TOWARDS A BETTER UNDERSTANDING OF THE INTERACTION BETWEEN VISUAL ATTENTION, PERCEPTION AND REACHING MOVEMENTS

By

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Abstract

By using both experimental and computational modelling approaches, this thesis presents evidence for continuous feedforward and feedback interactions between attention, perception, and movement. In Chapter 1 we investigate the spatial allocation of visual attention during reaching movements with the hand hidden from view. The results demonstrate proximity of the hand to a difficult-to-detect probe stimulus to increase the detection rate of the probe. As such, this demonstrates continuous proprioceptive feedback of the hand's location during movement to facilitate the allocation of visual attention and to its location. Complementing the feedback loop from movement to attention, in Chapter 2 we present further evidence for an ongoing feedforward influence of perception on movement. By building a computational model that considers movements to be made up of smaller submovements, we demonstrate perceptual priming to result in smaller numbers of submovements within a reach trajectory, capturing the ongoing feedforward effects of perception on movement. Taken together these experimental and computational modelling findings provide evidence for continuous feedforward and feedback connections between attention, perception, and the motor system, lending support to an integrated theoretical framework of movement.

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General Introduction

Traditional models of the motor system consider it to be the endpoint of a series of discrete and sequential processes (e.g., Keele, 1968). They assume that sensory information is passed through perceptual and cognitive processes before being transmitted to the motor system to prepare and execute the response as movement (e.g., Dietrich & Markman, 2003). However, in recent years an alternative theory has gained traction, proposing attentional, perceptual, cognitive, and motor systems to work in parallel and interact (e.g. Ostry & Gribble, 2016; Baldauf & Deubel, 2009; Strauss, Woodgate, Sami, & Heinke, 2015; Ostry, Darainy, Mattar, Wong, & Gribble, 2010; Song & Nakayama, 2009). This thesis provides further evidence for this interconnected theoretical framework of movement by demonstrating movement to continually affect and be affected by feedforward and feedback mechanisms to and from the attentional and perceptual systems.

In Chapter 1 we attempt to provide further evidence for a feedback loop from movement to attention during reaching movements, at odds with the traditional serial model of processing prior to movement. According to the traditional model of serial processing, prior to the onset of movement, attentional processes allocate visual attention to relevant parts of the visual scene. However, during reaching movements there is one movement-relevant location that is constantly changing: the hand. The hand’s ever-changing location means that, unlike static movement-relevant locations such as the target, a single location to which visual attention can be allocated to monitor the hand cannot be determined in the preplanning of movement. Instead, feedback from movement must be used to allocate visual attention to the location of the hand throughout the reach. Visual feedback of the hand’s location during movement has robustly been shown to be necessary for the completion of reaching movements (Churchill, Hopkins, Rönnqvist, & Vogt, 2000; Gentilucci, Toni, Chieffi, &

Pavesi, 1994), suggesting visual attention to be allocated to the hand when visual information of the hand's location is available. In this thesis, by hiding the hand from view, we explore whether continuous proprioceptive feedback of movement can similarly bias the allocation of visual attention to the location of the hidden hand during reaching movements.

In addition to not predicting movement feedback to continually influence attention, the traditional serial processing model also does not predict an ongoing feedforward influence of attentional and perceptual processes on movement preparation and execution. In Chapter 2 we seek to better understand this ongoing feedforward influence of attention and perception on movement by computationally modelling data collected using a choice reaching task (for review of choice reaching tasks see: Dotan, Pinheiro-Chagas, Al Roumi, and Dehaene, 2019; Song & Nakayama, 2009). By utilising a choice reaching task (CRT), whereby several targets are displayed simultaneously, the temporal unfolding of internal processes can be revealed in the trajectories of reaching movements (Song and Nakayama, 2006). By analysing movements from CRTs, curved trajectories demonstrate later selection of the correct target and hence greater competition between stimuli. As such, by using lexical and numerical stimuli as part of a CRT, the cognitive processes which underpin how we represent concepts such as numbers (Feigenson, Dehaene, & Spelke, 2004) and language (Spivey, Grosjean, & Knoblich, 2005) have been revealed. Similarly, by analysing the curvature of CTR trajectories, CRTs have also provided insight into the processes underlying attention and perception. Stimuli that require ignoring have been shown to induce trajectory curvature away from them whilst stimuli that may act as a target result in curvatures towards them (for review see Song and Nakayama, 2009). Furthermore, the amplitude of the deflection towards a distractor has been shown to increase with the pre-cueing of the distractor (Welsh & Elliot, 2004), heavily implicating attention and perception in the trajectories of reaching movements.

However, until now these effects from CRT experiments have largely been analysed using descriptive statistics. Descriptive statistics have, without doubt, added to our understanding of factors that influence movement. Yet, mechanistic explanations by the way of computational models allow for a deeper understanding of underlying processes. In Chapter 2 we seek to develop a computational model that, by considering movements to be made up of smaller submovements, gives a deeper insight into how the perceptual priming effect, induced by repeating target colour, influences reaching movements. As such by using both experimental and computational modelling approaches, the current body of work will provide further evidence for an interconnected theoretical framework of attention, perception, and reaching movements.

Chapter 1: The allocation of visual attention to the hand

1.1 Introduction

Consider the example of reaching for a mug on a table. You must locate the mug, reach towards it, avoiding the objects surrounding it and form your hand to the right shape to grasp it. The mundanity of such a frequent movement conceals the complexity required to execute it. Performing the reach requires specific information about the shape, orientation, location etc. of the mug, surrounding objects, and the hand. The visual scene in its entirety is extremely rich in information, too dense to be perceived in parallel. Selective attention allows us to successfully navigate such an environment, facilitating perception at relevant locations while largely ignoring the irrelevant information (Moray, 2017). The first experiment of this thesis attempts to provide further evidence of a feedback loop from movement to attention. It examines whether in addition to allocating visual attention to the target, proprioceptive feedback of the hand's location during movement, enables the continuous allocation of visual attention to the hand during reaching movements.

According to Allport (1987), the two primary functions of attention are to select information relevant for planning action, termed 'selection-for-action', and for the perception of objects, termed 'selection-for-perception'. In the years since this suggestion, dual-task paradigms have provided substantial evidence supporting a functional coupling of 'selection-for-action' and 'selection-for-perception,' which facilitates the perception of action-relevant objects and locations (for review see: Mahon, Bendžiūtė, Hesse, & Hunt, 2020). For instance, in a dual-task paradigm, Baldauf, Wolf, and Deubel (2006) asked participants to execute a short series of reaches while performing a discrimination task. They found discrimination of an 'E' from a '3' to be better at all movement relevant locations than at movement-irrelevant locations. Corroborating these findings, physiological evidence shows that when flashing a task-irrelevant dot during a series of reaching movements, the amplitude of the brain activity induced by the dot was larger when presenting the dot at action-relevant than at action-irrelevant locations (Baldauf & Deubel, 2009). As such, it can be assumed that, guided by information from the planning of movement, selective attention is employed to facilitate perception at action-relevant target locations.

Whilst prior research, such as that by Baldauf and Deubel (2006; 2009), suggests the preparation of movements to bias the allocation of visual attention to action-relevant locations, typically the only action-relevant location considered is that of the target. Due to the target being static in these paradigms, allocating attention to its location can be determined prior to the onset of movement. However, during reaching movements not every action-relevant location is static, as the hand by necessity is constantly moving. By continuously allocating attention to and around the location of the hand, one can monitor progress to the target, the shape of the hand, and perceive potential obstacles whilst ignoring action-irrelevant information.

Indeed, the necessity for visual information of the hand during reaching is well known. Early experiments showed removal of visual information of the location of the hand to result in less accurate reaches and longer movement durations (Carlton, 1981). Since Carlton's initial observations, increased movement duration without visual feedback has been robustly shown (Churchill, Hopkins, Rönnqvist, & Vogt, 2000; Berthier, Clifton, Gullapalli, McCall, & Robin, 1996; Schettino, Adamovich, & Poizner, 2003). Furthermore, the necessity of visual feedback has been extended to grasping movements, with Gentilucci, Toni, Chieffi, and Pavesi (1994) showing the absence of visual feedback to result in larger grip apertures. Moreover, recent research provides evidence for the allocation of visual attention to the location of the hand to be continuous. Perturbations to the visual representation of the hand's location during reaching movements have been shown to be corrected within an average of

160ms, regardless of where in the movement the perturbation occurred (Saunders & Knill, 2003). Whilst these experiments show that to some degree visual attention is allocated to the hand, during the process of reaching the spatial distribution of this attention is not clear. It is feasible that visual attention is allocated either to the entire reaching trajectory or to a broader area than specifically the location of the hand.

However, experiments showing heightened perception at the location of the hand when static demonstrate that feedback of the hand's location is used to allocate visual attention to its specific location in the absence of movement. Objects presented near the static hand are reliably perceived faster (Spence, Pavani, & Driver, 2000) and attended to for longer than those further away (Abrams, Davoli, Du, Knapp III, & Paull, 2008). Similarly, improved change detection (Tseng & Bridgeman, 2011) and decreased temporal fusion of sequentially displayed dots are found in the space surrounding the hand (Goodhew, Gozli, Ferber, & Pratt, 2013). It is possible in these studies that the mere presence of the hand as a visual stimulus draws visual attention to its location, leading to an increased ability to observe perceptual properties. However, there is evidence showing that proprioceptive feedback of the hand's location demonstrates the same attentional effects. Even when the hand is hidden from view, Reed, Grubb, and Steele (2006) showed increased target detection near the hand. Results such as these indicate a unique form of heightened attention surrounding the hand when still and the ability for proprioception to be used to locate the hand in these scenarios. However, it is possible that the same attentional mechanisms may not be in play during reaching movements as allocating visual attention continuously to the hand cannot be pre-planned and would instead require continuous feedback of the hand's location during movement.

Despite contradicting the serial model of processing, preliminary research involving dynamic hand movements suggests that proprioceptive feedback of the hand's location during movement does continually facilitate the allocation of visual attention to the hand.

When asking participants to perform reaching movements to a target whilst the hand was hidden from view, Jackson, Miall, and Balsley (2010) used a robot arm to perturb the hand to either the left or right of the planned trajectory. Soon after, a masked stimulus was presented on either the left or right side of the screen. The detection rate of the probe was found to be greater when the probe was presented on the side of the screen that the hand was perturbed into. However, it is possible that this effect occurs due to the direction of the force of the perturbation acting as a cue leading the allocation of visual attention to that side of the screen rather than requiring the continous feedback of the hand's location during movment. Yet Adam, Bovend'Eert, van Dooren, Fischer, and Pratt (2012) provide evidence that suggests continous proprioceptive feedback biases the allocation of visual attention to the location of the hand in the absence of cuing. When asking participants to move their hand which was hidden from view continuously from side to side, letters presented near the hand were identified more often than those further away. However, the rhythmic swiping action performed made the movement highly predictable and as such made it plausible that the allocation of visual attention to the hand's location was preplanned without the need for feedback of movement. Considering this, in order to better assess the presence of a feedback loop from movement to attention, an experiment exploring the continous allocation of attention during a number of reaching movements is required.

Thereby, in the current study we aim to determine whether proprioceptive feedback of the hand's location during movement also facilitates the allocation of visual attention to the hand's ever-changing location during reaching movements. To test this, participants performed reaches to a target while their hand was hidden from view. As the allocation of visual attention is not directly measurable, in the current experiment visual attention is operationalised through a probe detection task. During reaching, a small dot (probe) is displayed in a varied location on a screen over the concealed hand with participants then indicating if they noticed the dot. From this, the distance from the probe to the hand and from the probe to the target is used to predict the overt detection of the probe, made possible by the allocation of attention to its location. It is hypothesised that the closer the probe to the target, the higher the likelihood of perceiving it, which would confirm the allocation of attention to the location of the target, in line with previous research. Considering the hand's action-relevancy during reaching and evidence showing the allocation of attention to its location when static and dynamic, it is also hypothesized that the closer the probe to the hand, the higher the likelihood of perceiving it. Furthermore, considering evidence showing proprioceptive information facilitates the allocation of visual attention to the hand's location, we hypothesise these effects to exist despite the hand being hidden from view. By demonstrating in this way that feedback from movement influences the allocation of attention, we attempt to provide further evidence for an interconnected theoretical framework of movement, at odds with the traditional serial model of processing.

1.2 Method

1.2.1 Participants

19 right-handed University of Birmingham undergraduates were recruited using the university's research participation scheme. Of the participants recruited, 1 was male and 18 were female, with a mean age of 19.84 years old.

1.2.2 Setup

Participants were seated at a desk with a Polhemus motion sensor taped to the index finger of their dominant hand. The participants placed their dominant hand below a mirror which occluded it from view. The mirror reflected a 29-inch LCD screen placed above it, facing down so that the participant viewed stimuli at a distance of 50cm. A chin rest was used to maintain the viewing position, adjusted for height so that each participant could comfortably view the reflection of the screen in the mirror.

1.2.3 Stimuli

To indicate the start of the experiment, a green circle with a radius of a 0.075º was presented at the bottom of the screen representing the start box. During the experiment, a target appeared in one of three locations, positioned at 135º, 180º and 225º respectively from the start box at a distance of 0.6º (see Figure 1).

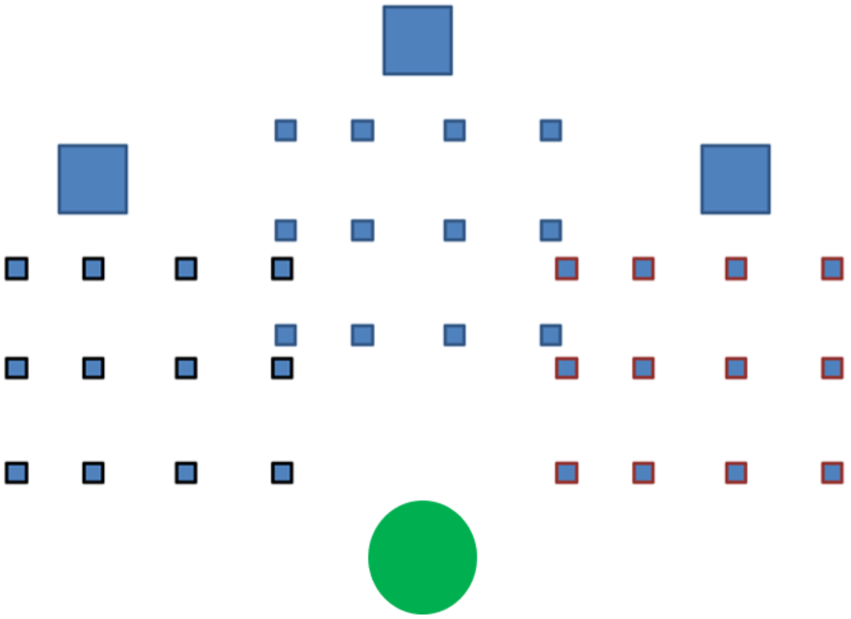

Figure 1: Illustration of possible target locations, black outlined boxes show probe locations for the left target, blue outlined for the centre target and red outlined for the right target. The green circle shows the location and presentation of the start button.

Two types of stimuli were presented to indicate movement or no-movement trials, respectively. In no-movement trials, the target consisted of a 0.15º sized black outlined square containing a black bar (see Figure 2B). In movement trials, the target consisted of the same black outlined square containing a black bar; however, with the addition of a small triangle adjoining one end (see Figure 2A) creating an arrow. The small size of the adjoining triangle was chosen to prevent the type of trial being detected from viewing the target in the periphery without attending to the target.

