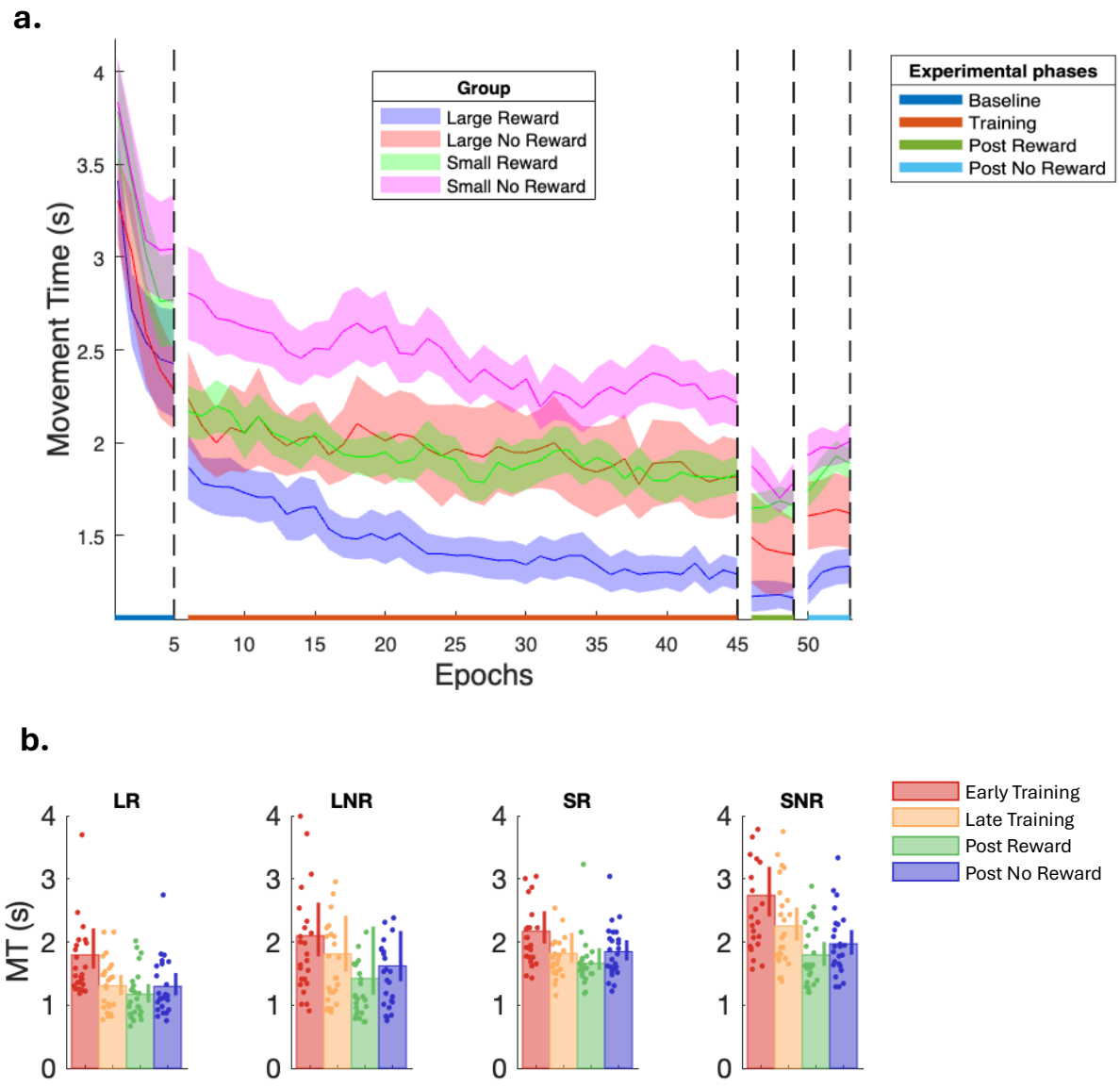


Figure 5.4: Changes in movement time (MT). a) MT changes across all phases in epochs of 5 trials, with the shaded area representing the standard error of the mean. b) Means for MT during early training, late training, post-reward, and post-no reward blocks for the Large Reward (Griffiths and Beierholm), Large No Reward (LNR), Small Reward (SR) and Small No Reward (SNR) groups. Each dot on the graph represents an individual value, while the error bars illustrate the 95% confidence interval of the mean.

Reward and Large Target Size Invigorated MV

MV showed a similar pattern of improvement to MT (Figure 5.5; Table 5.3). At baseline, there was an instantaneous effect of target size on MV baseline ($F(1, 96) = 4.52$, $p < .03$, $\eta^2 = .8$). In the training phase, reward feedback had a significant impact on MV ($F(1, 96) = 8.6$, $p < .005$, $\eta^2 = .83$). There was also a significant impact of timepoint ($F(1, 96) = 65.3$, $p < 0.001$, $\eta^2 = .98$), and of target size on MV, ($F(1, 96) = 14.4$, $p = 0.002$, $\eta^2 = .9$). There was no interaction between feedback, timepoint and target size ($F(1, 96) = 2.2$, $p = 0.14$, $\eta^2 = .68$).

In the post-assessment phases, all groups showed an increase in MV in the post reward compared to the post no-reward phase. There was a significant effect of phase, ($F(1, 96) = 58.3$, $p < 0.001$ $\eta^2 = .97$) and target size, ($F(1, 96) = 18.2$, $p < 0.001$, $\eta^2 = .9$) but no significant effect of reward ($F(1, 96) = 1.3$, $p = 0.026$ $\eta^2 = .55$) and no interaction between group, phase, and target size.

Table 5.3: Mean and standard deviation (SD) of maximum velocity values in training and post assessment phases.

