Changes of Mind in voluntary action
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Flexibility vs. stability of intentions

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Declaration

I, Anne Löffler, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

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14/09/2018

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Abstract

‘Changes of Mind’ can provide insights into the dynamic and continuous processes underlying decision making and action selection. Previous studies on Changes of Mind have exclusively focused on either perceptual or value-based choice. This thesis investigates the flexible neurocognitive mechanisms that shape voluntary actions, which require integration of internally-generated (endogenous) intentions and externally-cued (exogenous) sensory or value-based information. When information is noisy or changes dynamically, agents sometimes change their voluntary intentions and/or change the movements that are required to implement intentions into action. Continuous movement trajectories were used to capture both types of Change of Mind during ongoing action execution, revealing that ‘Changes of Intention’ are more frequent when intentions are weak or when the cost of pursuing an intention is high. These findings could be qualitatively reproduced by an attractor network model that continuously integrates endogenous and exogenous information over time, occasionally switching from one attractor state to a different one later on. In an fMRI study, the neural dynamics of intention reversals were investigated, providing evidence that neural patterns in a fronto-parietal network change dynamically to incorporate new decision- and action-relevant evidence after action onset. Finally, while behavioural flexibility is advantageous in many situations, an important hallmark of voluntary control is intention pursuit despite external changes or challenges. For example, people often need to persevere in the face of effort. Patients with post-stroke fatigue showed reduced perseverance compared to healthy controls when goal pursuit required continuous effort, which may cause adverse health-related outcomes. In conclusion, this thesis provides new insights into the continuous neurocognitive mechanisms that shape voluntary actions as they unfold. Reversibility of intentions allows agents to adjust their own actions to the current context, while stability of intentions is necessary for successful goal pursuit. Hence, volition requires balanced integration of endogenous intentions with dynamically-changing exogenous information.

Significance statement

Voluntary actions form a crucial part of our everyday life and are essential to our experience as responsible agents. Only through our actions can we control events in the outside world. Hence, one of the key questions in the field of cognitive neuroscience is how people generate intentions, and implement these intentions into motor actions. A particularly intriguing aspect of this is how the neurocognitive system allows for dynamic Changes of Mind. That is, when new information is obtained, how does the brain reverse an already made decision? And how is such a decision reversal translated into changes in ongoing action execution? Many theories of voluntary action differentiate between goals vs. means of actions, but there are few systematic experimental studies of the relation between them. Here, we present the first systematic framework for studying the shielding vs. updating of intentions, as well as movements.

A large range of converging methods was used, ranging from the measurement of continuous movement kinematics, computational modelling, through to neuroimaging techniques and a study on patients with post-stroke fatigue, in order to investigate the dynamic and continuous processes that shape voluntary actions as they evolve. Our findings show that the need to change an ongoing action plan can drive changes in the intention itself, in particular, when intentions are weak or are associated with costly movements in terms of time or effort. This provides important new insights into the reciprocal interplay between higher-order decision-making processes, and lower-level aspects related to movement execution. Hence, Changes of Mind provide a window into the fundamental neurocognitive mechanisms that shape behaviour, bridging the gap between decision-making and motor neuroscience.

Finally, our findings point to a crucial importance of a balance between flexibility and stability of intentions. Disturbances in this balance may be directly linked to a large range of neurological and psychiatric conditions, such as rigidity of behaviour in obsessive compulsive disorder or impulsivity in attention deficit hyperactivity disorder. Moreover, motivational deficits, such as apathy and fatigue can cause a reduction in sustained voluntary action, and hence, impairments in goal pursuit with potential consequences for rehabilitation and quality of life. This thesis paves the way for future studies into disturbances in the component processes underlying flexible action selection, with the potential to develop new diagnostic tools and interventions.