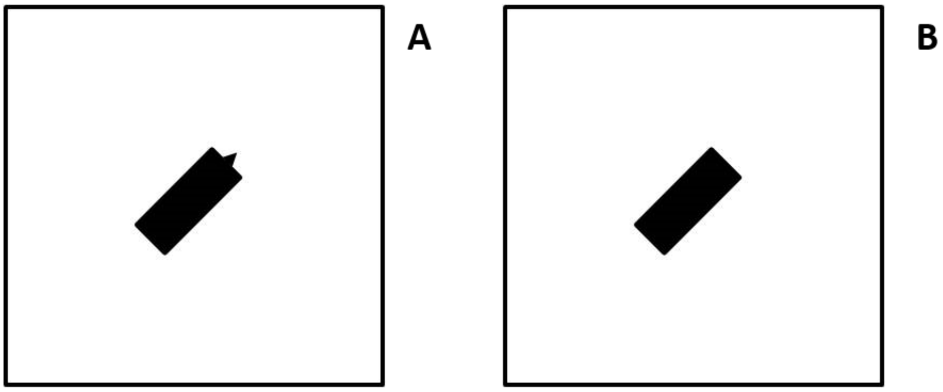

Figure 2: Example of target stimuli for movement trials (A) and no-movement trials (B)

For both types of trial, the black bar within the target was oriented in one of three ways: leftwards, central, and rightwards (see Figure 3). The central orientation for each target was oriented in the direction of a straight approach from the start box to the target. The left and right orientations were calculated by the angle of the central orientation +/- 45 degrees respectively. In movement trials, this orientation indicated the direction in which the target should be approached, with participants required to approach the target in the direction of the arrow. Varying the approach direction of the target was included to increase variance in distance from the hand to the probe.

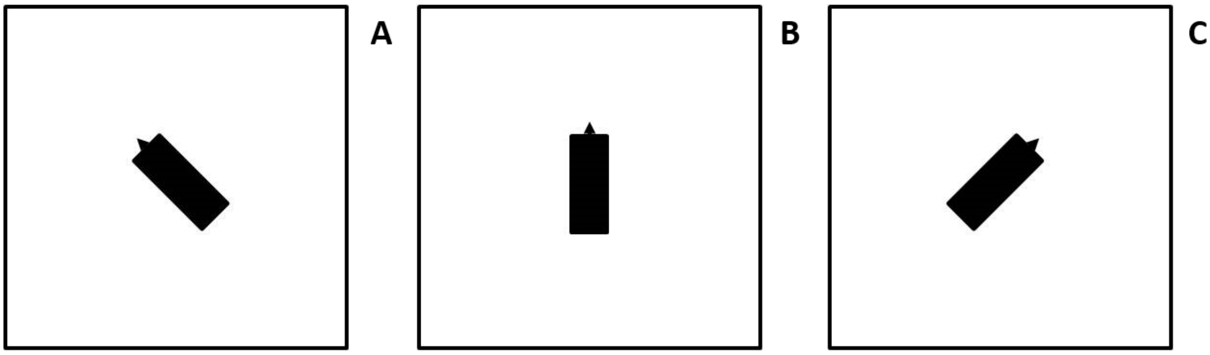

Figure 3: Example of left (A), centre (B), and right (C) orientations of target stimuli. The target pictured is the central target in movement trails.

To assess perception, a probe was presented in the form of a dot, 0.009º in diameter. The RGB value of the probe was set to black. The fourth RGB value, alpha, determining the transparency of the probe, varied based on the point of subjective equality (PSE) estimate during the staircase procedure and varied between 1 (near complete transparency) and 255 (opaque black) for each participant. The alpha value for the main task of the experiment was dictated by the final PSE estimate from the staircase method multiplied by 4. This multiplication of the final PSE estimate from the staircase method was done to account for the increased complexity in the body of the experiment compared with the staircase method. A multiplication method for altering the probe transparency was chosen in accordance with Webber’s law, which states the point of ‘just noticeable difference’ between stimuli is proportional to the original stimulus value. As such, by multiplying the final PSE of the staircase procedure, the task should decrease in difficulty by the same amount for each participant, regardless of their visual threshold. The multiplication factor of 4 was selected based on pilot data indicating this value to be sufficient for participants to see the probe on average 50 percent of the time.

The probe was presented in one of twelve locations for each target. These twelve locations were calculated according to a three-by-four grid dependent on the location of the target (see Figure 1). For the centre target, the grid was located directly below the target on the x-axis, centred on the midline of the target. For the left and right targets the grid was positioned below the target but offset on the x-axis so that the second column for the left target and third column for the right target were aligned with the centre of the target. This ensured that, for central approaches for all targets, the trajectory of the hand was likely to pass through the centre of the grid. To indicate whether the participant saw the probe, ‘Yes’ and ‘No’ boxes were presented on the left and right of the screen, respectively (see Figure 4). The side of the screen each box was presented on was randomised for each trial.

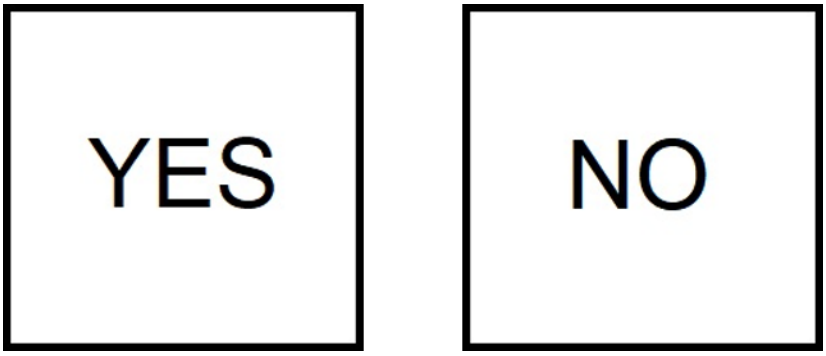

Figure 4: Yes/No response boxes for indicating if the participant saw the probe.

1.2.4 Design

The experiment followed a 2x3x3x12x2 design, manipulating movement (movement vs no-movement), target location, approach side, probe location and probe presence (probe present vs. probe absent). Stimulus onset asynchrony (SOA) was also varied. However, due to pilot data indicating a sizable fatigue effect due to the large number of trials, SOA was not included in the full factorial design in the experiment. Instead, early or late SOA was randomized for each trial with the added constraints of ensuring equal numbers of early and late SOAs for each block and participant.

1.2.5 Procedure

The experiment comprised of two parts. The first part of the experiment consisted of the staircase method; a standard psychophysics method used to determine an individual's visual threshold level (Cornsweet, 1962). In the second part of the experiment, participants completed the main experiment which, through the use of a probe detection task, investigated the spatial allocation of attention during hidden reaching movements.

The staircase method. The staircase method was used to determine each participant's visual threshold value. It is well known that the visual threshold at which an object can be differentiated from its background can vary between individuals (Judd, 1932). In the case of the current experiment, this would result in some participants needing a higher contrast between the probe and the background to achieve the same detection rate. Without accounting for this individual difference, the difficulty of the task would vary greatly between participants and add noise to the data. By using the staircase method to determine the individual's visual threshold level and using this to control the transparency of the probe in the body of the experiment, this source of variance can be removed.

During the staircase method, the start box appeared on the screen to signal the start of a trial. To begin the trial the participant moved their hand directly below the start box, which disappeared when they did so. The probe then appeared 300 or 400ms after the start box disappeared and remained on the screen for 100ms. Once the probe had been presented, Yes/No response boxes would be displayed on the screen. To indicate if they saw the probe, participants moved their hand directly below the appropriate response box, which then disappeared signalling the end of the trial.

The staircase method began with the alpha transparency of the probe being 253 (near opaque black) and possible values constrained from 255 to 1. This transparency value systematically changed from trial to trial, depending on if the participant had seen the probe. Psychtoolbox’s ‘MinExpEntStair’ function was used to determine the transparency of the probe. The function acts to suggest the probe transparency value for each trial that will provide the most information based on the principle of minimum expected entropy. As such, the final value suggests the level of transparency where the probe is perceived 75% of the time.

The staircase method took place over a series of 78 trials prior to the main experiment beginning. It was decided that the staircase method would not be done as part of practice trials due to the increased complexity of the task in the body of the experiment resulting in the target not being seen for reasons other than its transparency being less than the participants’ visual threshold.

The main experiment. After completion of the staircase method, participants completed a block of 78 practice trials consisting of the task for the main experiment. As part of this task, to indicate the beginning of a trial, the start box was presented on the screen. The participant then moved their hand directly below the start box, which disappeared when they did so. Immediately after the start box disappeared, the target was displayed, starting the trial. The location of the target was randomised. In a no-movement trial, the participant was instructed to look at the target but not move their hand. In a movement trial, the participant was to reach toward the target, approaching it in the direction indicated by the bar within the target. Once the participant’s hand was below the target, the target was removed from the screen. 200ms or 300ms after the target was displayed in no-movement trials and 300ms or 400ms after the target was displayed in movement trials, the probe was displayed for 10ms in one of twelve locations on a grid fixed to the location of the target. The stimulus onset asynchrony (SOA) of the probe was varied to prevent participants from learning to expect the probe at one particular time and only attend then. The SOAs were longer in movement trials than in no-movement trials due to the assumption that around 200ms are taken to fixate on the target in addition to a motor plan needing to be prepared. In 8.3% of trials, the probe was not displayed to avoid the potential bias of participants saying they saw the probe if always expecting it to be displayed. In no-movement trials, 1 second after the start of the trial the target disappeared. In movement trials the target disappeared once the participant's hand was directly below it.

For both types of trial, 400ms after the target was removed the Yes/No boxes were displayed. The participant moved their hand under the appropriate response box to indicate if they hand seen the probe. Once their hand was under a response box, the boxes were removed from the screen. The start box was then displayed once more, indicating the start of the next trial.

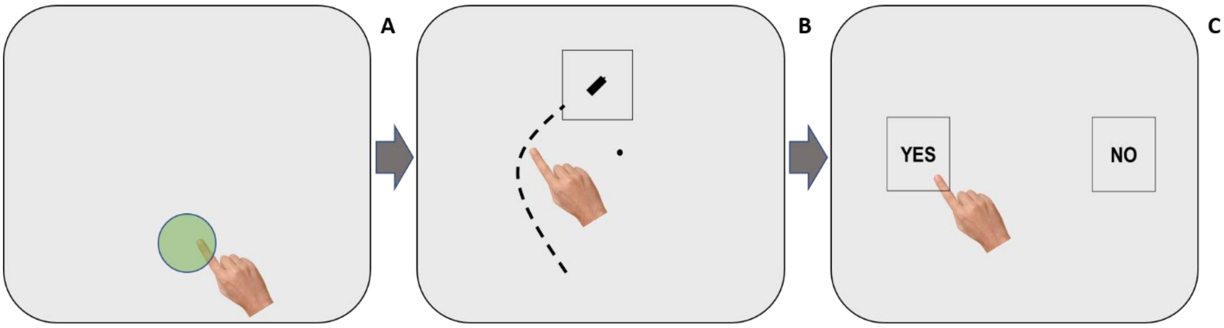

Figure 5: Illustration of the procedure of the body of the experiment. The participant first places their hand underneath the start button to begin the trial (A). The target then appears, as the participant reaches for it a probe is displayed (B). Once the target is reached the Yes/No boxes appear for the participant to indicate if they saw the probe (C).

After completing the block of practice trials, participants moved on to the experimental trials, which were identical to the practice trials. Participants completed 3 blocks of 78 experimental trials. Between each block there was an enforced rest period of at least one minute.

1.2.6 Analysis

A General Linear Mixed Model (GLMM) was used to analyse the data, utilising MATLAB's 'fitglme' function with a 'logit' link function. Like a logistic regression, a GLMM predicts a binary variable (probe seen vs not seen) from a continuous variable (distance), but while also accounting for the random effect of participant. Separate GLMMs for no-movement and movement trials were performed. For no-movement trials, the distance from the target to the probe was used as a predictor of whether the target had been seen. For movement trials, the distance from probe to the hand and the distance from target to the probe were used as predictors of seeing the probe.

1.3 Results

Predictor	Estimate	S.E.	tStat	DF	Sig.	Lower	Upper
No-movement Trails							
Distance from target to probe	-0.001	.000	-7.509	2047	<0.001	<-0.001	-0.001
Movement Trials							
Distance from hand to probe	<-0.000	.000	-2.154	1938	0.031	<-0.001	<-0.001
Distance from target to probe	-0.001	.000	-6.971	1938	<0.001	<-0.001	-0.001

Table 1: Summary of GLMM results predicting 'probe detected'

1.3.1 No-movement trials

For no-movement trials, a GLMM was performed with the dependent variable ‘distance from the target to the probe’ as a predictor of ‘probe detected’, considering the random effect of participant. The R^2 value indicates the model accounted for 12.8% of the variance. As hypothesised, in no-movement trials the distance from the target to the probe significantly predicted the likelihood of probe detection ($\beta < -0.01$, $t(2049) = -7.51$, $p < 0.01$). The negative relationship between ‘distance from the target to the probe’ and ‘probe detection’ indicates the rate of probe detection to decrease as the distance from the target increases.

1.3.2 Movement trials

A separate GLMM was performed for movement trials, with ‘distance from the hand to the probe’ in addition to ‘distance from the target to the hand’ as dependant variables predicting ‘probe detected’ while considering the random effect of participant. The R^2 value indicates the model accounted for 15.6% of the variance. As in movement trials, distance from the target to the probe also significantly predicted detection of the probe ($\beta < -0.01$, $t(1941) = 6.97$, $p < 0.01$). Notably, the distance from the hand to the probe was also a significant predictor of probe detection ($\beta < -0.01$, $t(1941) = 2.15$, $p = 0.031$). The negative relationship between both predictors and ‘probe detected’ indicates that as both the distance from the hand to the target and from the probe to the target increase, the likelihood of detecting the probe decreases.

1.4 Discussion

In this chapter, we investigated whether proprioceptive feedback of the hand’s location during movement facilitated the allocation of visual attention to the location of the hand in addition to the target. Corroborating the findings of Baldauf and Deubel (2009) and Baudauf, Wolf, and Deubel (2006), the results indicate visual attention is allocated to the location of the target, as the likelihood of the probe being seen was found to decrease in relation to an increase in the distance between the target and the probe. Notably, the results also indicate visual attention is allocated to the location of the hand during movement, an effect which relies on continuous proprioceptive feedback of the hand’s location. As such, in addition to demonstrating proprioceptive information to be able to locate the hand for the allocation of attention during movements, the presence of this continually moving site of attention provides evidence for an interconnected theoretical framework of movement, whereby movement can affect attention.

1.4.1 Is visual attention allocated to the hand and target locations by the same mechanism?

Up to this point we have considered that the observed effect of visual attention being allocated to the hand is due to its action-relevancy for the reaching movement, deployed in the same way in which attention is allocated to the target of a reach. According to models such as that by Allport (1987), it is suggested that in order to identify movement-relevant targets and hence allocate attention to them over other locations, the motor system must, to some extent, be involved. However, for the hand's location there exists another possibility which does not involve the motor system. It is plausible that given evidence of specialized neurons for the integration of proprioceptive and visual information, allocating visual attention to the hand's location can be done though purely sensory mechanisms. Observations of bimodal cells in the ventral premotor cortex of macaque monkeys have shown the visual receptive field of the cell to reflect the proprioceptive sense of the hand's location, moving in accordance with the movement of the hand (Graziano, Yap & Gross, 1994). With these findings implicating a biological coupling of proprioception and visual attention, it is possible that during movement, visual attention is allocated to the hand's location through purely sensory mechanisms. When using purely sensory mechanisms, the motor system needed for allocating visual attention to other action-relevant targets is not necessarily involved, meaning allocation of visual attention to the hand and target may use different mechanisms.