	Mean (SD)			
	Large		Small	
Maximum Velocity (cm/s)	Reward	No Reward	Reward	No Reward
Early Training	30.75 (7.4)	29.6 (10.5)	28.4 (6.5)	22 (6.6)
Late training	37.1 (8.2)	33.2 (12)	31.7 (7.1)	24.6 (5.8)
Post Reward	39.05 (9.1)	41 (15.74)	33.53 (7.09)	29.8 (6.04)
Post No Reward	37.41 (7.36)	35.45 (14.1)	31.01 (6.14)	26.46 (5.54)

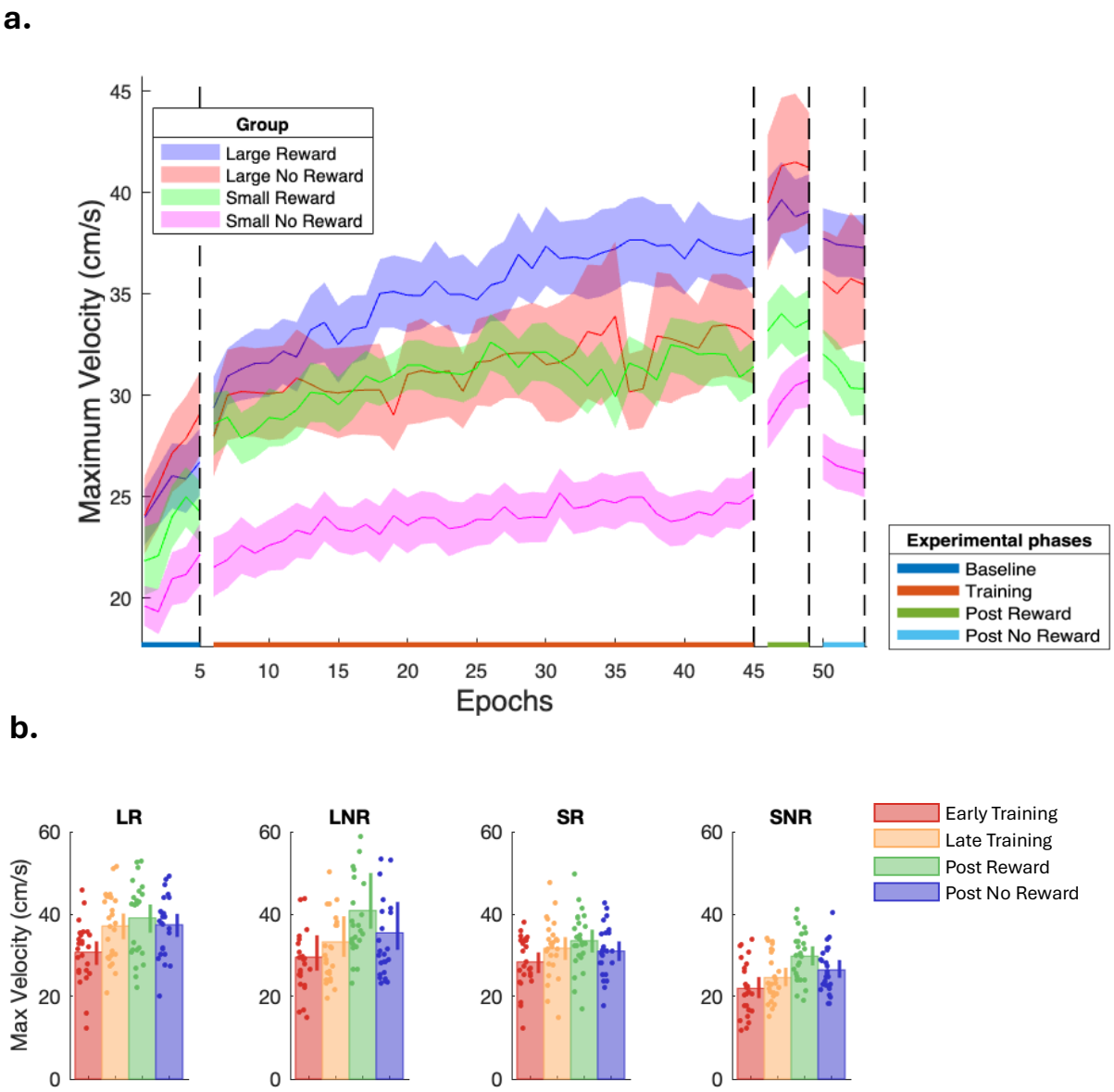


Figure 5.5: Changes in maximum velocity (MV). a) MV changes across all phases in epochs of 5 trials, with the shaded area representing the standard error of the mean. b) Means for MV during early training, late training, post-reward, and post-no reward blocks for the Large Reward (Griffiths and Beierholm), Large No Reward (LNR), Small Reward (SR) and Small No Reward (SNR) groups. Each dot on the graph represents an individual value, while the error bars illustrate the 95% confidence interval of the mean.

Large Target Size Enhances Movement Fusion

Our analysis revealed that all groups demonstrated a significant increase in FI throughout the training period. Target size exerted a notable effect on FI ($F(1, 95) = 11.730$, $p = 0.002$, $\eta^2 = .11$), as did the progression over time ($F(1, 96) = 74.193$, $p < 0.001$, $\eta^2 = .44$). The reward condition did not significantly influence FI ($F(1, 95) = 1.7$, $p = 0.19$, $\eta^2 = .02$). A significant three-way interaction was observed between target size, feedback, and timepoint ($F(1, 96) = 4.8$, $p = 0.03$, $\eta^2 = .05$

To further explore this interaction, multiple two-way ANOVAs were conducted:

Timepoint - Reward vs. Target Size

Early training indicated a significant effect of target size ($F(1, 96) = 7.4$, $p = 0.01$, $\eta^2 = .07$), with no effect for reward ($F(1, 96) = 0.74$, $p = 0.40$, $\eta^2 < .01$) and no interaction between the two factors ($F(1, 96) = 2.8$, $p = 0.11$, $\eta^2 = .03$). During late training, results were similar, showing a significant effect for target size ($F(1, 96) = 9.4$, $p = 0.004$, $\eta^2 = .09$), but no reward effect ($F(1, 96) = 2.7$, $p = 0.12$, $\eta^2 = .03$), nor an interaction ($F(1, 96) = 0.51$, $p = 0.48$, $\eta^2 < .01$).