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Abbreviations

AG	angular gyrus
CoM	Change of Mind
CoMov	Change of Movement
CoMov+Int	Change of Movement + Intention
CoInt	Change of Intention
CTL	control subjects
dlPFC	dorsolateral prefrontal cortex
FG	fusiform gyrus
IOG	inferior occipital gyrus
MELR	mixed-effects logistic regression
MFC	medial frontal cortex
MT	movement time
MVC	maximum voluntary contraction
MVPA	multivariate pattern analysis
OR	odds ratio
PCUN	precuneus
PPI	psycho-physiological interaction
PSF	post-stroke fatigue
RDM	random-dot motion
ROI	region of interest
SMA	supplementary motor area
SoA	Sense of Agency
SVM	support vector machine

Chapter 1.

Introduction

1.1 General introduction

Adaptive behaviour in a complex world requires continuous and dynamic decision-making processes. ‘Changes of Mind’ (CoM) are a striking example of our ability to flexibly reverse decisions after commitment to an initial choice, and change our actions accordingly. This flexibility can be highly advantageous in that it allows us to correct erroneous actions, and adjust our behaviour to the current context. For example, a CEO might need to change business strategies in response to changes in market demand. Yet, in other cases, decisions need to remain stable over time regardless of the current context. For example, deciding to quit smoking, go to the gym more regularly, or learn a new language – goal attainment often requires continuous pursuit of an intention. Understanding the mechanisms underlying the flexibility vs. stability of decisions, and their implementation into action, is highly relevant as choice reversals can have important implications for behavioural outcomes. The aim of this thesis is to investigate the dynamic and continuous neurocognitive mechanism underlying CoM. While the term ‘Change of Mind’ has many connotations, within the context of this thesis, it is defined as a reversal of one or more aspects of an initial action decision. More specifically, the focus of this thesis is on CoM in voluntary action.

1.1.1 What are voluntary actions?

Before addressing the topic of CoM in voluntary action, we first need to define what we mean by volition. In voluntary actions, people generate internal (endogenous) decisions about how to act, rather than merely following prepotent external (exogenous) cues or instructions (Passingham, 1987; Brass & Haggard, 2008; Haggard, 2008; Fried, Haggard, He, & Schurger, 2017). Internal decisions may be based on one's own goals, preferences or memory (Passingham, 1987; Haggard, 2008; Fried et al., 2017), and hence, are relatively independent from immediate external sensory cues. This 'freedom from immediacy' allows for deliberation and top-down control (Shadlen & Gold, 2004; Haggard, 2008) and is in sharp contrast to reflexes, which have a strong and direct stimulus-response link. Furthermore, as opposed to habits, voluntary actions are reasons-responsive and goal-directed, causing a higher demand for action planning and monitoring in volitional compared to habitual control (Fried et al., 2017). Finally, voluntary actions are typically accompanied by a subjective 'Sense of Agency' – the phenomenological experience of feeling in control over one's actions and their outcomes (Gallagher, 2000; Pacherie, 2008; Haggard & Tsakiris, 2009; Chambon, Sidarus, & Haggard, 2014). Sense of Agency is more pronounced in self-generated compared to externally-triggered actions (Haggard, Clark, & Kalogeras, 2002; Moore, Wegner, & Haggard, 2009). It is a crucial aspect of the conscious experience of our 'self' and enables us to feel responsible for our own actions and their consequences (Haggard & Tsakiris, 2009; Moretto, Walsh, & Haggard, 2011).

Voluntary actions require agents to make decisions about multiple action parameters, such as *what* to do, *when* to do it and *whether* to do it at all (Brass & Haggard, 2008). The current thesis is primarily concerned with the processes underlying *what* components of action selection, i.e., decisions about which one of two alternative courses of action to execute. In particular, what are the neurocognitive mechanisms that allow people to change their mind and switch from action A to action B? While this might be closely related to the decision about whether or not to execute action A, the inhibitory processes underlying such *whether* decisions have been addressed in detail by previous studies and are not the main focus of this thesis (Brass & Haggard, 2007; Kühn, Haggard, & Brass, 2009; Walsh, Kühn, Brass, Wenke, & Haggard, 2010; Parkinson & Haggard, 2013, 2014, 2015).