1.4.2 Potential sources of unaccounted for variance

The finding that perception is better closer to the hand is consistent with the wealth of evidence showing increased perception at the location of the hand in static scenes (Abrams, Davoli, Du, Knapp III, & Paull, 2008) and showing increased perception at other task-relevant locations (for review see: Mahon, Bendžiūtė, Hesse, & Hunt, 2020). However, the variance accounted for by the model is relatively small, suggesting additional factors also affect the allocation of perception during reaching movements. Considering this, two possible reasons why the model accounted for such a small proportion of the variance in the data will now be discussed in addition to how the effects of these factors may be minimised in future research. The first reason is the possibility that visual attention is not allocated to the hand throughout the trajectory but rather only at the end of the trajectory. The second reason is the possibility that visual attention is allocated to a location that spatially precedes the hand rather than to the location of the hand itself. In addition, the potential pitfalls of the experimental design will be considered, such as the effects of using a hidden hand paradigm and the effects of the predictability of the target locations on the variance in the data and their wider implications.

Allocation of visual attention to the hand only at the end of the reach. One possible explanation of why the model only accounted for a relatively small amount of the variance in the data is that visual attention is only allocated to the hand in later portions of the trajectory. Despite being investigated for over a century, the relative contributions of preplanning and online feedback to movement has reached little consensus (Desmurget & Grafton, 2000). Undoubtedly, preplanning has a role in the production of action, with evidence showing simple movments to be performed successfully in the absence of online feedback (Desmurget, et al., 1999). Yet, to complete successful movements in the real world, a mechanism for compensating for the ever-changing environment is necessary. One such way of enabling flexibility around the changing environment is to guide reaches using sensory feedback. However, the substantial temporal delay that accompanies sensory feedback (Paillard, 1996), makes guiding a movement entirely using sensory information highly inefficient (Gerdes & Happee, 1994). Consequently hybrid models have been suggested, featuring an initial movment guided by preplanning, followed by online sensory feedback at the end of the reach to facilitate corrections for endpoint accuracy (Jeannerod, 1988; Milner, 1992). Early studies such as that by Carlton (1981), offered support to this notion of online feedback only at the end of the trajectory, as it was found that removing vison of the first 75% of the reach had no effect on the accuracy of the movement, unlike removing visual feedback in the last 25% of the movement which significantly affected movement accuracy. If this is the case, in our analysis we could expect to find distance from the hand to the probe to be a significant predictor of probe detection due to its strong predictive power at the end of the reach despite its weak predictive power at the beginning of the reach. Thus, position in the trajectory may add variance to the model which cannot be accounted for by distance from the target to the probe or by distance from the hand to the probe.

The hand facilitates perception but not at its location. Another possible source of variance in the model is the site of the allocation of visual attention spatially preceding the hand. When asking participants to perform continuous swiping movements from one side of the screen to the other, Festman, Adam, Pratt, & Fischer (2013) found no significant main effect of distance between the hand and the probe on discrimination of a ‘T’ from an ‘L’ at the probe location. Strikingly however, an interaction was found between proximity and movement direction, finding discrimination to be best when the hand was moving towards the probe. In principle, an interaction between movement direction and proximity is understandable. When monitoring a scene for obstacles in the real world, there would be little reason to monitor the space already passed through but ample reason to monitor the approaching space. Yet, in the current study we do not differentiate between probes presented in front of or behind the hand. In this case it is possible that the distance from the hand to the probe is still significantly predictive of probe detection due to its strong predictive power when the probe spatially precedes the hand. However, to investigate the possibility of an interaction between proximity and movement direction in the future, including the spatial relationship between the hand and the probe in the analysis may account for more variance.

The effects of experimental design: *the hidden hand paradigm.* In addition to potential theoretical sources of variance in the model, experimental design may also contribute to the unaccounted-for variance observed. One such experimental design feature that may add to the variance in the model is hiding the hand from view. In everyday reaching movements, lack of vision of the hands is possible but unusual. To locate the hand, a spatial representation is built by combining both proprioceptive and visual information (Holmes & Spence, 2002) with the weighting of each source of information in proportion to the amount of noise it contains (Körding & Wolpert, 2004). Due to visual information being more temporally and spatially precise than proprioception, a heavy weighting is placed on visual information during reaching movements (Sober & Sabes, 2005). However, in conditions where visual information is unreliable, e.g. during low light conditions, a reliance on proprioceptive information increases (Mon-Williams, Wann, Jenkinson, & Rushton, 1997). Due to the hidden-hand paradigm used in the current study, locating the hand is reliant solely on proprioception. In real world situations where there is no visual information on the location of the hand, such as in the dark, there would also be limited visual information available about potential obstacles. Consequently, in these situations it would make little sense to attend as closely to the location of the hand as when visual information is available. Consequently, if less visual attention is allocated to the hand when proprioception is being used to locate it, the predictive power of ‘distance from the hand to the probe’ would be weaker than if the hand was visible, resulting in a large proportion of variance in the model being unaccounted for.

Predictability. An additional design feature that may add to the variance in the model is the predictability of the task. Despite attempting to create more reach trajectories by varying the approach direction of the target, there are still only nine possible reaches required. Furthermore, approaching the target from the preferred angle is not enforced, meaning that participants could perform just three different reach trajectories during the experiment. Through both learning and through the initial instructions given to the participant before the experiment began, the trajectories become highly predictable. This predictability could result in the participant not having to allocate visual attention after initial trials due to being able to rely on ‘muscle memory’, as suggested by Similä and McIntosh (2015). Neurophysiological evidence strengthens the notion of an interaction between predictability and perception, with activity in the visual cortex being shown to decrease with the predictability of the target (Alink, Schwiedrzik, Kohler, Singer, & Muckli, 2010). Furthermore, when using highly predictable targets, McIntosh and Buoncore (2012) failed to replicate kinematic and temporal effects of a distractor (as shown by Tipper, Howard, & Jackson; 1997), strengthening the claim that increased predictability decreases the allocation of visual attention. As such, it is possible that, in the current study, after learning the movements associated with the relatively small number of possible targets, as the experiment progresses less attention needs to be allocated as memory is relied upon and hence the allocation of visual attention to the location of the hand is reduced. In this case, the predictive power of the distance from the hand would be decreased in later trials, increasing the unaccounted-for variance in the model.

Aside from its effects on the variance in the model, predictability potentially has wider implications for the interpretation of the results due to the likelihood of preplanning. When repeating the same movements many times, information can be gathered on the trajectory and the speed of the hand, making it possible to predict where the hand would be at any point in time during the reach. Consequently, this could result in visual attention being allocated at the predicted location of the hand based on the preplanning of movement and not using the proprioceptive sense of hand position. Whilst no conclusions can be drawn from the present study as to the effect of predictability on the allocation of visual attention to the hand’s location, measures can be taken to mitigate this possibility in future studies. By randomising the location of the target to anywhere within a specific region and manipulating the hand from its intended location (potentially through the use of robotics), the exact trajectory of a reach would become unpredictable, preventing preplanning/leaning effects from affecting the allocation of visual attention and perception and ensuring the hand is located via proprioception.

1.4.3 Conscious vs. subconscious perception

The findings do not only support previous literature showing visual attention to be allocated to the location of the hand but also cast established theories, such as Glover's planning-control theory, into doubt. Glover proposes two distinct, but temporally overlapping systems in the production of action: planning and control, each relying on their own qualitatively different visual representations. Prior to the start of movement, the planning system uses a range of cognitive and visual factors to select an appropriate target and plan the kinematics of the reach. After the initiation of the movement, the reach is influenced increasingly by the control system. The control system acts to monitor the visual scene and occasionally adjust the trajectory of the reach based on a limited visual representation of the planned reach and the target location, provided by the planning system and proprioception. Unlike the planning system, the control system's visual representation must deal with rapidly updating information. To enable the speed required for an accurate spatial representation of the ever-changing scene, Glover suggests the control system operates outside of conscious awareness (Glover, 2004). As the probe occurs after the onset of movement, Glover would therefore categorise information about the probe to be under the influence of the control system. If conscious perception and the control system are separate as Glover's theory stipulates, the detection of the probe (i.e. a conscious process) would not be influenced by the control system (i.e. the trajectory). As such, the results of the current study do not support Glovers hypothesis of a complete separation between conscious perception and action in the control phase of movement.

Considering our findings of heightened conscious perception surrounding the hand, in combination with literature also showing subconscious perception, Glover's planning-control theory may be too simplistic in its view of all action-relevant information during control being processed identically. There exists a substantial quantity of data showing subconscious perception during movement to influence trajectory of the reach. However, the research that shows this primarily focuses on subconscious manipulations to the hand or target position. For instance, revisiting Saunders and Knill's (2003) study (as discussed in Section 1.1), participants were shown to correct visual perturbations during the reach, despite unawareness of the perturbation occurring. Similarly, the ability to adjust movement considering subconscious changes to the visual relationship between the target and the hand mid-reach has been robustly shown (Goodale, Pelisson, & Prablanc, 1986; Preblanc & Martin, 1992; Pisella, et al., 2000), demonstrating that some action-relevant information is processed subconsciously. Yet, where this research differs from the current study is the type of movement-relevant information being perceived.

The previous studies discussed, such as that by Saunders and Knill (2003), consider perception of the hand and target's spatial relationship. In contrast, the current study presents an additional and unforeseen object (the probe) to be perceived. Consequently, a different perceptual mechanism may be employed which is more apt for dealing with potential obstacles. In this case, conscious perception may be advantageous as it would allow for a more thorough consideration of how to respond, whilst subconscious perception of the hand-to-target relationship would ensure the fast processing needed for continuous monitoring. As such, perception of action-relevant information may not be as simple as conscious for the planning system and subconscious for the control system as Glover's (2002) planning-control model suggests, but instead also be dependent on the type of action-relevant information being presented.

1.5 Conclusion

In conclusion, as predicted, the findings indicate attention to be allocated to both the hand and target during reaching movements, with the likelihood of detecting the probe decreasing with the increase in distance from the target to the probe and from the hand to the probe. As such we interpret this as evidence for a feedback loop from movement to attention, contrasting the traditional serial model of processing and as such providing evidence for the newer interconnected theoretical framework of movement. However, there is a possibility that the allocation of visual attention to the location of the hand during reaching movements observed may be the result of preplanning, bypassing proprioception. As such, future research should investigate the spatial distribution of visual attention while the hand is manipulated to perform an unforeseen trajectory to avoid the possibility of preplanning.

Chapter 2: Explaining perceptual priming: a computational modelling approach

2.1 Introduction

Complementary to the influence of movement on attention and perception shown in Chapter 1, evidence of an ongoing feedforward influence of attention and perception on movement after the onset of movement also exists. When reaching for a target which changes location on a screen, participants have been shown to adjust the trajectory of their reach mid-movement (Goodale, Pelisson, & Prablanc, 1986), demonstrating the movement to continually adjust with the influx of visual information facilitated by the continuous allocation of visual attention to the target. Additionally, hindering perception of the hands by hiding them from view has been shown to result in less accuracy, longer reaches, and kinematic changes to hand position when grasping (Churchill, Hopkins, Rönnqvist, & Vogt, 2000; Berthier, Clifton, Gullapalli, McCall, & Robin, 1996; Schettino, Adamovich, & Poizner, 2003). Furthermore, by facilitating the allocation of attention to the correct target by cuing or by perceptual priming, deviations in curvature of reaching trajectories towards distractors have been shown to be reduced (Song and Nakayama, 2006), suggesting attention and perception to continually influence movement.

To date, the effects of attentional and perceptual processes on movement have largely been described rather than explained. Whilst descriptive analyses have, without doubt, added to our understanding, mechanistic explanations by way of computational models allow for a deeper understanding of underlying attentional and perceptual processes. In particular, when considering movements to consist of the execution of one or more motor plans, descriptive analyses offer no explanation of how such motor plans form the observed trajectory. Contrastingly, by considering movements to be made up of smaller submovements, each representing an individual motor plan, computational modelling offers a more appropriate way to explore motor plans (Friedman, Brown, & Finkbeiner, 2013; Flash & Hogan, 1985). In the present study we aim to build a submovement-based computational model of reaches, in order to capture the ongoing feedforward influence of perceptual priming on movement and its constituent motor plans.

2.1.1 Perceptual priming and movement

For some time, the effects of perceptual priming, induced by target colour repetition, have been shown with reaction time (RT) paradigms. A series of studies by Maljkovic and Nakayama (1994) showed that when asking participants to find an odd-coloured target amongst distractors, RTs diminished with the repetition of target colour. However, whilst RTs are effective at showing that perceptual priming influences the time taken to execute a movement, they provide little information on how perceptual priming might influence movement and the selection and execution of motor plans prior to movement completion. As such, when using RTs it cannot be determined whether perceptual priming affects the preparation of movement in line with the traditional model of serial processing or whether perceptual priming may continue to affect the movement itself after its onset in favour of the newer interconnected theoretical framework of movement.

To investigate how perceptual priming might influence the preparation of movement, and the movement itself after its onset, a choice reaching task (CRT) can be employed. Utilising reaching movements and a visual search task, Song and Nakayama's Choice Reaching Task (CRT) has become a standardised paradigm, used to observe the continuous temporal unfolding of internal processes. The CRT comprises of several targets displayed on a screen with participants reaching towards the appropriate target as quickly and accurately as possible. By presenting alternative choices spatially and observing fluctuations in the direction of the reach trajectory, it is possible to observe how competition between choices is resolved over time. According to Desimone and Duncan's (1995) Biased Competition Theory, each object in the visual field competes for representation and processing. Stimuli displayed simultaneously each have the potential to be the target, leading to competition between items. As potential targets are identified, competing motor plans, specifying the kinematics of a reach, are formed for each possible target by the motor system (Cisek & Kalaska, 2005; Freeman, Ambady, Midgley, & Holcomb, 2011). While perceptual competition between targets decreases with the parallel accumulation of information about each target, competition between motor plans correspondingly decreases (Smith & Ratcliff, 2004; Strauss, Woodgate, Sami, & Heinke, 2015; Narbutas, Lin, Kristan, & Heinke, 2017). This results in one motor plan dominating, causing the movement to begin. However, perceptual priming may temporally bias the competition towards motor plans to distractors (Song and Nakayama 2006) leading to a curved trajectory.

2.1.2 Analyses of Choice Reaching Tasks

The ability for CRT to capture the continuous temporal dynamics of internal processes, and the versatility of potential stimuli, makes it an attractive paradigm for a range of research domains. Furthermore, with the transition of CRTs from motion trackers to mouse tracking and the release of open source software such MouseTracker (Freeman & Ambady, 2010) and MouseTrap (Kieslich & Henninger, 2017), CRTs have become comparable to simple reaction time experiments in programming. Yet, whilst conducting a CRT may be as straightforward as a RT experiment, the same cannot be said for analysing them. The continuous nature of reaching trajectories produces large amounts of data, with analysing such large and multifaceted data sets posing a significant challenge to researchers. Numerous methods exist to analyse CRT data (for review see Dotan, Pinheiro-Chagas, Al Roumi, & Dehaene, 2019) each with their advantages and disadvantages. Here the pros and cons of these existing methods will be discussed, considering the added value that a submovement extraction model can provide in gaining insight into perceptual priming’s ongoing feedforward influence on the preparation and execution of motor plans and hence reaching movements.