Reward Groups - Target Size vs. Timepoint

Within the reward group, significant main effects were found for both timepoint ($F(1, 96) = 30$, $p < 0.001$, $\eta^2 = .24$) and target size ($F(1, 96) = 6.1$, $p = 0.02$, $\eta^2 = .06$), with no interaction (($F(1, 96) = 2.8$, $p = 0.11$, $\eta^2 = .03$). The no-reward group exhibited similar patterns with significant effects for timepoint ($F(1, 96) = 22$, $p < 0.001$, $\eta^2 = .19$) and target size ($F(1, 96) = 7.1$, $p = 0.01$, $\eta^2 = .07$), and no interaction ($F(1, 96) = 2.8$, $p = 0.11$, $\eta^2 = .03$).

Target Size Groups - Timepoint vs. Reward

For small target groups, a significant main effect of timepoint was observed ($F(1, 96) = 25$, $p < 0.001$, $\eta^2 = .21$), without a main effect of reward ($F(1, 96) = 2.5$, $p = 0.13$, $\eta^2 = .03$) or interaction ($F(1, 96) = 1.1$, $p = 0.30$, $\eta^2 < .01$). In large target groups, a significant main effect of timepoint emerged ($F(1, 96) = 9.4$, $p = 0.004$, $\eta^2 = .09$), without a main effect of reward ($F(1, 96) = 2.7$, $p = 0.12$, $\eta^2 = .03$), but a significant interaction between timepoint and reward was detected ($F(1, 96) = 4.9$, $p = 0.03$, $\eta^2 = .05$).

Post-hoc analysis of the significant interaction in large target groups indicated differences between early and late training within both large reward ($t(96) = -5.2$, $p < 0.001$) and large no-reward ($t(96) = -3.2$, $p = 0.003$) conditions. However, no significant differences were found between the large reward and large no-reward groups at early ($t(96) = 0.31$, $p = 0.76$) or late training ($t(96) = 1.7$, $p = 0.10$). Interaction plots showed that the FI values in the large no-reward group initially exceeded those in the large reward group, but by the end of the training, this trend reversed, reflecting the significant interaction reported (Figure 5.6).

In the post-assessment phases, there was a significant effect of target size, ($F(1, 96) = 13.8$, $p < 0.001$) but no significant effect of phase, ($F(1, 96) = 1.01$, $p = 0.317$) and no significant effect of reward, ($F(1, 96) = 0.19$, $p = 0.66$).