1.1.2 Neural basis of voluntary action

It has been suggested that voluntary actions are generated in a distinct medial pathway of action selection, whereas externally-triggered (exogenous) actions result from lateral premotor areas (Okano & Tanji, 1987; Passingham, 1987; Haggard, 2008; Passingham, Bengtsson, & Lau, 2010; Krieghoff, Waszak, Prinz, & Brass, 2011). While premotor cortex receives direct inputs from sensory areas, medial frontal areas have widespread connections to other cortical areas and the limbic system, which provide internal information about physical and emotional states, motivation, and memory (Passingham et al., 2010). Although a strict dissociation of lateral and medial action pathways has been challenged (Nachev, Kennard, & Husain, 2008; Nachev & Husain, 2010; Hughes, Schütz-Bosbach, & Waszak, 2011), a large number of neuroimaging, stimulation and patient studies have provided converging evidence that medial frontal cortex (MFC) is crucially involved in the generation of voluntary actions. For example, preparation and initiation of voluntary movement has been linked to activity in the supplementary motor area (SMA), pre-SMA, cingulate cortex and medial prefrontal cortex (Deiber, Honda, Ibañez, Sadato, & Hallett, 1999; Cunnington, Windischberger, Deecke, & Moser, 2003; Soon, Brass, Heinze, & Haynes, 2008; Fried, Mukamel, & Kreiman, 2011; Zapparoli et al., 2018). In addition to voluntary decisions about *when* to act, MFC appears to be involved in generating voluntary *what* decisions (Bode, Bogler, & Haynes, 2013; Soon, He, Bode, & Haynes, 2013; Zapparoli et al., 2018). More specifically, the pattern of neural activity in MFC predicts endogenous decisions between alternative choice options, such as images of different object categories (Bode et al., 2013) or more abstract decisions about whether to add or subtract two numbers (Soon et al., 2013).

Additionally, such ‘free’ decisions are encoded in parietal cortex, including precuneus, angular gyrus and supramarginal gyrus (Bode et al., 2011; Soon et al., 2013; Zapparoli et al., 2018). It has been proposed that precuneus may contribute to endogenous choice by resolving conflict when alternative options appear to be equal, hence preventing behavioural stalemate (Bode et al., 2013). However, the specific contributions of parietal and frontal cortex to voluntary action remain largely unclear. A recent functional magnetic resonance imaging (fMRI) study suggests that parietal cortex is specifically involved in voluntary *what* decisions, whereas MFC forms an ‘intentional hub’ that integrates all three *what*, *when* and *whether* components of voluntary action (Zapparoli et al., 2018).

In addition to neurophysiological and -imaging approaches, patient studies can provide unique insights into the neurocognitive mechanisms that underlie voluntary action by identifying specific patterns of impaired volition (Kranick & Hallett, 2013). For example, tics/Tourette syndrome and anarchic hand syndrome are characterised by reduced voluntary control. Anarchic hand syndrome is typically caused by fronto-median lesions, including the SMA, that result in a loss of voluntary control over movements of the contralesional limb (Marchetti & Della Sala, 1998). Other neurological conditions affect patients’ subjective Sense of Agency over their actions, rather than movement control per se. For example, in alien hand syndrome, patients do not experience actions of the affected limb as their own (Kranick & Hallett, 2013). As opposed to anarchic hand syndrome, alien hand syndrome is typically caused by lesions in parietal cortex (Marchetti & Della Sala, 1998), which appears to be critical for conscious movement intention (Desmurget et al., 2009; Desmurget & Sirigu, 2009) and Sense of Agency (Farrer et al., 2008; Chambon, Wenke, Fleming, Prinz, & Haggard, 2012; Ritterband-Rosenbaum, Nielsen, & Christensen, 2014). Similarly, delusions of control in schizophrenia are characterised by a reduced Sense of Agency and may be the result of impaired connectivity between lateral parietal cortex – specifically, angular gyrus – and frontal areas (Voss, Chambon, Wenke, Kühn, & Haggard, 2017).