Summary measures. Much like RTs, summary measures quantify an entire trajectory into a single figure which represents one aspect of the reach. Two of the most used summary measures for CRTs are Maximum Deviation (the maximum distance of the reach trajectory from a straight line connecting the start location to the target; see Figure 6 for an illustration) and Initiation Latency (the amount of time after the targets appear before movement is initiated). Despite their simplicity, summary measures such as MD and IL have been shown to be highly successful at showing differences between trajectories performed at different levels of perceptual priming. When pointing for the odd-coloured targets, Song and Nakayama (2006), in addition to replicating Maljkovic and Nakayama’s (1994) finding of the total time of the reach to decrease with the number of target colour repetitions, also found IL and MD to decrease between two and six repetitions of target colour.

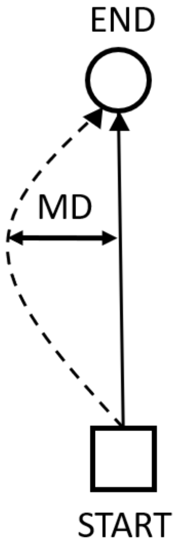

Figure 6: Illustration of maximum deviation (MD). The solid line shows the straight trajectory from the starting point to the target. The dashed line shows the actual trajectory of the reach. MD is calculated as the maximum distance of the reach trajectory from a straight line connecting the starting location to the target.

Using the insight gained from the summary measures MD and IL, theories of the processes underlying perceptual priming's effect on motor plans and hence reaching movements, have been proposed. For instance, the decrease in ILs with repetition of target colour have been interpreted as showing the time taken to form a motor plan to decrease. The reason for this perhaps being the repetition of target (colour), facilitating the rapid deployment of attention to the target and allowing it to be identified faster, hence the quicker preparation of a motor plan (Woodgate, 2017; Song & Nakayama, 2009). Similarly, considering research showing MD to be correlated with relative amounts of activation of competing targets (Song & Nakayama, 2006; Welsh & Elliot, 2004), decrease in MD with target colour repetition has been suggested to show perceptual priming to decrease the competition between targets. As such, it is clear that the summary measures MD and IL are sufficient to capture a difference in movement resulting from perceptual priming. Yet, by the nature of summary measures being a single value, the continuous temporal detail that has the potential to provide information about ongoing competing motor plans is lost.

Time dependent measures. It is clear from previous research that perceptual priming is a relatively fast effect, influencing initial saccades (McPeek, Skavenski, & Nakayama, 2000) and directions of reach (Song & Nakayama,2006). As such, it is possible that perceptual priming only affects the early selection of motor plans; yet by only using summary measures information about the time-course of perceptual priming's effect on movement is lost. To observe how perceptual priming's feedforward influence on movement unfolds in time, a more detailed family of analyses can be utilised (namely time-dependent measures) which account for the coordinates of a trajectory at each point in time.

Direct Coordinate Comparison. One way in which differences in trajectories at different points in time can be analysed is by direct comparison of coordinates (Spivey, Grosjean, & Knoblich, 2005). Although not previously applied to perceptual priming data, direct coordinate comparison has been successful at showing differences in trajectories between other conditions. For instance, subtle differences in the timing where conditions' trajectories differ have been found when reaching leftward versus rightward (Spivey, Grosjean, & Knoblich, 2005; Faulkenberry, Cruise, Lavro, & Shaki, 2016; Chapman, et al., 2010), a difference which Spivey (2005) suggests reflects the kinematics of the dominant vs non-dominant hand or the position of the mouse. By applying this method to perceptual priming data, differences in the times at which trajectories deviate with varying levels of perceptual priming could be explored, providing a sense of the time course of its influence on movement.

To do this, the data must first be normalised to the same time scale, generally 101 timestamps (0 -100% of movement time) via linear interpolation. This removes the effect of differing initiation latencies. The data is then normalised to a standard space for direct comparison of coordinates between trials and conditions. Once the data has been normalised there are two options for comparing coordinates, depending on the number of conditions being compared. If only two conditions are being compared, such as priming vs. no priming, paired sample t-tests can be used to compare coordinates on a given axis for each point in time individually. Alternatively, a functional analysis of variance (FANOVA) can be used when comparing the coordinates of three or more conditions (Ramsay & Silverman, 2007), such as for number of target colour repetitions.

Extending the traditional ANOVA, a FANOVA uses functional (continuous) data such as trajectories made up of continuous sets of coordinates. For example, when repeating the target colour multiple times, forming a ‘streak’, to induce perceptual priming, a FANOVA could be used to compare trajectories from each length of streak at each point in time. Instead of the single F-statistic produced by a regular ANOVA, a FANOVA provides a functional F-statistic that is used to determine if and where the trajectories differ. By doing this, the time-dependent characteristics of perceptual priming’s influence on movement can be revealed and thus insight is gained into their underlying processes and motor plans. However, despite showing differences in trajectories, functional t-tests and FANOVAs offer little indication of which of the observed differences in trajectories relate to perceptual priming and which may be the result of a confound. For example, early differences in trajectories found under different perceptual priming conditions, whilst potentially resulting from the differences in perceptual priming, could also potentially result from another confounding factor such as target location. By directly comparing the coordinates of the two trajectories, we can observe that a difference exists and where in the trajectory it exists but cannot differentiate between the potential causes of the variance.

Multiple Regression. To differentiate the temporal effects on the trajectory caused by a factor of interest, such as perceptual priming, from the effects of other factors, a multiple regression analysis can be used (Scherbaum et al., 2015). For each point in time either the deviation of the coordinates on a given axis (calculated as the distance from a straight line joining the start and end of the trajectory) or the angle of the movement is calculated. This value is then entered into a multiple regression as the dependent variable, with factors hypothesised to affect the trajectory, such as priming and confounds, entered into the regression as separate independent variables. A separate multiple regression is performed for each timestamp. Each multiple regression returns a beta weight for each of the independent variables. The beta weights are then averaged across participants, producing a curve for each independent variable which represents the predictors' influence on the trajectory at each point in time. To determine if and where predictors affect the trajectory, t-tests are performed against zero for each predictor at each timestamp. To avoid significant results due to multiple comparisons, the significant effects of predictors are only accepted if significant t-tests are produced by a specific number of consecutive timestamps (usually 8-10) (Dale, Kehoe, & Spivey, 2007; Scherbaum, Gottschalk, Dshemuchadse, & Fischer, 2015).

By using a multiple regression in this way, Scherbaum et al. (2015) have shown perceptual priming of the target location to influence only the early sections of the reach and hence potentially only the initial selection of a motor plan, providing a better understanding of perceptual priming's effect on movement. In addition, the flexibility of multiple regressions makes them useful for analysing data sets with suspected confounds. For instance, reaching for the wrong target may reduce the effect of perceptual priming in a subsequent trial. To differentiate the effect of these errors on the data from the effects of perceptual priming, in a direct coordinate comparison, trials where the previous trial's response was incorrect can be excluded. The issues with pruning the data in this manner are twofold: firstly, the data describes only a very specific type of trial. Secondly, there is a potential loss of statistical power due to a reduced number of trials (Notebaert & Verguts, 2007). In multiple regressions these confounds can be included as predictors in the model, meaning the entire data set can be used. Futhermore, if a new potential counfound is suspected, such as the direction of reaching found by Spivey (2005), older data sets can be reanalysed in light of this by adding the suspected confound as an additional predictor. Thus the flexibility of multiple regressions makes them a particularly useful method of analysis in rapidly developing fields of psychology.

However, a great deal of caution must be taken when constructing and interpreting the results of a multiple regression. The regression coefficient for each predictor in a multiple regression is highly influenced by the inclusion of other correlated factors in the model (multicollinearity). For example, if in a CRT the left target is always blue and the right target is always red, by including motor priming (in the form of location repetition) and perceptual priming (in the form of target repetition) as predictors in the model, both predictors would have a smaller predicted effect on the trajectory than if either one were omitted from the model. Similarly, regression coefficents are also highly influenced by adding superfluous predictors into the model (overfitting). When overfitting, the model becomes too complex and the regression coefficients begin to reflect the random error in the data rather than the actual effects of the predictors. As such, while multiple regressions are powerful tools for quantifying the effects of different factors, such as perceptual priming, they are relatively fragile when considering the outcome's dependence on the quality of the model, rendering them far from the ideal analysis tool.

Velocity dependent measures. The methods discussed so far are Cartesian based. Yet, in addition to coordinate position information, trajectory data also contains information about the varying speed in a reach. Coordinates and speed have been suggested to reflect separate processes with coordinates reflecting the accumulation of evidence and speed reflecting online confidence (Dotan, Mayniel, & Dahaene, 2018). Furthermore, when adding movement curvature into a multiple regression, a correlation between speed and confidence was still found to be significant (Dotan, Mayniel, & Dahaene, 2018), suggesting speed provides additional information which position alone cannot. As such, it is possible that information on the execution of motor plans may in part or in whole be manifested in the speed. By combining position and speed information into velocity plotted against time (to produce a velocity profile), all available information can be utilized to examine the influence of perceptual priming on motor plans and hence movement.

Indeed, research analysing position and velocity measures have found changes in an independent variable to be reflected in velocity but not position. When performing a reaching task with electroencephalography (EEG) recording, Perfetti, et al. (2011) found acceleration and maximum velocity but not movement extent to be correlated with 8.05–10 Hz activity in bilateral parietal regions. They use this correlation to suggest the involvement of parietal regions in motor planning; an interaction that would have been missed had coordinates alone been analysed. Interestingly, they also found a disassociation between acceleration and peak velocity, with peak velocity being correlated with activity in parieto-occipital areas, where acceleration was not. As such, different mechanisms could be assumed for each measure, giving a clearer understanding of how motor plan selection and execution occurs, emphasising the value of velocity-based analysis. Consequently, when analysing data with the aim of exploring the influence of perceptual priming on motor plans and movement, by not considering speed-derived information, effects of perceptual priming may be missed, providing at best a limited explanation of its influence on movement.

Submovements and motor plans. Thus far the analyses discussed do not directly take into account the underlying mechanisms behind the reaching movements such as the competition between motor plans. However, a common way of modelling reach movements in motor control research, the submovement model, forms an ideal basis for reflecting these motor plans (Woodworth, 1899; Flash & Hogan, 1985). By constructing a submovement model of reaching movements and applying the model to trajectory data collected under a range of perceptual priming conditions, a mechanistic description of how perceptual priming influences competition between motor plans can be provided. This in turn would lead to a deeper understanding of the influence of the ongoing feedforward effect of perceptual priming on movement planning and execution.

These submovements are discrete and ballistic by definition, with curved trajectories being achieved by overlapping the straight trajectories of multiple submovements (Flash & Hogan, 1985). Hence, the peaks and troughs apparent in the velocity profile of a reach can be interpreted as the sum velocity profiles from smaller overlapping submovements (Roitman, Massaquoi, Takahashi, & Ebner, 2004; Flash & Henis 1991). The velocity profile of an individual submovement has been shown to follow the same broadly bell-shaped distribution across a large range of paradigms (Vellbo & Wessberg, 1993; Doeringer, 1999; Rohrer, et al., 2002). From a computational modelling standpoint, the consistency of the shape of submovement velocities makes them a convenient way of considering how reaching movements are produced, as when using a function to define this profile, larger velocity profiles can be decomposed into their constituent submovements.

To date, submovement models have been utilised in relatively few studies. However, two areas where submovements have been successfully applied are the analysis of movement differences with stroke recovery and aging. When decomposing continuous reaching movements of stroke patients, the duration and speed of submovements increased up to 54 months post-stroke (Rohrer, et al., 2004). Notably, however, overlap of submovements increased with recovery only until one year where it plateaued, suggesting qualitatively different underlying processes to be affected in the different stages of stroke recovery. Analysing submovements has also shown qualitative differences in movement production with age (Pratt, Chasteen, Abrams, 1994). When extracting submovements from the continuous reaches of older and younger adults, both groups performed similar initial ballistic submovements. However, with practice younger adults modified their submovements to the demands of the task, whereas older adults failed to modify their movements despite extensive practice (Pratt, Chasteen, & Abrams, 1994). This suggests a role for motor learning for younger, but not older, adults, which could play a role in age-related motor disorders. Findings such as those discussed exemplify the value of using submovement extraction to explain the processes underlying effects such as perceptual priming’s influence on movement.

A possible way to interpret submovements is to consider each one to reflect the implementation of a motor plan. For instance, each submovement must have critical parameters which every motor plan must possess, such as onset, speed, direction and duration. In addition, it can be assumed that a motor plan, much like a submovement, would follow a straight trajectory as it provides the most direct route from A to B. By extracting submovements from a given reach trajectory it is posibile to quantify both the number of motor plans executed and the critical parameters of each. Given this information it is possible to make hypotheses on the function of each motor plan and therefore gain a deeper understanding of how movement is produced and influenced by different factors.

2.1.3 Overview

It is clear from Song and Nakayama's (2006) research showing differences in MD and IL between perceptual priming conditions that perceptual priming causes differences in reach trajectories. In the present study we aim to build a computational model that, by extracting the individual submovements from a reach, captures the differences between reach trajectories recorded at different levels of perceptual priming. By considering each of these submovements to represent an individual motor plan, we hope to capture different numbers of motor plans executed at different levels of perceptual priming. It is hypothesised that the number of submovements extracted and hence the number of motor plans executed will mirror the differences observed by Song and Nakayama (2006), finding a lower number of submovements at higher numbers of target repetitions. This finding would demonstrate the less frequent switching between targets and hence the smaller number of motor plans executed as competition is reduced with increased perceptual priming. By building and interpreting the results of a submovement extraction model, considering competing motor plans this research aims to provide a mechanistic explanation of the ongoing feedforward influence of perceptual priming on movement.

2.2 Experimental Data

The data used to test the model was taken from Woodgate's (2017) Experiment 2.2, and broadly follows the methodology of Song and Nakayama (2006). Woodgate's (2017) methodology is as follows.

2.2.1 Method

Participants. 11 participants, aged 19-20 (mean 19.2), were recruited from the student population at the University of Birmingham by volunteer sampling.

Stimuli. Odd Colour (OC) displays were presented on a Samsung SyncMaster 940N LCD screen (19”, 1280 x 1024), placed vertically 45cm from the participant in a semi-darkened room. OC displays consisted of a black background with three square targets positioned equidistant (12.2cm) from the centre screen. The middle target was presented directly above the centre of the screen. The left and right targets were presented at 120^{o} and 240^{o}, respectively, from the centre of the screen. The target was differentiated from the two distractors by colour. Therefore, the target was either green (u’=0.11, v’=0.24, L=64.43) amongst red (u’=0.46, v’=1.03, L=22.43) squares or red amongst green. A small white fixation cross (0.9cm) was presented centrally on the screen at all times.

Procedure. Participants sat at a table facing the viewing screen. A small white trigger switch was positioned 10cm in front of the participants, centred on the midline of the body. A passive 4mm reflected marker was attached to each participant’s index fingernail on their right hand.

To begin a trial the participant held down the trigger switch. This triggered motion capture cameras (Qualisys ProReflex MCU240, 200Hz) to begin continuously recording the position of the fingernail reflector for 3000ms. The switch also began a 1000ms delay period in which the participant was to fixate on the fixation cross in the centre of the screen. After the fixation period, an OC target display was then presented. The participant was instructed to reach and touch the screen at the location of the odd-coloured target as quickly and accurately as possible. 400ms after the onset of the OC, a warning tone sounded. Participants were instructed to start the reach before the tone sounded to increase the likelihood of the reach beginning before the correct location of the target was decided. Beginning the reach resulted in the depression of the trigger switch, providing a clear indication of the onset of movement. Similarly, the time the screen was touched was used to indicate the end of the reach.