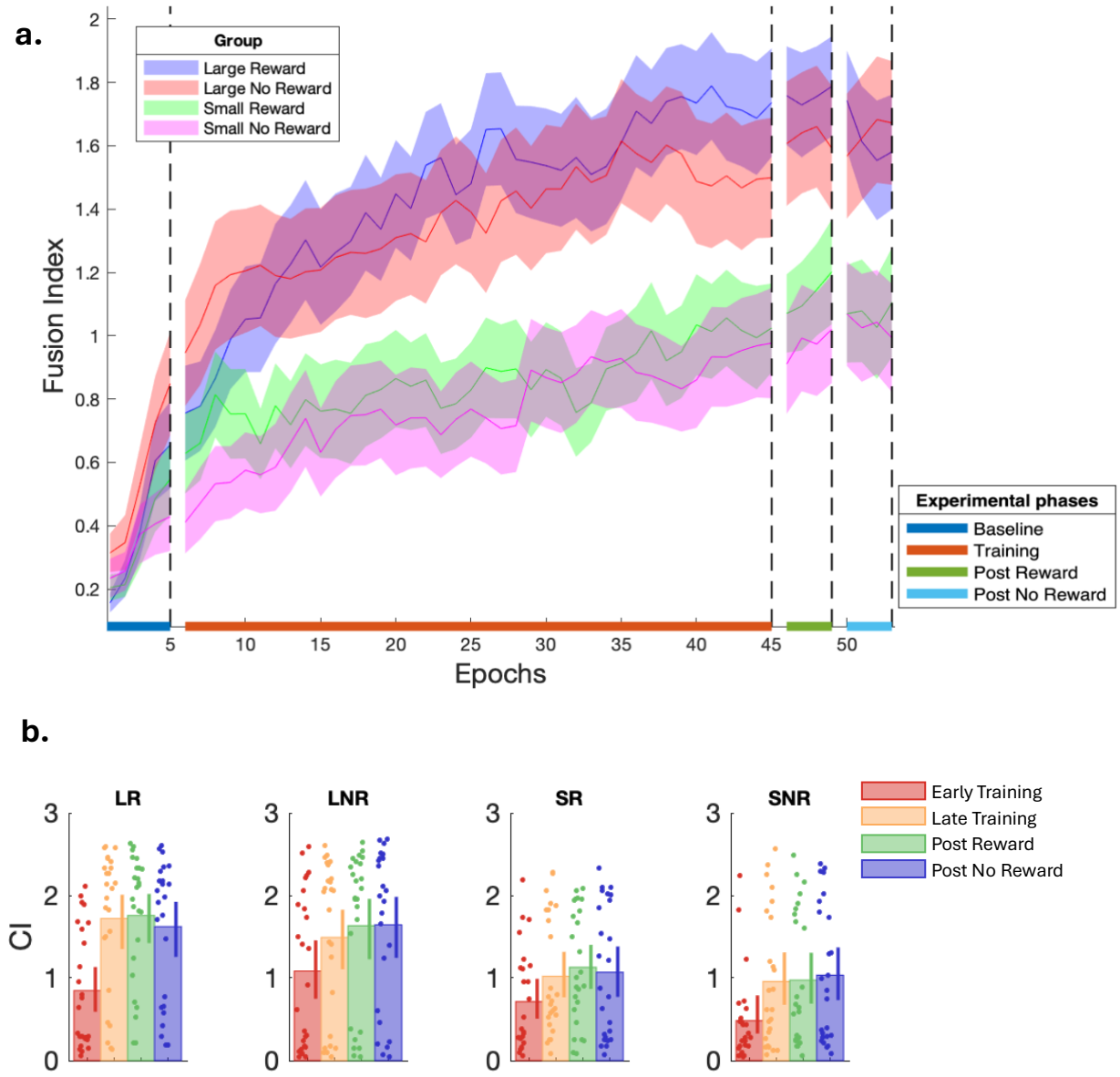


Figure 5.6: Changes in fusion index (FI). a) FI changes across all phases in epochs of 5 trials, with the shaded area representing the standard error of the mean. b) Means for FI during early training, late training, post-reward, and post-no reward blocks for the Large Reward (Griffiths and Beierholm), Large No Reward (LNR), Small Reward (SR) and Small No Reward (SNR) groups. Each dot on the graph represents an individual value, while the error bars illustrate the 95% confidence interval of the mean.

	Mean (SD)			
	Large		Small	
	Reward	No Reward	Reward	No Reward
Fusion Index				
Early Training	0.85 (0.72)	1.1 (0.93)	0.71 (0.62)	0.48 (0.54)
Late training	1.72 (0.84)	1.49 (0.95)	1 (0.72)	0.96 (0.8)
Post Reward	1.76 (0.77)	1.63 (0.95)	1.13 (0.7)	0.97 (0.8)
Post No Reward	1.62 (0.86)	1.64 (0.96)	1.1 (0.8)	1 (0.82)

Table 5.4: Mean and standard deviation (SD) of fusion index values in training and post assessment phases.

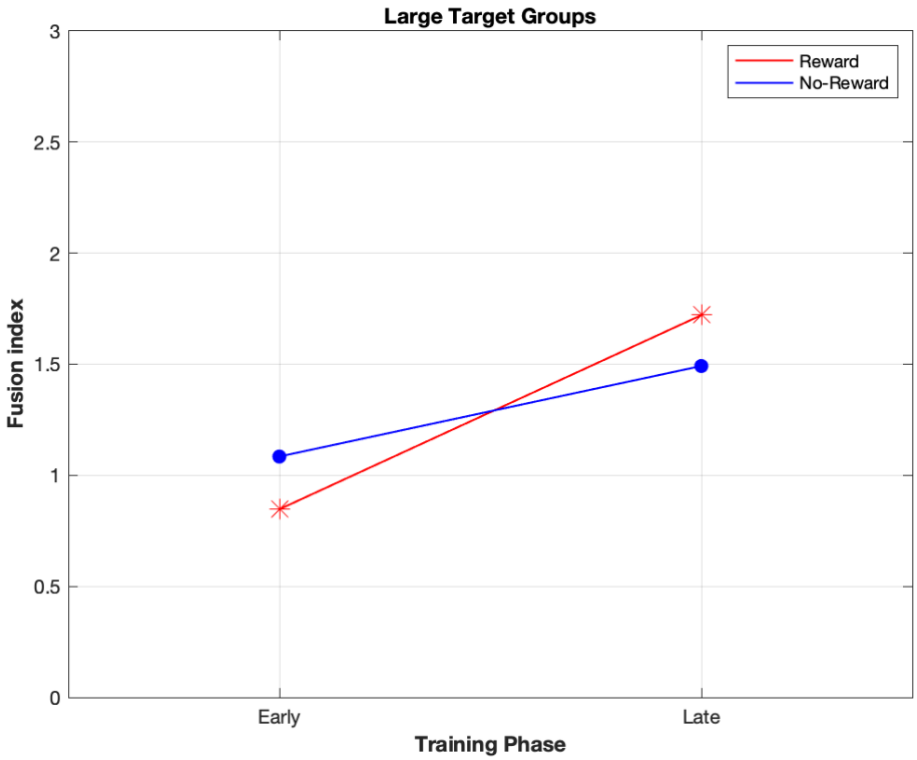


Figure 5.7: Interaction Plot of Reward Feedback and Timepoint on FI in Large Target Groups
The plot represents the interaction between reward feedback and timepoint on the FI in large target groups. Initially, the FI values are higher in the no-reward group compared to the reward group; however, as training progresses, this trend reverses, with the reward group surpassing the no-reward group by the end of the training period.

5.5 Discussion

In this study, we aimed to investigate how the level of difficulty of a task can affect reward-based movement fusion. We manipulated the target sizes to create two levels of difficulty: an easy task with large targets and a difficult task with small targets. We divided participants into two sub-groups: one with rewards for performance speed and the other without rewards. Our hypothesis was that reward could improve performance across all target sizes, but through different mechanisms. For larger target sizes, the reward would decrease MT by promoting both movement velocity and movement fusion, leading to long-lasting and energy-efficient performance gains. For smaller target sizes, the reward could lead to faster discrete movements by increasing the maximum velocity of individual sub-movements, but the fusion would be inhibited. This, in turn, would lead to transient decreases in movement time when the reward was removed. The results of the study showed that reward and target size had a positive impact on MT. However, there was a significant main effect of target size, but no effect of reward on movement fusion, indicating that a large target size was the only facilitator of movement fusion and reward had no impact on it. Moreover, the reward-based improvement in MT was transient, as all groups showed an increase in MT when the reward was removed.