In conclusion, volition is associated with specific behavioural, neuroanatomical and neurophysiological markers that dissociate voluntary actions from purely externally-triggered actions. However, previous studies have often treated volition as a single cognitive ‘event’ leading to a single action, and hence, have used paradigms that may only provide limited insights into the complex and dynamic mechanisms underlying real-life actions. While some authors have acknowledged that voluntary actions evolve in time (Brass & Haggard, 2008; Schurger, Sitt, & Dehaene, 2012; Filevich & Haggard, 2013), few studies have investigated the neurocognitive mechanisms that allow for reversals of action decisions after movement onset.

1.1.3 Changes of Mind (CoM)

Previous studies on voluntary action have largely focused on a) the processes that lead up to an action *before* its initiation or b) the mechanisms that are involved in the evaluation of an action *after* it has been completed. For instance, research investigating the neurocognitive mechanisms prior to action has revealed how voluntary action decisions are generated (Bode et al., 2011; Bode et al., 2013; Soon et al., 2013), at which point in time these decisions enter consciousness (Libet, Gleason, Wright, & Pearl, 1983; Libet, 1985; Haggard & Eimer, 1999; Soon et al., 2008; Bode et al., 2011), and how voluntary decisions are implemented into motor action (Rushworth, Walton, Kennerley, & Bannerman, 2004). By contrast, studies on mechanisms after action completion have investigated the evaluation of action outcomes with respect to predicted outcomes (Blakemore, Wolpert, & Frith, 2000; Sato & Yasuda, 2005), post-action inference about prior intentions (Wegner, 2002; Wegner, Sparrow, & Winerman, 2004; Aarts, Custers, & Wegner, 2005), or the experience of responsibility for consequences of an action (Moretto et al., 2011; Caspar, Christensen, Cleeremans, & Haggard, 2016). In fact, action-related processes are often separated into *prospective* mechanisms that occur before action onset and *retrospective* mechanisms occurring after action completion (Moore et al., 2009; Chambon et al., 2014). By contrast, less is known about the processes that occur *during* ongoing action execution – in particular with regard to continuous decision processes that allow people to change their mind after an action has already been initiated, but before it has been fully executed. This may be largely due to the nature of paradigms that have typically been used to study volition. More specifically, there are five main characteristics of real-life voluntary actions, which are essential to understanding how voluntary actions unfold over time, but which have not been captured by many previous studies. The study of CoM offers one way to address these important topics:

1) *Extended time span:* While previous paradigms have often operationalised voluntary actions in terms of discrete and fast key presses, real-life actions are continuous and can take seconds, minutes, hours or weeks to complete. This prolongs the time period in between prospective and retrospective mechanisms, providing many opportunities for potential decision reversals during ongoing action execution.

2) *Large number of affordances:* Previous paradigms have often limited action choices to decisions about when to press a single button, or which one of two buttons to press. In real life, a significantly larger number of possible courses of actions (affordances) co-exist at a given point in time. The ability to flexibly switch between those alternatives may be particularly relevant when actions are initiated based on uncertain or incomplete information.

3) *Counterfactual outcomes*: Different affordances may be associated with different action outcomes. Given the exclusive and serial nature of actions, pursuing one action outcome often means momentarily forfeiting another one. Consequently, voluntary actions can have several counterfactuals, and the mere notion of "I could have done otherwise", is an important hallmark of volition (Kulakova, Khalighinejad, & Haggard, 2017; Rens, Bode, & Cunnington, 2018). In fact, people sometimes “do otherwise” and switch to an alternative course of action. Failures to switch may cause feelings of regret when the outcome of a chosen action is unsatisfactory (Frith & Haggard, 2018).