Participants completed 4 blocks of 96 trials. Two of these blocks contained the blocked condition, and two the mixed condition. In the blocked condition, the target colour remained the same for all trials in the block. For example, always reaching for the red target among green distractors. In one block of the blocked condition the target remained red and in the other block the target remained green. In the mixed condition, however, the colour of the target changed on some trials, creating ‘streaks’ of repeating target colour. For instance, three consecutive trials featuring red targets amongst green distractors followed by a green target amongst red distractors would constitute a streak of three. In this example the first red trial and the first green trial are referred to as ‘switch trials’. Whereas the second consecutive red trial would be referred to as Streak 2 and the third as Streak 3. Streak lengths varied from 2 to 6 repetitions of target colour.

2.2.2 Results & Discussion

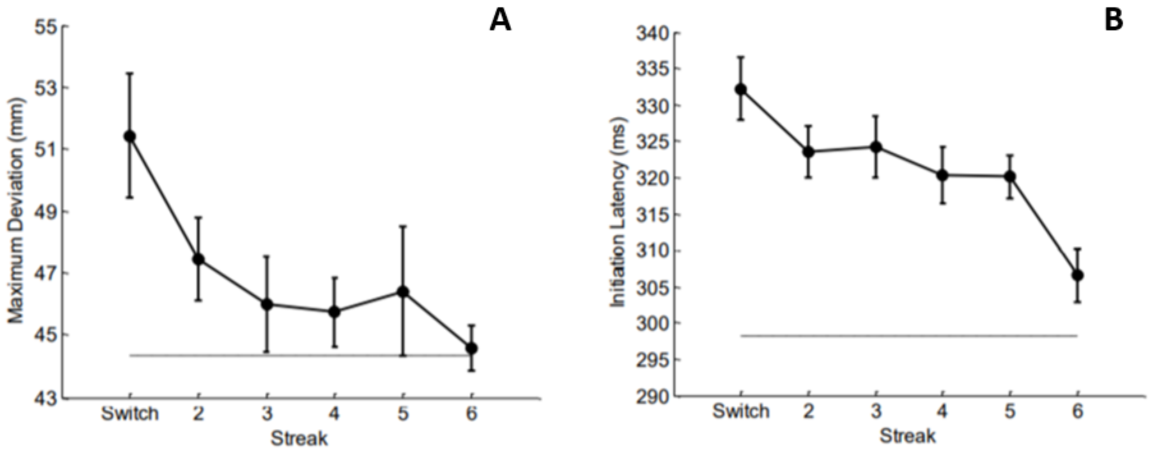

Figure 7: (A) shows Maximum Deviation (mm) plotted against streak. (B) shows Initiation Latency (ms) plotted against streak. Adapted from Woodgate (2017).

For detailed results see Woodgate (2017). In summary, ANOVA analyses indicated significant decreases in both IL ($F(5,50)=9.60$, $p<0.001$,η_p^2 $=0.49$) and MD ($F(5,50)=5.04$, $p=0.001$, η_p^2 2 $=0.34$) with an increase in target colour repetition (perceptual priming). However, different numbers of target colour repetitions were needed to show a decrease in IL and MD. Whilst IL was shown to decrease gradually at first and more drastically towards the maximum number of target repetitions (see Figure 7B), MD was shown to decrease dramatically after just one target repetition, becoming comparable to that of the blocked condition (see Figure 7A).

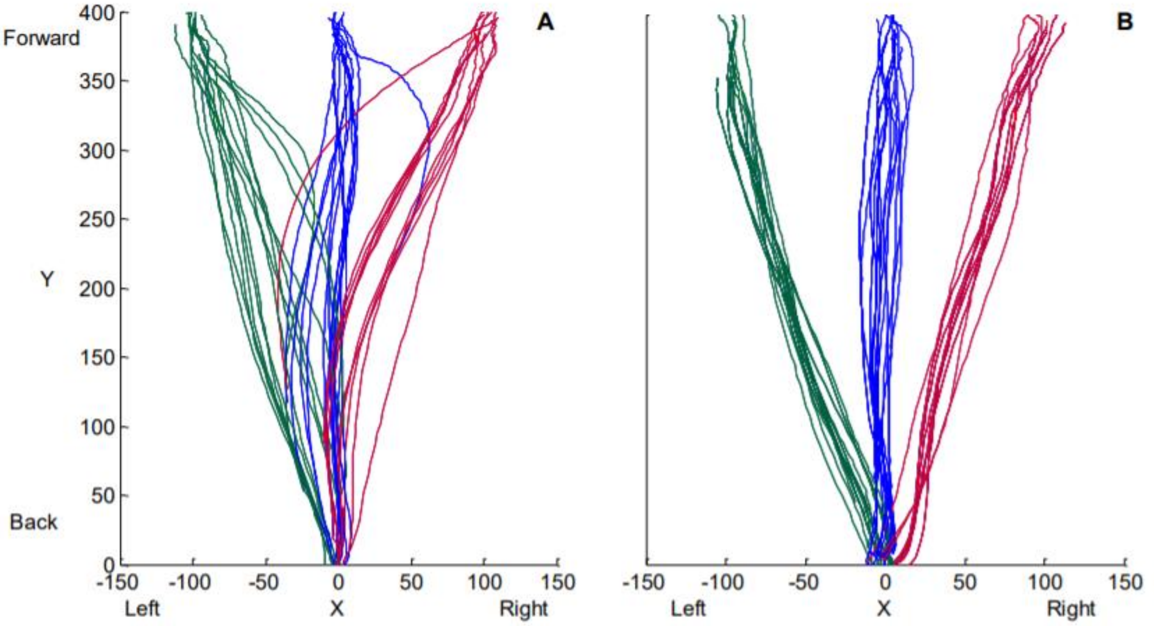

Figure 8: Illustration of Woodgate's (2017) reaching trajectories. X and Y coordinates (mm) of reaching trajectories. (A) shows switch trial trajectories. (B) shows streak 6 trajectories. Green, Blue and Red lines show trajectories to the left centre and right target respectively. Taken from Woodgate (2017).

By showing a decrease in both MD and IL with the increased repetition of target colours, Woodgate (2017) demonstrated CRTs to replicate the RT experiments of Maljkovic

& Nakayama (1994), capturing the effect of perceptual priming. Whilst the decrease in IL with the repetition of target colour suggests motor plans to be formed faster with perceptual priming, the decrease in MD suggests perceptual priming to lead to less competition between targets. This reduced competition between targets results in the correct target being selected initially, leading to only a single motor plan being executed and hence a straighter trajectory being observed with the increase in target colour repetition.

However, both MD and IL purely describe the effects of perceptual priming and as such do not directly account for the concept of motor plans. Submovement models, on the other hand, provide a much more apt way of exploring perceptual priming's effect on motor plans. By considering each submovement to represent an individual motor plan, a mechanistic explanation of the effect of perceptual priming on movement can be developed, providing a deeper understanding of the ongoing feedforward influence of perception on movement preparation and execution.

2.3 Fitting the submovement model

The task of splitting a larger movement into its constituent submovements is not trivial. How this computational model is constructed can greatly affect the quality of the extraction. As currently no standard, widely-used model of submovement extraction exists, the mathematical description of a single submovement, the method of fitting submovements to the data, and the constraints put on the model, vary from model to model and are selected based on limitations of the data and the hypothesis being tested. In this thesis, the model presented is largely based on that used by Friedman, Brown, & Finkbeiner (2013), however with adaptions to the function that defines the fit of the model to the data and constraints for our data.

2.3.1 Data preparation

Out of the original 11 participants' data from Woodgate (2017), 7 were used in the analysis due to missing data. Only trials from the mixed condition were used due to assessing the effects of priming. The trajectories were filtered using a Butterworth filter to reduce noise. The resultant velocity profile for each trial was cropped to within the movement start and end times.

2.3.2 Mathematical description of submovement model

In line with Friedman et al. (2013), the velocity profile ($\dot{V}(t)$) of a submovement is defined using Flash & Hogan's (1985) minimum jerk criterion as:

$$\dot{V}(t) = \frac{A}{D}\left(30\left(\frac{t-T_0}{D}\right)^4 - 60\left(\frac{t-T_0}{D}\right)^3 + 30\left(\frac{t-T_0}{D}\right)^2\right) \tag{1}$$

where t is time, T_0 is start time, D is duration and A is amplitude. Whilst the start time and duration of a submovement remain constant across the different axes of the submovement, the amplitude of the submovement can vary between axes. Thus, this equation is calculated three times, once for each of the axes of movement, yielding three velocity profiles: $\dot{V}_x(t)$, velocity on the x axis; $\dot{V}_y(t)$, velocity on the y axis; and $\dot{V}_z(t)$, velocity on the z axis. As such, each submovement is defined by five parameters: A_x (amplitude on the x axis), A_y (amplitude on the y axis), A_z (amplitude on the z axis), T_0 (start time) and D (duration).

According to the minimum jerk criterion, each submovement has a straight trajectory. Therefore, to have a curved trajectory, multiple submovements must overlap, with their individual velocity profiles summating to produce the observed overall velocity profile. Accordingly, the resultant velocity profile of the entire reach (*F(t)*) can be defined as:

$$F(t) = \sum_{i=1}^{N} \begin{cases} 0 & t < T_{0i} \\ \dot{V} & T_{0i} \leq t \leq T_{0i} + D \\ 0 & t > T_{0i} + D \end{cases} \qquad (2)$$

where *N* is the number of overlapping submovements with individual velocity profiles which are summed to produce a resultant velocity profile for each axis ($F_x(t)$, $F_y(t)$ *and* $F_z(t)$).

In addition, the summation of the absolute of the velocity profile of each submovement was calculated, termed the absolute velocity profile (*M(t)*). This is defined as:

$$M(t) = \sum_{i=1}^{N} \begin{cases} 0 & t < T_{0i} \\ |\dot{V}| & T_{0i} \leq t \leq T_{0i} + D \\ 0 & t > T_{0i} + D \end{cases} \qquad (3)$$

Two overlapping submovements that are additive inverses would cancel each other out in equation two. However, when adding the absolutes of the velocity profiles, these submovements would result in a larger velocity than either individually, thus preventing submovements with this relationship from being invisible to the cost function.

2.3.3 Method of fitting submovements

A different cost function to Friedman et al. (2013) was used due to differences in experimental design. Despite recording all three axes of movement, Friedman et al. (2013) include only data from the x and y axes due to little movement on the z axis. Since all axes are involved in our reaches (see Figure 11 for an illustration), all three axes are included in the model. In addition, Friedman et al.'s (2013) data comprised of movements in a roughly square environment. In contrast, our data was collected in a space where the physical bounds of the space were much larger in the y axis (forwards/backwards) than in the z (up/down) and x (left/right) axes. Because the y axis was much larger, this enabled participants to move faster along this axis, producing a velocity profile whose large size would dominate the fitting process. Consequently, instead of calculating the difference between the model and the data by summing all axes, percentage difference between the model and the data for each axis were calculated separately before being summed. By using percentage differences, different relative costs being calculated for each axis due to different sizes of velocity profiles are avoided; for instance, avoiding a situation where a lower cost would be calculated for an axis where the velocity is much smaller than for an axis with a much larger velocity due to larger physical bounds of the space.

As such, to evaluate the fit of the model to the data, an error function was used, defined as:

$$E = \sum_{t} \frac{|F_x - G_x|}{|G_x|} + \frac{|F_y - G_y|}{|G_y|} + \frac{|F_z - G_z|}{|G_z|} + \frac{\left|\sqrt{{M_x}^2 + {M_y}^2 + {M_z}^2} - \sqrt{{G_x}^2 + {G_y}^2 + {G_z}^2}\right|}{\sqrt{{G_x}^2 + {G_y}^2 + {G_z}^2}} \tag{4}$$

where G_x, G_y, and G_z are the velocity profiles for each axis in the data and F_x, F_y, and F_z are the velocity profiles for each axis predicted by the model. The first three terms determine the percentage difference of the model from the data for each axis separately. The fourth term, as proposed by Friedman et al. (2013), calculates the difference between the tangential absolute velocity profile and the tangential velocity profile. This prevents the selection of completely overlapping submovements in opposite directions (that are physically impossible), which summed would cancel out to produce the velocity profile from the data.

The solution that best fits the data was found using MATLABs *fmincon* minimization function, with the Sequential Quadratic Programming (SQP) algorithm. This acted to minimize the error function in Equation 4. One to ten submovements were fitted iteratively for each trajectory. For each number of submovements, the parameters of the constituent submovements were optimised simultaneously. The maximum number of function evaluations and iterations was set to 50,000. For each number of submovements, the function was run ten times with the initial parameter guesses changed to randomised values each time to increase the likelihood of finding the globally optimal solution. The iteration which produced the lowest error was selected as the optimal solution (Rohrer & Hogan, 2006; Friedman, Brown, & Finkbeiner, 2013).

2.3.4 Constraints

Technical constraints. To ensure physically implausible submovements were not selected, the model was run with four technical constraints, which are as follows:

$$\begin{gathered} |A_x| > 0.5;\ |A_y| > 5;\ |A_z| > 0.5 \\ 0 >\ T_{0i} < MT - 167ms \\ T_{0i} + D_i > MT \\ T_{0i+1} > T_{0i};\ D_{i+1} > D_i \end{gathered} \tag{5}$$

where MT represents the end time of the entire reach. The first constraint ensures the submovements respect the physical constraints of the space. In this case the distance on the y axis (reaching forwards/backwards) was much larger than the possible distances on the x (left/right) or z (up/down) axes. The second constraint ensures the submovement starts after the start time of the entire movement and ends before the end time of the entire reach minus the minimum duration of the submovement (167ms). The third constraint ensures the submovement ends before the end of the reach. The fourth constraint limits the submovement to start after the start of the previous submovement and end after the end of the previous submovement. This prevents impossible submovements which encompass multiple smaller submovements from occurring.

Theoretical constraints. Two theoretical constraints were also imposed, reflecting the assumptions of the model. These were:

$$\begin{gathered} 167ms > D_i > 1.5s \\ T_{0i-2} <\ T_{0i} + D_i \end{gathered} \tag{6}$$

The first theoretical constraint was implemented to reflect the current literature on submovement duration, constraining the duration of the submovement to a minimum of 167ms and a maximum of 1.5s (Rohrer & Hogan, 2006). It is conceivable that only two submovements can be planned and executed simultaneously (Song, 2020 in private communication) and hence the final constraint limits the maximum number of submovements overlapping at any one time to two. This is achieved by requiring the current submovement to start after the submovement two previous had finished.

2.4 Study 1: Minimum error method

The first attempt to extract the number of submovements took the simplest approach, selecting the number of submovements that produced the smallest error. Termed 'the minimum error method' this approach is defined as:

$$n(o,j) = \min_{i}\left(e_{ijo}\right) \tag{7}$$

where $n(o,j)$ represents the number of selected submovements for a given streak and trial, i the number of submovements and e_{ijo} the error of the fit for each trial.