Reward and Large target size improved movement performance

As anticipated, the introduction of rewards had a positive impact on the motor performance of all groups. Specifically, the groups that received rewards showed shorter movement times and higher velocities in comparison to the groups that did

not receive rewards, and the group with the large target size exhibited superior performance. Post-assessment evaluations also demonstrated an improvement in performance across all groups when rewards were provided. These findings are consistent with previous studies that have shown how rewards can enhance motor performance across different tasks, such as tasks that involve eye movements (Manohar et al., 2015), arm movements (Codol et al., 2020b) and ankle movements (Goodman et al., 2014a). In this study, we replicated these results by using finger-reaching movements on mobile phones. Additionally, the larger target groups displayed a significant improvement in performance, supporting Fitts's law, which states that larger targets result in faster and more accurate movements in target-reaching tasks.

The Link Between Fusion and Persistence of Reward-Based Improvement

Our findings regarding the non-significant impact of rewards on movement fusion and the transient nature of reward-based motor performance enhancements might initially appear to conflict with the results of Sporn et al. (2022). They reported a substantial influence of rewards on the fusion of sequential movements and a sustained improvement in motor performance even after rewards were withdrawn. Nevertheless, our study contributes to the discussion by illustrating a scenario where movement fusion occurs independently of rewards and does not result in long-lasting performance gains once the reward is removed. This aligns with Sporn et al.'s findings, which suggest that the persistence of reward-based motor improvements depends on the reward facilitating an improvement in fusion. Our results support this by indicating that without a reward-induced enhancement in fusion, the associated performance gains are not sustained. This highlights the importance of fusion as a

critical component for retaining learned motor improvements rather than just a byproduct of training. Our findings also raise intriguing questions about the role of task-specific elements. For instance, the larger targets in our study may have created a ceiling effect, where fusion was easily achieved without the need for rewards, thus precluding observable reward-based improvements. This is consistent with previous research that has shown that tasks with lower difficulty levels can result in early performance plateaus (Agarwal et al., 2022, Bonassi et al., 2020). On the other hand, the small target conditions may have presented a floor effect, making it difficult to achieve fusion despite the motivational incentives provided by rewards (Jacklin, 1984). This suggests that there is a threshold of task difficulty beyond which rewards may not effectively promote certain aspects of motor learning, like fusion. In addition, the duration of training may also influence the outcomes of our study. While Sporn et al. demonstrated that reward-facilitated fusion can lead to the formation of a robust motor primitive over time, our participants engaged in a relatively short training period. It is possible that fusion as a motor learning outcome requires more extended practice to manifest, suggesting that a longer training duration could potentially reveal the reward-based differences in fusion that we did not observe. In light of these considerations, future studies could benefit from longitudinally examining the effects of rewards on movement fusion across varying levels of task difficulty and training duration. This would help to clarify the conditions under which rewards may yield lasting improvements in motor performance, particularly in terms of movement fusion and its role as a fundamental mechanism in motor learning.

Differential Mechanisms of Performance Improvement in Large and Small Target Groups

The training resulted in an improvement in performance for all participants. However, the mechanisms behind these improvements varied depending on the size of the target. For larger targets, the performance gains were linked to increases in both MV and FI. This supports our hypothesis and is consistent with the findings of Sosnik et al. (2004), who suggested that less demanding accuracy requirements promote the fusion of movement sequences. Participants dealing with smaller targets showed performance gains primarily through an increase in MV without a corresponding rise in FI of movement. This pattern suggests that when faced with stringent accuracy demands, participants may prioritize speed in individual movements rather than integrating these movements into a fluid sequence. The absence of significant fusion in these conditions implies that increasing task difficulty may constrain the development of more efficient movement strategies, leading participants to rely on faster but potentially less efficient movements. The use of target size manipulation can greatly impact motor learning and rehabilitation. Practitioners can adjust the level of difficulty to influence whether learners focus on the speed of individual movements or the integration of movements into a more efficient and cohesive sequence. This approach can be a useful tool in shaping motor strategy development.

Task Difficulty and Fusion of Sequential Movement

This online study highlights that task difficulty significantly influences how people learn motor skills, pushing them to prioritize either speed or efficiency. However, the study's manipulation of task difficulty through target size may not have been optimal

for promoting movement fusion. The lack of clear reward benefits and the differing performance patterns between the easy (large target) and difficult (small target) conditions suggest that the chosen difficulty levels might have missed the "sweet spot" for maximizing learning, known as the challenge point (Guadagnoli and Lee, 2004). The small target task may have been too challenging, hindering fusion and favoring individual movement speed, while the large target task might have been too easy, leading to a ceiling effect where reward had little impact. Finding this challenge point is inherently difficult, as it is affected by individual differences in skill level and learning rate, the dynamic nature of skill acquisition, and the complexities of objectively quantifying both task difficulty and movement fusion (Guadagnoli and Lee, 2004, Pollock et al., 2014). Future research should focus on refining the task's challenge point to better understand how difficulty interacts with reward to drive the development of efficient, fused movements.

Handedness

One consideration when interpreting the current findings is the potential influence of handedness. Although the sample predominantly consisted of right-handed participants, the fixed target arrangement on the smartphone screen might have introduced a spatial bias. Left-handed individuals, holding the phone in their right hand, would have performed the task primarily with their dominant hand on the left side of their body. While the task primarily relied on finger movements, minimizing the involvement of shoulder movement and midline crossing, subtle biomechanical differences in wrist pronation and supination between left-handed and right-handed individuals could still exist. These differences might have introduced slight variations in movement trajectories or efficiency when reaching for certain targets (Bradshaw et

al., 1990). However, given the emphasis on finger dexterity and the minimal role of gross arm movements in this task, it is unlikely that handedness played a substantial role in the observed effects. Future studies could further explore this factor by employing a counterbalanced design where the target arrangement is mirrored for half of the participants, ensuring that both left-handed and right-handed individuals perform an equal number of movements towards both sides of their body. This would provide a more robust assessment of any handedness-related effects on reward-based fusion in sequential reaching movements.

Limitations

The COVID-19 pandemic posed many difficulties in conducting research, especially for studies that are normally done in a controlled laboratory setting. To address these challenges, this study was designed to allow participants to contribute remotely using their personal smartphones. Although this approach facilitated the continuation of research when lab-based experiments were not possible, it also introduced several limitations that require further discussion.

Device Variability

The reliance on participants' personal phones introduced a degree of variability that is absent in standardized lab environments. Differences in screen size, touch sensitivity, and device responsiveness could affect task performance, introducing an uncontrolled variable into our study.

Posture and Ergonomics

The lack of control over participant body posture is a significant limitation. Different postures may impact manual dexterity and task execution, with various positions potentially affecting arm and hand kinematics (Buffington et al., 2006). This factor

alone could contribute to the observed variability in the results since the body position can influence motor strategies employed during task performance.

Phone Orientation

We were also unable to standardize the orientation in which participants held their phones, which could affect arm configuration and the mechanics of reaching movements. The orientation of interaction with a touchscreen device could also impact performance, adding another layer of uncontrolled variability.

Environmental Conditions

The ambient environment in which participants performed the task was also beyond our control. External factors such as background noise, interruptions, and even lighting conditions could affect concentration and performance, which could potentially impact the outcomes.

These limitations highlight the challenges of adapting laboratory-based experiments to a remote format. They highlight the importance of considering these factors when interpreting the study's findings and designing future remote or hybrid experimental protocols.

5.6 Conclusion

Our investigation has led us to a better understanding of our initial hypothesis. The study confirmed that larger targets are associated with improved fusion of movements and reduced movement time (MT), suggesting that task structure significantly affects motor performance. However, contrary to our hypothesis, rewards did not enhance the fusion of sequential movements. Additionally, the performance improvements observed in groups receiving rewards did not persist after the reward was removed, even among those engaging with larger targets. This

finding highlights the temporary nature of reward-based enhancements in motor tasks and suggests that the intrinsic features of the task, such as target size, may be more important for sustained motor learning than previously thought. These results have significant implications for the development of training programs and interventions, which may benefit from a greater emphasis on task design to achieve lasting improvement in motor skills.

Chapter 6

GENERAL DISCUSSION

In this thesis, we conducted a detailed examination of the role of rewards in motor performance in health and disease. This subject is of great importance for both theoretical advancement and practical applications in rehabilitation. Through a series of empirical investigations, we explored the impact of rewards on different movement types and components, assessing the variability in response among individuals with different health statuses and age groups. In this discussion, we will synthesise the key results, reflect on their broader implications, and consider the potential pathways for future research that could further refine our understanding and application of reward systems in health and disease.

6.1 Summary of the results

In Chapter 2, we investigated the impact of ageing on reward-based changes in action selection and action execution of reaching movement. The results indicated that monetary rewards enhanced the execution of reaching movements for both older and younger adults, with both groups showing significantly faster maximum velocities and shorter movement times under reward conditions. However, the improvement was more pronounced in younger adults. Despite these improvements, the accuracy of the movements was not compromised. Additionally, rewards also

improved reaction times across all ages, although this increase in speed came at the cost of reduced selection accuracy, affecting both age groups equally.

In Chapter 3, we explored the effects of monetary rewards on action selection and execution during reaching movements in both paretic and non-paretic arms of chronic stroke patients. We also examined how intensive upper-limb rehabilitation influenced these reward-based changes in motor performance. Our findings indicate that rewards positively influenced the execution of movements without compromising accuracy in both arms, with a more pronounced effect in the non-paretic arm. Although reaction times were enhanced by rewards, this improvement was accompanied by a reduction in selection accuracy for both arms. Additionally, intensive rehabilitation led to improvements in both the selection and execution components of the paretic arm, without affecting the reward-based enhancements observed in these components.

In Chapter 4, we explored the neural mechanisms underlying reward-enhanced motor performance, focusing on the role of the M1. We used cTBS to modulate M1 activity, assessing its impact on the selection and execution of reaching movements. Our findings indicate that while rewards significantly improved the execution without compromising accuracy, they adversely affected the selection process, leading to faster but less accurate selection decisions. Notably, modulating M1 activity with cTBS did not influence either the execution or selection aspects of the task, suggesting that the cTBS did not effectively modulate M1 activity.

In chapter 5, we explored how manipulating task difficulty influence the fusion of reward-based sequential reaching movements. Our results indicate that while rewards improved both movement time and maximum velocity, particularly when the task was made easier by increasing target size, they had no significant effect on the

fusion of movements. Instead, task difficulty was the primary factor affecting fusion, as evidenced by significantly higher FI values in participants who engaged with larger targets compared to those working with smaller targets, regardless of reward presence.

6.2 Theoretical implications

Consistently across all studies within this thesis, rewards have demonstrated a profound ability to invigorate motor execution, characterized by shortened movement times and increased reaching velocities, without compromising the accuracy of the reaching movements. This enhancement was observed across a diverse demographic, including healthy individuals of varying ages and those experiencing upper limb weaknesses due to stroke. The uniform response to rewards, observed in tasks ranging from discrete arm reaching with robotic manipulanda to finger reaching on cell phones, underscores the fundamental role of reward in enhancing motor execution. However, few points are needed to emphasis regarding the theoretical implications of these results and the addition they added to the body of evidence.