2.4.1 Results

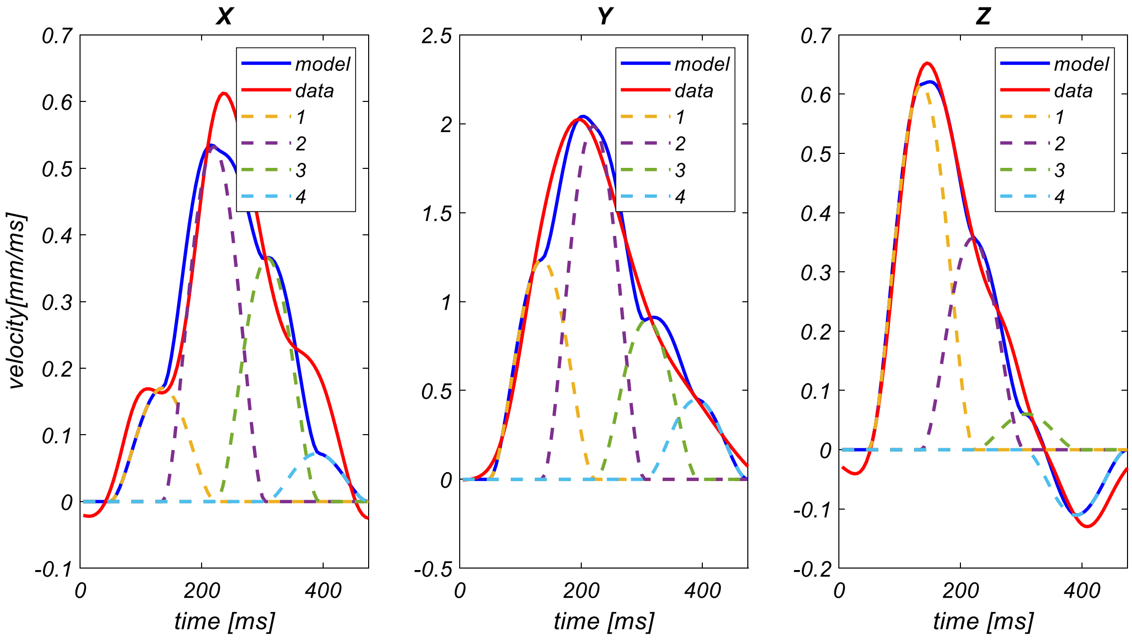

Figure 9: Illustration of submovements extracted using the minimum error method. In this trial, four submovements were extracted, each represented in the illustration as a dashed line and labelled in the legend. The model reflects the sum of these four submovements. The trial illustrated, occurred at streak 3.

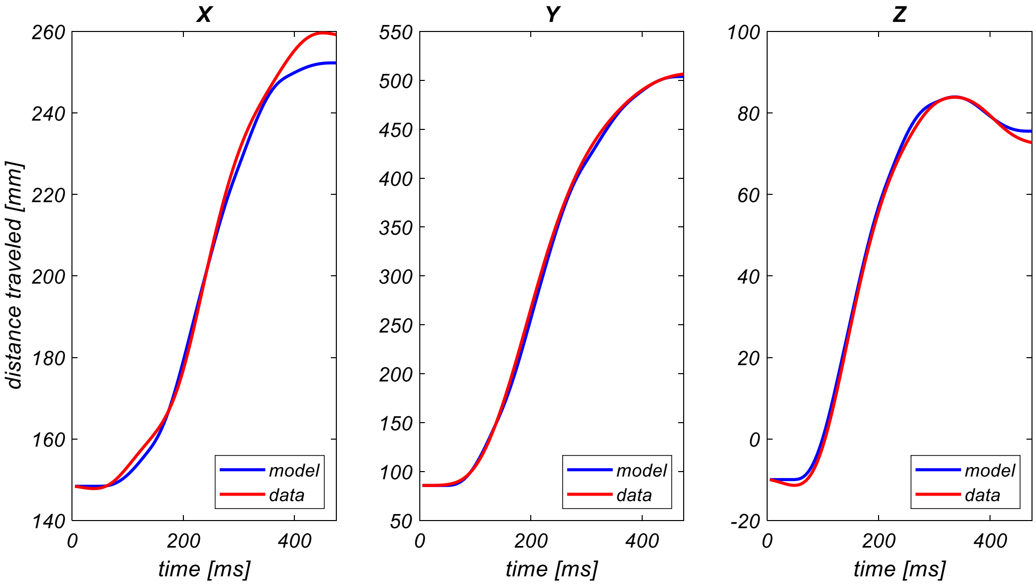

Figure 10: Illustration of the reach trajectory in each axis separately for a single trial. The original data is displayed in blue while that reconstructed from the minimum error model is displayed in red.

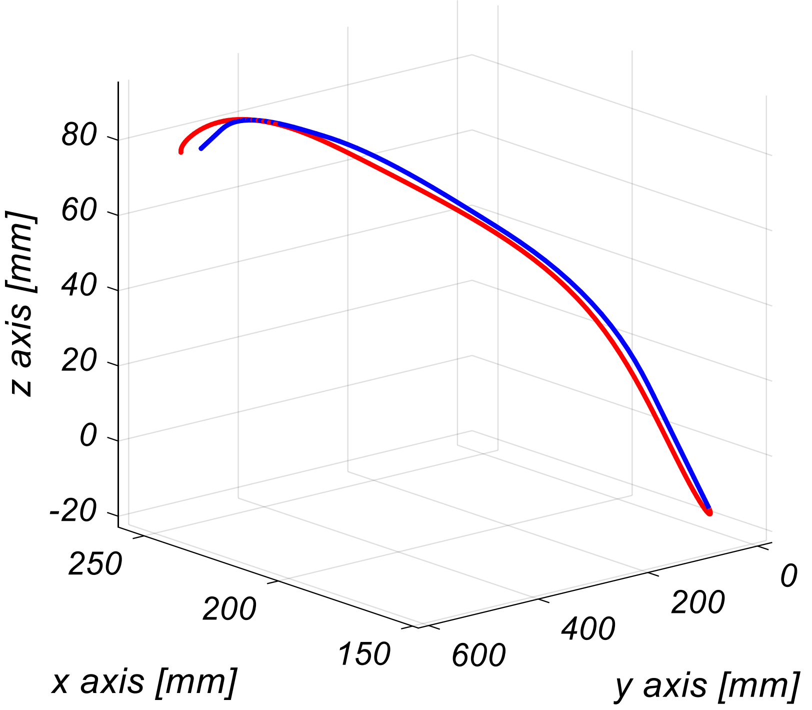

Figure 11: 3D Illustration of the reach trajectory. The original data is displayed in blue and the trajectory reconstructed from the minimum error model, in red.

Figure 9 demonstrates the minimum error method’s ability to select submovements with appropriate qualities (amplitude and timing) and quantity to fit the velocity profile of the data relatively closely in all three axes. Similarly, Figures 10 and 11 show the reconstructed cartesian trajectory from the model to fit relatively closely to the data on all axes.

ANOVA Results: To determine if there was a significant difference in the number of submovements selected using the minimum error method at different levels of streak, an ANOVA analysis was performed. ANOVA revealed no significant difference between streaks (F(5,36) = 0.238, p = 0.943).

Comparison of switch trial with streak 6 trials: To look specifically for a difference between the number of submovements selected by the minimum error method for switch trials and streak 6 trials, paired sample t-tests were performed. Despite switch trials (M =5.33, SD = 0.69) having a higher mean number of submovements than streak 6 trials (M = 5.02, SD = 0.71), the difference was found to not be significant (t(6) = 2.19, p = 0.07).

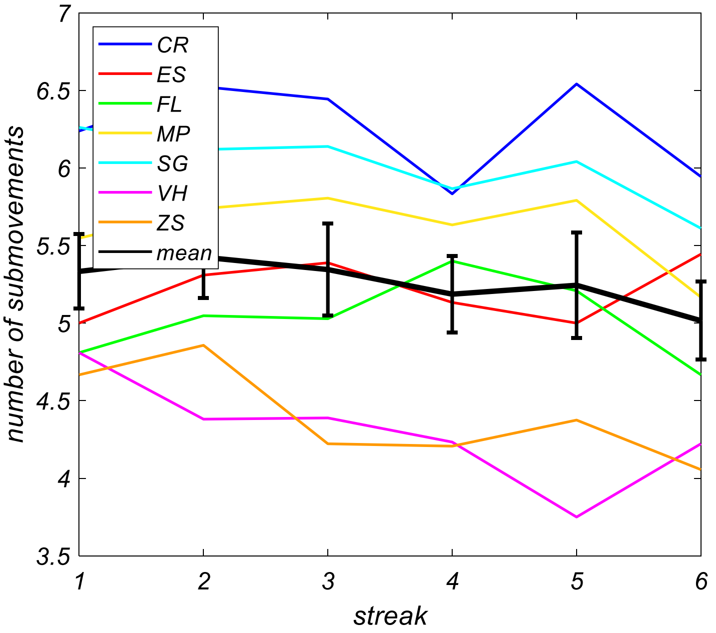

Figure 12: Mean number of submovements selected by minimum error method at each streak for each participant. Error bars represent standard error.

2.4.2 Discussion

Selecting the number of submovements by using the smallest error provides a relatively accurate fit of the model to the data velocity profile (see Figure 9) and cartesian coordinates (see Figures 10 and 11). However, the number of submovements selected by the method is very large. If assuming all submovements result from target competition, with an average of over five submovements in each trial, this would assume an average of four changes of mind about which stimulus is the correct target. Given the assumption that perceptual priming reduces target competition with the increase in target colour (Song and Nakayama 2006; Woodgate 2017), four changes of mind after six repetitions of target colour is highly unlikely. Instead it is probable that additional motor plans and hence submovements exist which do not result from target competition. For example, one or more small submovements may exist to perform small corrections at the end of a trajectory to facilitate hitting the target accurately.

Given the high numbers of submovements extracted by this method, a method of only selecting the submovements resulting from target competition is required to better understand the ongoing feedforward effect of perceptual priming on movement preparation and execution.

2.5 Study 2a: Threshold method: low threshold

To reduce the susceptibility of the model to selecting submovements not resulting from perceptual competition between targets, a second method of selecting the number of submovements was developed. By assuming that high levels of perceptual priming reduce perceptual competition between targets, only a single motor plan to the primed target is thought to be executed. As such, the error of the fit of a single submovement at high levels of perceptual priming can be thought to tolerate additional submovements not resulting from perceptual competition. This error can then be used as a threshold by which the number of submovements and hence motor plans resulting from perceptual competition in other conditions can be judged. This selection criteria was defined as:

$$n(o,j) = \min_{i}\left(\left\{i \middle| e_{ijo} < (\bar{e}_{16} + D)\right\}\right) \tag{8}$$

where *n* represents the number of selected submovments, *o* the trial number, *j* the streak length, *e* the mean error of the fit for one submovement in streak 6 trials and *D* represents the tolerance.

In the current study, the streak 6 trials represents the highest level of perceptual priming, at which it can be assumed that little target competition exists and hence a motor plan is executed only to the primed target. Based on this assumption, the threshold value was calculated as the mean error for fitting one submovment at streak 6 trials plus one standard deviation. The number of submovements is selected as the minimum number of submovements required to produce a fit with an error lower than this threshold. The inclusion of data within one standard deviation above the mean allowed for a small portion of trials to have abnormally high errors or contain multiple submovements while assuming that the majority of trials consist of one submovement. Contrasting with previous models, such as those by Friedman, Brown, and Finkbeiner (2013) and Rohrer and Hogan (2006) which maintained a constant threshold value across all participants, in the current model the threshold value (see Equation 8) was calculated separately for each participant to allow for individual differences.

2.5.1 Results

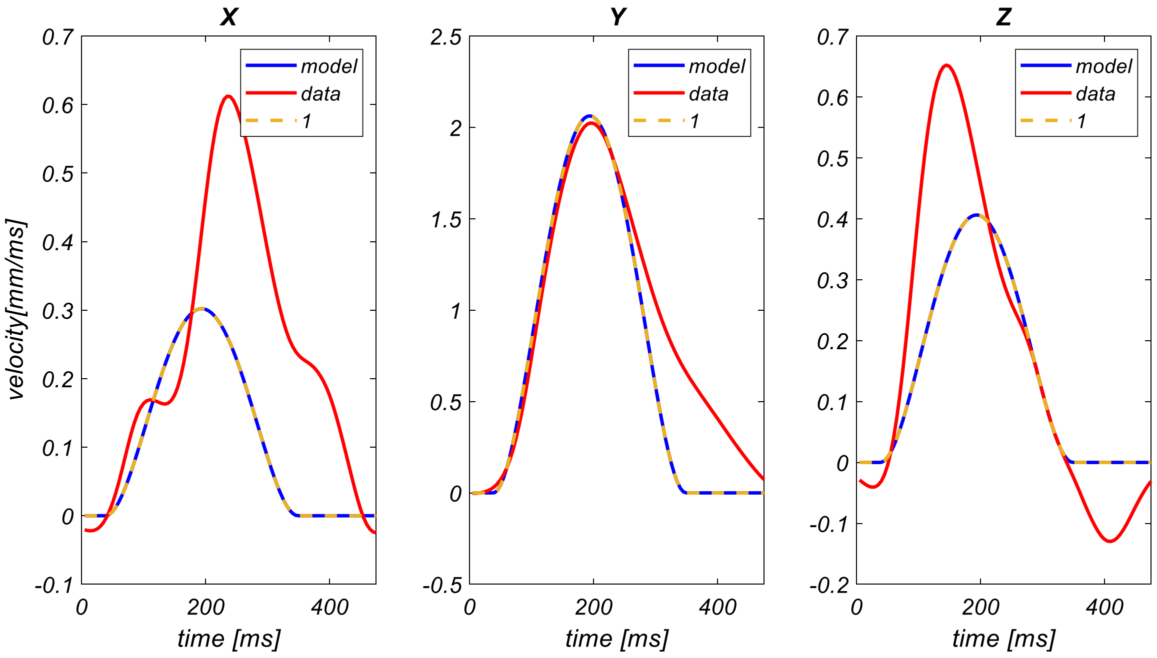

Figure 13: Illustration of submovements extracted using the low threshold method. For this trial just one submovement is extracted making up the entirety of the model's prediction. The trial illustrated occurred at streak 3.

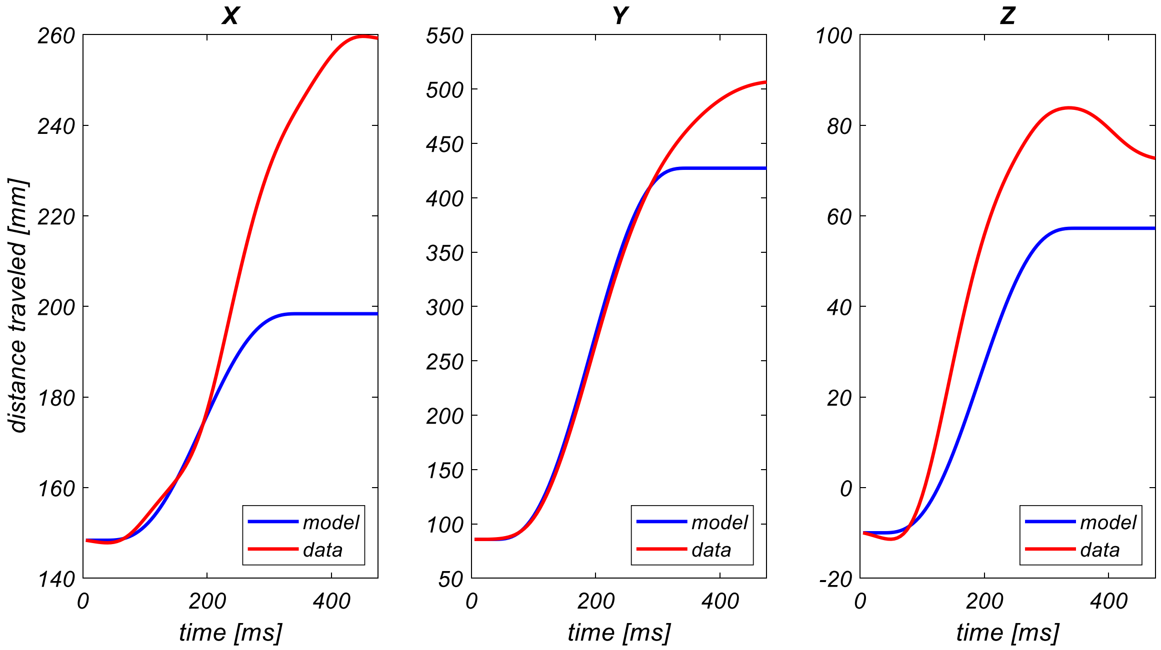

Figure 14: Illustration of the reach trajectory in each axis separately for a single trial using the low threshold method. The original data is displayed in red while that reconstructed from the model is displayed in blue. The reconstructed trajectory from the model is seen to plateau as at this point the model predicted the velocity to be 0mm/ms and so no further distance was travelled.