The Complex Interplay Between Age, Reward Processing, And Motor Performance

The nuanced differences observed between age groups in response to rewards can be interpreted through the lens of lifespan psychology and neurodegeneration. Older adults exhibited a less pronounced reward-based enhancement in motor performance compared to younger adults, supporting physiological studies indicating an age-related decline in dopaminergic function and reward sensitivity (Eppinger et al., 2012, Morgan, 1987, Gantz et al., 2018). This thesis extends these findings by providing behavioural evidence of such changes. Additionally, the findings suggest

that older adults may rely more heavily on intrinsic motivation rather than external rewards. This propensity has been observed in various contexts, such as the workplace (Shi et al., 2023), and in this thesis, we replicated similar trends in reward-based arm reaching movements. This supports theories suggesting that older adults prioritize emotionally satisfying goals over the pursuit of future gains, which reflect a broader shift in motivational orientation (Hess, 2014, Ziaei and Fischer, 2016, Shi et al., 2023). Further, this thesis corroborates previous findings that older adults adapt their motor strategies to maintain the quality of performance, potentially to compensate for age-related declines in sensorimotor function (Seidler et al., 2010). In our study, older adults demonstrated a preference for accuracy over speed in both the selection and execution phases of motor tasks. This strategic prioritization supports the hypothesis that older adults may adopt more conservative strategies to preserve performance accuracy, potentially as a compensatory mechanism in response to sensory and motor declines (Seidler et al., 2010).

Overall, our findings contribute to our understanding of cognitive ageing, demonstrating that while age-related slowing occurs in motor performance, the ability to utilize motivational cues is maintained. This suggests that motivational interventions could still be effective in enhancing motor performance among older adults, despite the general cognitive slowdown.

Reward and Motor Control After Stroke

In this thesis, we also provided evidence that chronic stroke patients retain sensitivity to reward incentives, which can lead to improvements in motor performance. This challenges the notion of a diminished reward system after stroke (Oestreich et al., 2020, Rochat et al., 2013a, Wagner et al., 2023b, Widmer et al., 2019) and suggests

potential for harnessing reward mechanisms to enhance motor recovery. The preserved sensitivity to reward suggests that neuroplasticity and functional reorganization within the brain might compensate for initial disruptions caused by the stroke, leading to a restoration of reward processing and its influence on motor control. While the study showed that reward sensitivity is preserved, the differential magnitude of reward-based enhancement observed between the paretic and non-paretic arms suggests potential alterations in the neural pathways connecting reward processing and motor control within the affected hemisphere. This could involve changes in the strength of connections, compensatory recruitment of alternative pathways, or altered functional dynamics within the reward-motor network (Cramer, 2008, Seitz and Donnan, 2015, Ward, 2005).

Ineffectiveness of cTBS in Modulating M1

The inability of cTBS to significantly modulate the impact of rewards on motor performance in this study highlights several important considerations. The variability in neuromodulation response could be attributed to individual differences, including neuroanatomical structures, baseline neurophysiological states, or genetic predispositions that influence neuronal excitability (McCalley et al., 2021). This variability underscores the necessity for personalized approaches in neuromodulation, where protocols are tailored based on individual neurophysiological profiles. Additionally, the findings raise questions about the efficacy and specificity of cTBS as a tool for modulating M1. Factors such as the precision of coil placement, the intensity of the stimulation, and the duration of the protocol might not have been optimally configured to achieve effective modulation. This highlights the need for more accurate targeting and potentially the use of real-

time monitoring techniques like neuroimaging during the application of cTBS to ensure that the desired brain areas are being effectively targeted and modulated (Lynch et al., 2022). Such improvements could enhance the impact of interventions and contribute to a better understanding of the neural mechanisms underlying reward processing in motor tasks.

Dissociation Between Action Selection and Execution

The reward-based changes in selection and execution in this thesis provide compelling evidence for a dissociation between action selection and action execution, highlighting the distinct neural systems underlying these processes (Diedrichsen and Kornysheva, 2015). This is supported by several key observations:

- Differential Effects of Rewards: The observed effects of rewards on action selection and execution differed significantly. While rewards led to faster reaction times, indicating improved efficiency in action selection, they also resulted in decreased selection accuracy, suggesting a speed-accuracy trade-off. Conversely, rewards enhanced movement execution speed (increased maximum velocity and decreased movement time) without compromising movement accuracy. This suggests that the neural systems involved in selecting an action and executing it respond differently to motivational incentives.
- Independence from Motor Impairment: The similarity in selection accuracy between the paretic and non-paretic arms of stroke patients further strengthens the argument for dissociation. Despite significant motor impairments in the paretic arm, the cognitive processes involved in selecting the correct target remained largely unaffected. This indicates that action

selection is independent of the motor system's integrity and relies on separate neural substrates.

Fusion of Sequential Movement and Task Difficulty

The online study underscores the critical role of task design in shaping motor learning strategies. By manipulating task difficulty, we can influence learners' priorities, encouraging them to focus on either speed or efficiency, which ultimately impacts the development of motor skills. However, our findings suggest that we may not have effectively identified the optimal "challenge point" for promoting movement fusion in this context. The Challenge Point Framework (CPF) posits that learning is maximized when tasks are moderately difficult, striking a balance between being achievable yet demanding (Guadagnoli and Lee, 2004). In our study, the lack of a significant effect of reward on fusion, coupled with the distinct performance patterns observed in the large and small target groups, suggests that the chosen difficulty levels may not have adequately captured this optimal learning zone. It is possible that the small target task, while intended to be challenging, exceeded the participants' capacity for effective fusion, leading to a focus on individual movement speed rather than the integration of movements into a fluid sequence. Conversely, the large target task may have been too easy, resulting in a ceiling effect where fusion was readily achieved without the need for further optimization through reward incentives. These findings highlight the need for further exploration around the challenge point to fully understand the impact of task difficulty on reward-based fusion.

6.3 Practical implications

The findings of this thesis provide compelling evidence for the potential of reward-based interventions to enhance motor performance across diverse populations, including healthy individuals of varying ages and those with upper limb impairments due to stroke. The consistent positive influence of reward observed across a range of motor tasks underscores its fundamental role in shaping motor behavior and improving execution. This paves the way for integrating reward-based strategies into rehabilitation practices, but several key considerations should guide their implementation.

Age-Related Differences

As demonstrated in Chapter 2, older adults exhibit a less pronounced reward-based enhancement compared to younger adults and may prioritize accuracy over speed. Rehabilitation programs for older adults should consider incorporating intrinsic rewards that align with their values and goals, such as personal achievement, mastery, and social connection. Additionally, focusing on accuracy-based feedback and rewards might be more effective than solely emphasizing speed.