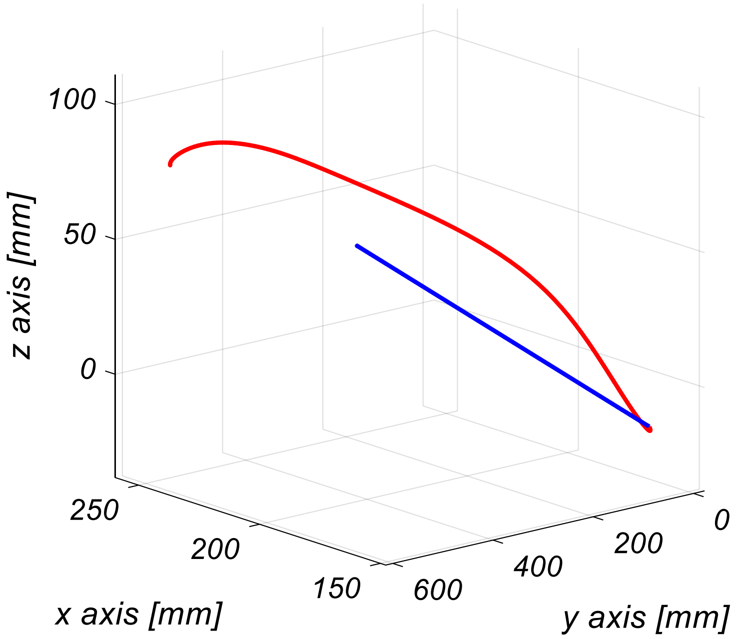

Figure 15: 3D Illustration of the reach trajectory. The original data is displayed in red and the trajectory reconstructed from the model, in blue. The reconstruction of the data from the model is shown to be a straight line due to the model selecting a single submovement.

Figure 13 presents an illustration of submovements extracted from a single trial using the threshold method. It demonstrates the threshold method to capture the overarching shape of the velocity profile in each axis showing its resistance to small fluctuations in velocity. However, it also demonstrates the threshold method's failure to capture the relatively large fluctuations in velocity such as that observed near the end of the movement in the z axis. Additionally, from Figures 14 and 15 we can see that due to the model only selecting a single submovement that terminates before the recorded end of the reach, the reconstruction of the trajectory in cartesian coordinates from the model stops short and hence fails to hit the target. Moreover, Figure 15 demonstrates the model's failure to capture the shape of the trajectory due to only selecting a single submovement which by definition is straight.

ANOVA Results: To determine if there was a significant difference between the number of submovements selected using the threshold method at different levels of streak, an ANOVA analysis was performed. The ANOVA revealed no significant difference between streaks (F(5,36) = 1.009, p = 0.427).

Comparison of switch trial with streak 6 trials: To look specifically for a difference between the number of submovements selected by the threshold method for switch trials and streak 6 trials, paired sample t-tests were performed. A significant difference between the number of submovements selected by the threshold method in switch trials and streak 6 trials were found (t(6) = 3.32, p < 0.05). Compared to the mean number of submovements in streak 6 (M = 1.17, SD = 0.06) trials, the mean number of submovements in switch trials (M = 1.30, SD = 0.13) were found to be significantly higher.

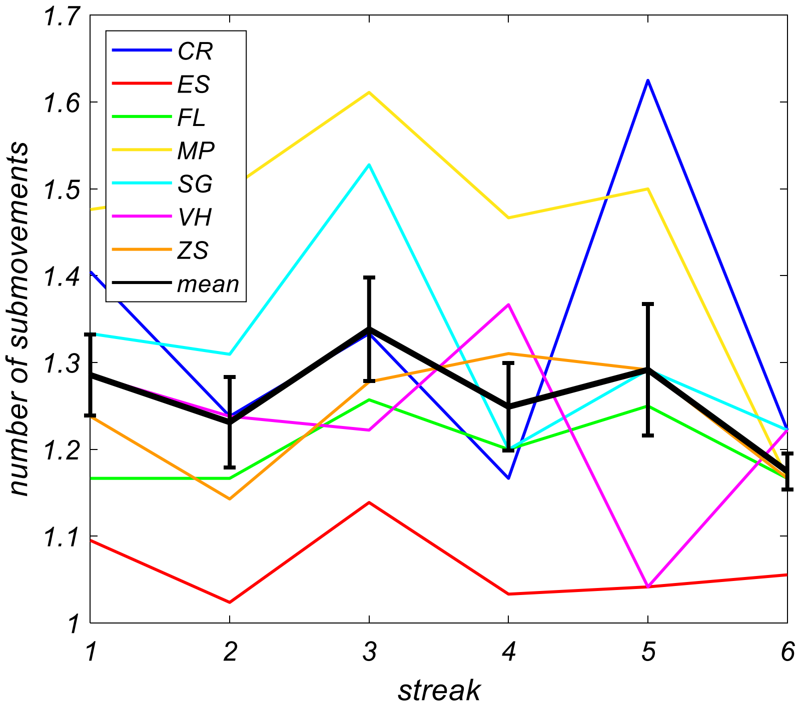

Figure 16: Mean number of submovements selected by low threshold method at each streak for each participant. Error bars represent standard error

2.5.2 Discussion

As expected, the number of submovements selected using the threshold method (M = 1.27, SD = 0.19) were found to be much smaller than the number selected by the minimum error method (M = 5.30, SD = 0.75), demonstrating the threshold method to be robust against small fluctuations in velocity. Moreover, unlike the minimum error method, the threshold method demonstrated a significant difference between numbers of submovements in streak 6 and switch trials. This indicates the threshold method to be successful at quantifying the number of motor plans resulting from perceptual competition while ignoring the additional motor plans extracted by the minimum error method.

However, despite finding a significant difference between switch trials and streak 6 trials using the threshold method, Figure 15 illustrates a lack of systematic decrease in the number of submovements with an increase in perceptual priming. One potential reason for the lack of systematic decrease observed is that using the fit error for one submovement creates a threshold with a tolerance that is too high. By using a threshold that tolerates additional submovements that do not relate to perceptual priming, the susceptibility of the model to including these additional submovements is reduced as intended. However, the fit that is ultimately selected is comparatively poor as the tolerance for inaccurate fits of the model to the data is high. Consequently, the model fails to pick up on small differences in the number of submovements, resulting in the lack of systematic decrease in the number of submovements and the increase in perceptual priming, as observed. As such, while being effective at detecting if there are differences in the number of submovements and hence motor plans resulting from perceptual competition under considerably different levels of perceptual priming, the submovement method is not sensitive enough to detect small differences in the number of submovements. This lack of model sensitivity when using a threshold designed to ignore several submovements, is an unavoidable issue as by its nature it tolerates fits which ignore multiple distinct peaks of velocity. However, by creating a threshold that allows more submovements in streak 6 trials, the tolerance of the model of poor fits to the data would be reduced.

2.6 Study 2b: Threshold method: high threshold

When creating a threshold that allows for more submovements, in order to reduce the tolerance of the model of poor fits to the data, the question of how many submovements to allow in streak 6 trials arises. It is conceivable that the reach trajectory may consist of three types of movement, each serving a distinct function within the reach. With participants required to initiate the reach within 400ms of the target being displayed, it is plausible that an initial movement to release the button and prevent the warning tone occurs, irrespective of the perceptual competition between targets. Following the release of the button, one or more motor plans are executed depending on the perceptual competition between the targets bringing the participant in the region of the correct target. Finally, to facilitate hitting the target accurately, an additional motor plan is executed, as observed by the presence of a corrective submovement at the end of a reach. As such, if assuming that, in addition to the single submovement resulting from target competition in streak 6 trials, a submovement exists for each of the purposes of lifting the finger and endpoint corrections, three submovements can be expected in streak 6 trials. By creating a threshold that allows for these additional two submovements at streak 6, the error of the fit of the model to the data would be reduced allowing for a more accurate fit of the model to the data.

The high threshold method implements this assumption, assuming three submovements to occur in streak 6 trials, defined as:

$$n(o,j) = \min_{i}\left(\left\{i \middle| e_{ijo} < (\bar{e}_{36} + D)\right\}\right) \qquad (9)$$

where n represents the number of selected submovements, o the trial number, j the streak length, e the mean error of the fit for three submovements in streak 6 trials, and D the tolerance.

2.6.1 Results

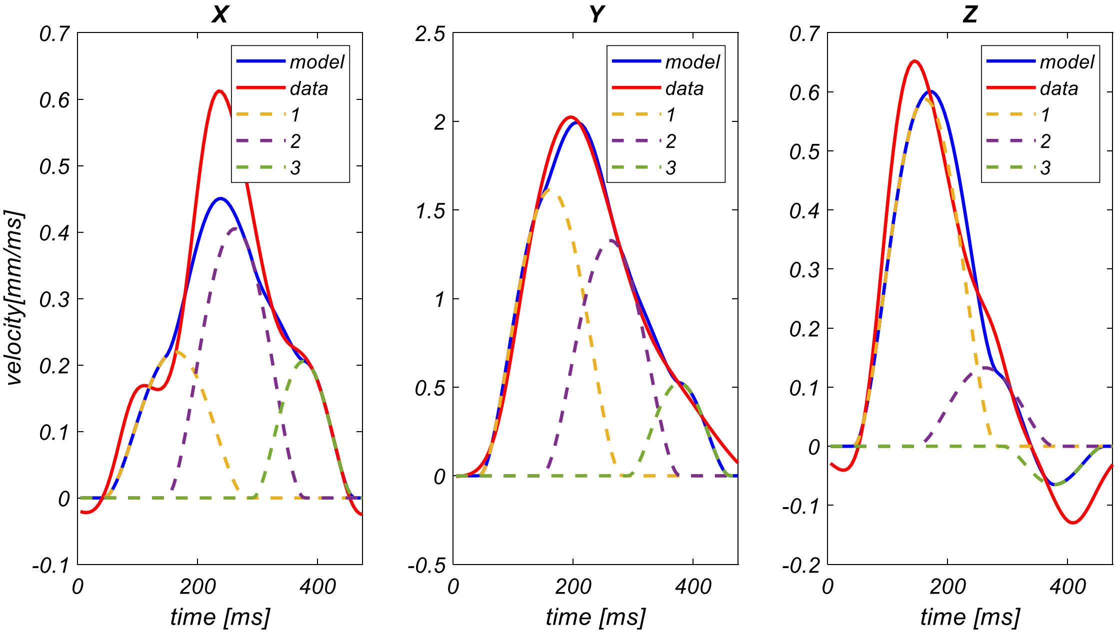

Figure 17: Illustration of submovements extracted using the high threshold method. In this trial three submovements were extracted, each represented in the illustration as a dashed line and labelled in the legend. The model reflects the sum of these three submovements. The trial illustrated, occurred at streak 3.

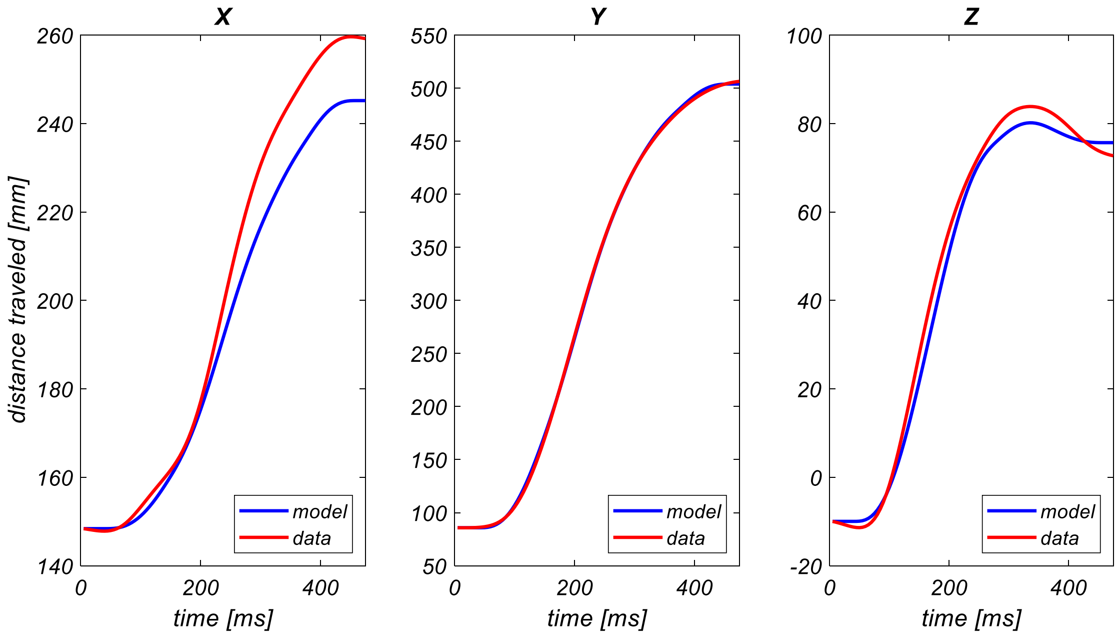

Figure 18: Illustration of the reach trajectory in each axis separately for a single trial, as selected by the high threshold method. The original data is displayed in blue while that reconstructed from the model is displayed in red.

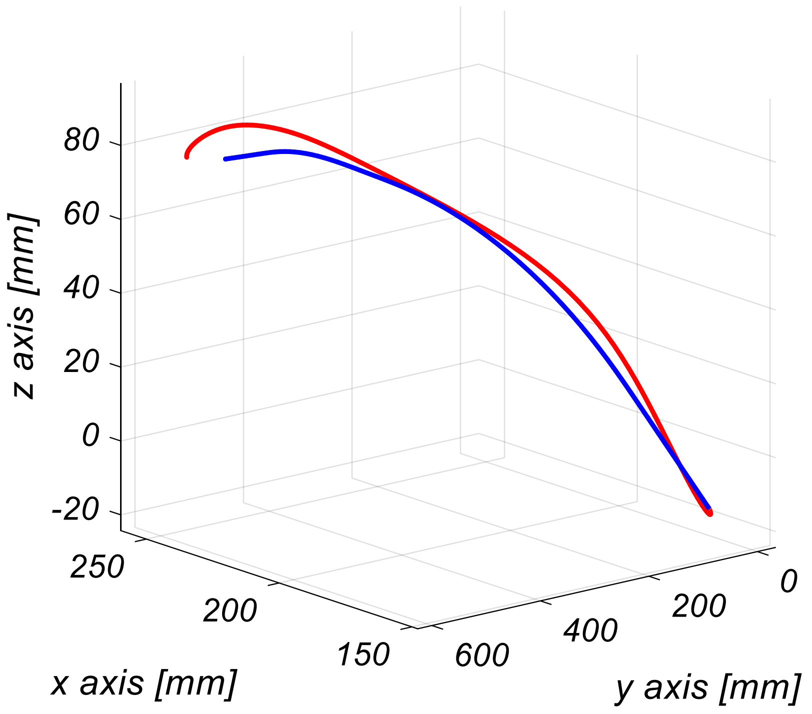

Figure 19: 3D Illustration of the reach trajectory using the high threshold method. The original data is displayed in red and the trajectory reconstructed from the model, in blue.