Stroke-specific considerations

While reward can improve motor performance in both paretic and non-paretic arms of stroke patients, the magnitude of this effect and the specific components of motor control that are most responsive to reward might differ between individuals. Rehabilitation programs should be individualized to address the specific impairments

and needs of each patient, considering factors such as lesion location, stroke severity, and overall functional goals.

6.4 Limitations

Lack of control groups in the stroke study

One limitation of the stroke study discussed in Chapter 3 is that it did not include a control group of age-matched healthy individuals. Adding such a group would help to determine whether the responses of stroke patients to rewards are typical or different from those of people without neurological impairments. This would provide stronger evidence about the specific effects of stroke on reward processing and motor performance. Although a group of age-matched healthy individuals was tested using a similar task design in Chapter 2, it is important to note that the Kinarm devices used in the two studies were different. The end-point Kinarm was used in Chapter 2, while the Exoskeleton Kinarm was used in the stroke study in Chapter 3. These devices have significant differences in how they support the arm, including variations in holding position and gravitational support, which can affect task performance significantly. Because of these differences in the mechanical and functional properties of the devices, it was not appropriate to make a direct comparison of the results between healthy individuals and stroke patients across these chapters.

Challenges in Modulating M1 Activity with cTBS

As discussed in Chapter 4, our attempt to modulate M1 activity using cTBS did not yield the expected changes in performance during the reaching task. We initially hypothesized that this lack of effect might be due to the stimulation targeting a small

brain area (specifically, the representation of the FDI muscle) that is not critically involved in whole-arm reaching movements. Consequently, we proposed exploring the same cTBS protocol with a simpler task reliant on index finger movements, anticipating a more pronounced effect. However, recent findings from a master's student within our lab further challenge the effectiveness of cTBS in modulating M1 activity. Utilizing the same cTBS protocol, the student investigated its impact on a serial reaction time task involving both index and little finger movements. Initial MEP results indicated that cTBS was ineffective in inhibiting M1 excitability, even when targeting muscles directly involved in the task. The observed ineffectiveness of cTBS in modulating M1 activity in both our reaching task and the subsequent finger movement task necessitates exploring alternative methods for investigating the role of M1 in reward-based motor control.

6.5 Future research

Implementing Rewards in Rehabilitation Programs

The research presented in this thesis has laid a foundational understanding of how rewards can enhance motor performance across different populations. However, several gaps remain that must be addressed to translate these findings into clinical applications. A critical next step is to integrate reward mechanisms into structured rehabilitation programs and rigorously assess their efficacy through randomized controlled trials (RCTs). These trials should compare the outcomes of rehabilitation programs that incorporate rewards with traditional approaches or control groups that do not use reward mechanisms. Key areas for these RCTs include assessing improvements in motor function, evaluating the impact on activities of daily living, measuring changes in overall quality of life, and gauging patient satisfaction. Such

comprehensive evaluations are crucial for determining how reward mechanisms can enhance patient independence and emotional, physical, and social well-being.

In addition to conducting trials, there is also a significant need to develop practical implementation frameworks. These frameworks should provide clear and actionable guidelines for integrating reward-based interventions into existing rehabilitation protocols. Essential components of these frameworks include defining optimal reward schedules to maximize motivation, identifying which types of rewards are most effective for different patient demographics, developing methods for effective reward delivery, and outlining how to synchronize reward-based interventions with other therapeutic practices. This synchronization ensures that reward mechanisms complement rather than conflict with other rehabilitation efforts. Furthermore, exploring the underlying motivational dynamics within rehabilitation settings is vital. Understanding how different patients respond to various rewards will aid in tailoring interventions to meet individual needs, thereby increasing the overall effectiveness of the rehabilitation. Long-term follow-up studies are also important to assess the sustainability of improvements gained through reward-based interventions. These studies can provide crucial insights that inform continuous adjustment and optimization of rehabilitation practices.

Alternative TMS protocols

Exploring other TMS protocols, such as intermittent theta burst stimulation (iTBS) (Läppchen et al., 2015) or paired-pulse TMS (Sommer et al., 2001), might offer different mechanisms for modulating M1 activity and potentially elicit more consistent effects. In addition, combining TMS with neuroimaging methods like fMRI or EEG (Peters et al., 2013) could provide valuable insights into the neural correlates of

reward processing and motor control, allowing for a more comprehensive understanding of M1's involvement.

Task Difficulties and Movement Fusion

In terms of task difficulty, future studies could employ a wider range of target sizes or utilize adaptive algorithms that adjust task difficulty based on individual performance, allowing for a more precise identification of each participant's challenge point. Additionally, investigating the influence of other task parameters, such as movement distance or target location, could provide further insights into the optimal conditions for promoting fusion and skill acquisition. By systematically exploring the challenge point and its interaction with reward, we can gain a deeper understanding of how to design effective training interventions that promote efficient and skilled motor performance.

6.6 Conclusion

This thesis has provided a comprehensive exploration of how rewards influence motor performance across various demographics, including healthy individuals, older adults, and chronic stroke patients. The findings have significant implications for both theoretical understanding and practical applications, particularly in the realm of rehabilitation. The findings highlight the nuanced interplay between reward processing, age, and motor control, revealing both preserved and altered responses in healthy ageing and stroke. While the neural mechanisms underlying these effects require further investigation, the dissociation between action selection and execution underscores the complexity of reward-based motor control. This thesis has significant implications for rehabilitation practice, paving the way for the development

and implementation of reward-based interventions to optimize motor recovery and improve the quality of life for individuals with motor impairments. By further exploring the intricacies of reward processing, refining intervention strategies, and investigating the optimal conditions for motor learning, we can harness the power of rewards to unlock new avenues for enhancing human movement and promoting well-being.

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