Figure 17 demonstrates the high threshold method’s ability to select submovements with appropriate qualities (amplitude and timings) and quantities to fit the velocity profile of the data somewhat closely in all three axes, capturing the general shape of the data. Similarly, Figures 18 and 19 show the reconstructed cartesian trajectory from the model to fit extremely closely in the y axis and relatively closely in the x and z axes, capturing the shape of the data.

53 out of a total of 1342 trials were removed from the analysis due to no number of submovements, resulting in an error that was below the threshold.

ANOVA Results: To determine if there was a significant difference between the number of submovements selected using the threshold method at different levels of streak, an ANOVA analysis was performed. The ANOVA revealed no significant difference between streaks (F(5,36) = 1.011, p = 0.425).

Comparison of switch trial with streak 6 trials: To look specifically for a difference between the number of submovements selected by the minimum error method for switch trials and streak 6 trials, paired sample t-tests were performed. Despite switch trials having a higher mean number of submovements (M = 2.88, SD =0.32) than streak 6 trials (M = 2.82, SD = 0.20), the difference was found to be not significant (t(6) = 0.38, p = 0.72).

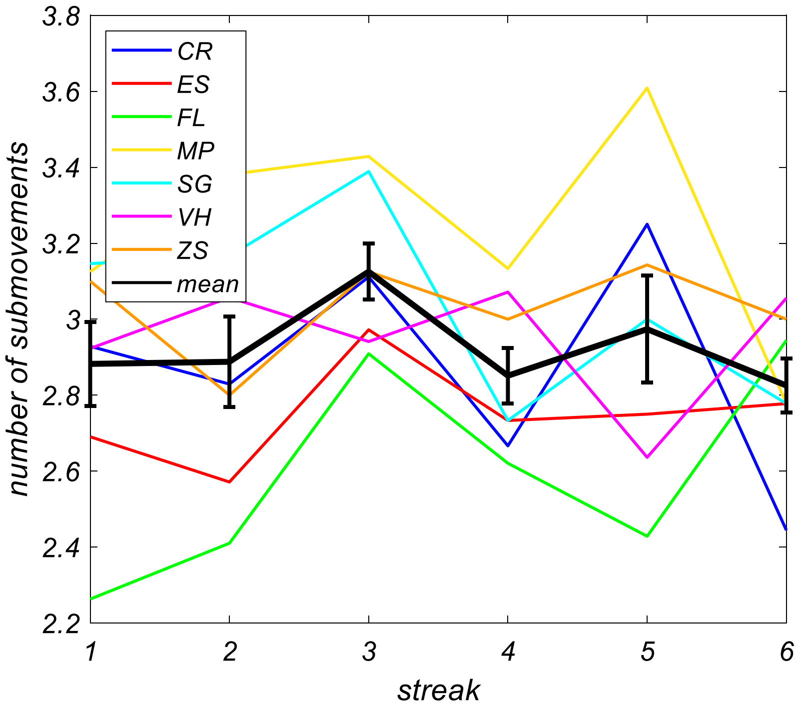

Figure 20: Mean number of submovements selected by the high threshold method at each streak for each participant. Error bars represent standard error.

2.6.2 Discussion

As expected, the number of submovements selected by the high threshold method (M = 2.93, SD = 0.23) were found to be larger than the number selected by the low threshold method (M = 1.27, SD = 0.19) and smaller than the number selected by the minimum error method (M = 5.30, SD = 0.75). This demonstrates that whilst the high threshold method can filter out some peaks of velocity picked up by the minimum threshold method, it is more sensitive than the low threshold method. Moreover, when comparing Figures 15 and 19, and 14 and 18, it is clear that the increased sensitivity of the high threshold method allows for a closer fit of the model to the data than achieved by the low threshold method.

However, when using the high threshold method, there were no significant differences in the number of submovements in switch trials and streak 6 trials. Considering that the high threshold method allows more submovements than the low threshold method does, submovements that do not result from target competition such as those that lift the hand from the button and facilitate endpoint corrective movements are included in the analysis. Consequently, the effect of repetition of target colour reducing the number of submovements found when using the low threshold method is lost. As such, a method that provides a close fit of the model to the data while being able to identify the submovements resulting from target competition is needed.

One way in which a close fit can be achieved and the submovements relating to target competition identified, is by using the minimum error method to select the total number of submovements with additional methods for identifying the function of individual submovements. As discussed in the introduction to section 2.6, the three possible functions of motor plans and hence submovements can be considered to be lifting the hand from the button, moving towards the target, and endpoint correction for hitting the target accurately. Considering that button release movements occur at the beginning of a reach and endpoint-accuracy submovements occur at the end of a reach, knowing their approximate timings makes identifying them possible. Cropping the trajectory within a certain distance (in cartesian coordinates) or time (in velocity profile) from the start and end of a reach should isolate button release and endpoint corrective movements from those resulting from perceptual competition between targets. Any submovements not deemed to be button release movements or endpoint corrective movements could then be considered to reflect competing motor plans resulting from the perceptual competition between targets. Once submovements have been labelled with their appropriate function, analyses between the streak length and number of submovements resulting from target competition, can be performed. As it is assumed that perceptual priming reduces the competition between targets, by isolating the analyses to the submovements that result from target competition, a more sensitive and accurate method of investigating the ongoing feedforward influence of perception on the preparation and execution of movement is provided.

In addition to analysing perceptual priming effects on target competition submovements, being able to identify the function of submovements also allows us to explore other effects of perceptual priming on reaching. For example, it may be the case that repetition of target colour increases the number of endpoint corrective movements. If large, perceptual priming leads to only a single motor plan being performed after lifting the hand from the button, and fewer opportunities for correcting the trajectory of the reach are available. As a result, despite the movement ending near the target, more endpoint corrective movements may be required to reach the target. In contrast, in switch trials, motor plans to multiple targets are performed due to high perceptual competition, providing frequent opportunities to correct the movement during the reach and thus requiring no endpoint facilitating corrective movements to hit the target. As a result, when considering the total number of submovements in a reach, both switch trials and streak trials may consist of relatively similar numbers of submovements despite the submovements serving different functions. In this case, despite priming having a substantial effect, little or no correlation would be found between priming and the number of submovements, as observed when using the minimum error method or the high threshold method to select submovements. By exploring the effect of target colour repetition on submovements serving each function, a better understanding of the way in which perpetual priming effects the entirety of a reach can be sought, deepening the understanding of the ongoing feedforward influence of perception on the preparation and execution of movement.

2.7 General discussion of the submovement model

The initial aim of this chapter was to show that a submovement model can capture differences in reaching trajectories collected at different numbers of target colour repetition, in order to show the feedforward influence of perception on movement. By demonstrating the model's ability to capture a significantly larger number of submovements in switch trial reaches than in streak 6 trial reaches, this aim has been achieved. By interpreting the quantitative and qualitative information from submovements at different perceptual priming levels, it is possible to suggest a mechanistic explanation of perceptual priming's effect on movement. Higher numbers of submovements in switch trials indicate a larger number of motor plans to occur in these conditions, which reflects executing motor plans to multiple targets as a consequence of high target competition. Prior to switch trials, the repetition of target colour primes movements to targets of that colour by increasing the activation of that target and hence decreasing the competition between targets. In a switch trial, the carry over of perceptual priming from the previous trials results in a higher level of activation for the distractor than the target, initiating movement towards that stimulus. As slower cognitive processes act, the correct target is ultimatly selected, causing the rapid switching of motor plans and hence the increase in number of submovements and curvature.

2.7.1 Appropriate definition of a submovement velocity profile

Aside from the method of selecting the number of submovements in a reach, an additional factor that influences the number of submovements determined by the model is the equation used to define the velocity profile of a single submovement. Considering the leftward skewed velocity profiles described by Milner (1992) and observed in our data (see Figure 17, y and z axes), the idea of minimum jerk as the best way of defining a submovement velocity profile should be questioned.

Originally developed from kinematic data, Flash and Hogan’s (1985) minimum jerk model assumes a movement to be as smooth as possible. The resultant velocity for a single movement is a symmetrical, bell-shaped distribution, defined by just three parameters. From a practical standpoint, the small number of parameters make the minimum jerk model convenient for extracting submovements as they help to minimize the already high computational expense of the optimization procedure (Rohrer & Hogan, 2006). In addition, when comparing to kinematic data, the minimum jerk velocity profile has been shown to fit the data within a small percentage difference (Flash & Hogan, 1985). Furthermore, from a scientific standpoint, simpler computational models can be considered better, leading to a preference for the minimum jerk model over other more complex models. Consequently, the minimum jerk model has become one of the most common ways of defining a submovement’s velocity profile when extracting submovements and thus is easy to compare between experiments.

However, despite its common place in the literature, the minimum jerk model may not be the best way of defining a submovement velocity profile. When comparing twenty-two different models defining submovement velocity profiles, Plamondon’s (1992) support-bounded lognormal model (LGNB), was found to provide a substantially better fit than all other models including the minimum jerk model (Plamondon, Alimi, Yergeau, & Leclerc, 1993). Unlike the minimum jerk model, the LGNB model allows for asymmetric velocity profiles. To achieve this, in addition to the three parameters required by the minimum jerk model (amplitude, start time and duration), the LGNB model requires an additional two parameters: kurtosis (fatness of the curve) and skewness (asymmetry of the curve). These additional parameters give the model the flexibility to take on the shape of more velocity profiles in less submovements. For example, in a highly skewed velocity profile, two overlapping, symmetric, minimum jerk submovements would be required to produce the skewness observed, whereas just one LGNB submovement would produce the same result. As such, due to the skewness observed in our data, by using the LGNB model as opposed to the minimum jerk model that was used, fewer submovements and a better fit may have been selected, yielding more accurate submovement extraction. Additionally, if the skewness of the velocity profile changes as a function of priming, for example an increase in priming leading to fewer but more skewed submovements, the increase in the number of minimum jerk submovements required to fit the data may weaken the statistical relationship between perceptual priming and number of submovements.

2.7.2 Limitations of the submovement model

While submovement extraction begins to provide a mechanistic explanation of perceptual priming's effect on movement, submovement models alone are not a full explanation of perceptual priming's effect on the selection and execution of motor plans. In our current submovement model the aim is only to explain the trajectory, but evidence also shows the initial latency is affected by the repetition of target colour (Song & Nakayama, 2006). To model this effect, a possible approach could be to draw on the popular drift diffusion model (DDM).

Since its initial application to perceptual decision-making by Ratcliff in 1978, the DDM has gained popularity as it is able to explain a broad range of behavioural evidence (Ratcliff, Smith, Brown, & McKoon, 2016) as well as its illustration of neurophysiological results (Gold & Shadlen, 2007). The DDM assumes that evidence from sensory information is accumulated in a stochastic manner over time. The accumulation of evidence continues until one of two thresholds, representing two alternative choices, is reached. By using a DDM with an early boundary for this initial target decision and a second boundary for changes of mind, Resulaj, Kiani, Wolpert, and Shadlen (2009) showed how the continued processing of information in the ‘processing pipeline’ can produce the observed curved trajectories in reaching movements. Similarly, Friedman, Brown and Finkbeiner (2013) demonstrated that modelling the angle and amplitude of a submovement on the state of accumulated evidence prior to a decision being made, is sufficient to explain curvature in reaching movements that results from different stimulus quality and viewing time.

By extending the models suggested by Resulaj et al. (2009) and Friedman et al. (2013), the observed latency and curvature effects of priming may be explained. Although not directly addressed in either model, the DDM contains an additional feature: bias. Bias reflects the starting point of evidence. If no bias is present, the starting point of evidence is zero, the midpoint between the two choices’ thresholds. However, if bias is present, evidence starts accumulating at a point closer to one threshold than the other. The closer the bias is to the threshold the less evidence is needed for the threshold to be reached. Therefore, the more likely it is to be reached and the less time required to reach it and begin executing the first motor plan.

By representing the direction of priming by bias, both the decreased initiation latencies and decreased curvature with target colour repetition could be explained. For example, as the number of repetitions of the green target colour increases, the bias moves closer to the threshold that represents choosing the green target. If taking the idea of an early threshold for the initiation of movement from Resulaj et al.’s (2009) model, then less evidence and thus less time would be needed to reach the initiation threshold due to the decreasing distance of the bias from the threshold. As such, the decrease in initiation latency with priming could be explained. When coupling this with Friedman et al.’s (2013) idea of intermittent sampling of evidence translating into the direction of submovements prior to the final decision being made, the high curvature on switch trials resulting from opposite priming to the target colour the previous trials, could be explained. If, on switch trials, bias is closer to the incorrect choice (e.g. red target when in fact green is the odd one out), early samples would show evidence to be closer to the incorrect target, causing initial submovements and hence motor plans to head in that direction. However, as evidence accumulates over time, later samples would show evidence to be closer to the correct target threshold, resulting in later submovements and motor plans executed in the direction of the correct target. As such, combining a DDM with a submovement extraction model would be a logical next step towards fully explaining the feedforward effect of perceptual priming on reaching movments.

2.7.3 Future applications

While it is clear there is some progress to be made in honing the accuracy of the submovement extraction model, the future applications are numerous. In addition to researching vision and motor psychology, the versatility of stimuli that can be used in a CRT has meant that it can be utilized for research in a range of psychological domains. From demonstrating phonological competition in language processing (Spivey, Grosjean, & Knoblich, 2005) to the processing of numbers (Ishihara, et al., 2006), subliminal information (Xiao & Yamauchi, 2017), and social stereotypes (Freeman, Penner, Saperstein, Scheutz, & Ambady, 2011), the CRT has given insight into the temporal unfolding of internal processes where previously reaction time data was relied upon. No matter the topic of research, using a CRT still yields the same complexities of data analysis, generally producing descriptions of effects from MDs and ILs. The submovement extraction model developed is flexible in its application to any CRT data, providing a mechanistic explanation of the workings of underlying internal processes in a range of fields. As such, the submovement extraction model developed can be considered a tool to be used in future research as well as being applied retrospectively to existing data to address ongoing research questions.

2.8 Conclusion

To conclude, by building a submovement model we have been able to successfully capture differences in movement trajectories under different levels of perceptual priming, providing an insight into the motor plan mechanism by which the movements are created. By capturing a change in motor plans, further evidence is provided for the ongoing feedforward influence of perception on movement preparation and execution, adding strength to the claim of an interconnected theoretical framework of movement over the traditional serial model. However, whilst the low threshold method was successful at showing this, its fit to the data was poor in comparison to the high threshold method and the minimum error method. Future research should seek to develop a way of classifying the functions of each submovement and motor plan observed. By doing this, the motor plans resulting from target competition can be identified, giving a more accurate and clearer picture of the ongoing feedforward influence of perception on movement preparation and execution.

3.0 Summary

Considering the findings from Chapter 1 which showed visual attention to be allocated to both dynamic (the hand) as well static (the target) locations during reaching movements, as intended further evidence is provided in this thesis for proprioceptive feedback of movement to continuously influence the spatial allocation of visual attention and hence perception. Similarly, the ability of the submovement model, developed in Chapter 2 to capture differences in reaching movements resulting from different levels of perceptual priming, provides further evidence for an ongoing feedforward influence of attention and perception on movement. Taken together, these experimental and computational modelling findings lend support to an integrated theoretical framework between attention, perception, and movement, at odds with traditional serial models. However, both chapters raise additional questions that the current body of work cannot answer. Future research should seek to investigate the effects of factors such as predictability and vision of the hands on the allocation of visual attention and perception in order to remove the possibility of the effects found in Chapter 1 being due to preplanning. In addition, future research should also aim to develop a way of identifying only submovements that result from target competition to better understand the interconnected framework between attention, perception, and movement.

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