4) *Hierarchical organisation*: Voluntary actions are driven by higher-order goal intentions that specify a desired action outcome (e.g., “I want to eat an apple”). These goals then need to be implemented into specific motor actions through lower-level processes involved in movement selection and planning (e.g., reaching for an apple). Hence, voluntary actions are organised in a hierarchical manner and CoM may occur on each level of the hierarchy. That is, decision reversals may either reflect a change in *what* goal is selected, or a change in *how* the goals is implemented into action (see section *1.4.2* below).

5) *Multiple sources of information:* Voluntary actions need to integrate several pieces of information from different sources, including rewards and costs associated with an action, bodily states, and memories. Additionally, information from the external environment needs to be taken into account in order to select an appropriate action in a given situation. For example, external contexts can impose constraints on voluntary decisions by limiting the number of affordances. Hence, voluntary actions may be more accurately described as a mix of various endogenous and exogenous factors, rather than being entirely internally generated. Importantly, each source of evidence may change dynamically over time, which can potentially trigger CoM.

The need to integrate external information for successful action selection implies that perceptual processes are highly relevant for voluntary action. In fact, one aspect that will be further explored throughout this thesis is that CoM about endogenous actions may be triggered by changes in the external environment – or changes in how the external environment is *perceived*. Consider a person that intends to cross the road (voluntary intention). The person needs to take into account whether the traffic light is red or green (perceptual information) in order to select an appropriate course of action (stop vs. cross the road). If the traffic light changes just as the person approaches the crossing, a quick change of action might be necessary (e.g., if the traffic light switches to red: Stop). In some situations, the perceptual information might be perturbed by noise (e.g., fog), introducing uncertainty in the perpetual decision about the traffic light. Moreover, perceptual information may be a lot more complex than the mere colour of a traffic light, which further increases difficulty of the perceptual decision. For example, in the absence of a traffic light, the person needs to consider how many cars are coming from each direction, how fast they are going, if they are accelerating or not etc. A large number of studies has investigated such difficult perceptual decisions and has provided evidence that people continuously evaluate incoming sensory signals and sometimes change their mind about an initial perceptual choice (e.g., Resulaj, Kiani, Wolpert, & Shadlen, 2009). Hence, before further considering CoM in voluntary action, studies on CoM in perceptual decision making will be reviewed as these can provide important insights into theoretical and practical aspects of studying decision reversals and their underlying neurocognitive mechanisms.

1.2 CoM in perceptual decision making

Most previous studies on CoM in perceptual decision making have used the random-dot motion (RDM) task. In this task, participants have to judge the direction of moving dots by reaching for a target that corresponds to the observed net dot motion (e.g., left target for leftwards moving dots; **Figure 1.1**). Choice difficulty varies according to the dot-motion coherence, i.e., the percentage of dots that move into the same direction. On some trials, participants' movement trajectories indicate a CoM, i.e., the response is initiated towards one target (e.g., on the left), but is then redirected and ends in the other target (e.g., on the right; Resulaj et al., 2009; Albantakis & Deco, 2011; Albantakis, Branzi, Costa, & Deco, 2012; Burk, Ingram, Franklin, Shadlen, & Wolpert, 2014; Moher & Song, 2014; van den Berg et al., 2016). These findings provide strong evidence that perceptual information continues to be evaluated after an initial choice has already been implemented into action, which can occasionally induce a CoM if evidence in favour of the alternative choice option is obtained after response onset.

Importantly, by measuring continuous movement trajectories to capture CoM, these studies provided evidence that decision-making processes can run in parallel to action execution. Interestingly, CoM in the RDM task occurs even when the external stimulus disappears at action onset (Resulaj et al., 2009). This is due to sensorimotor delays (‘non-decision time’), causing evidence presented right before action onset to be processed *while* the action is executed. Hence, the onset of an action does not mark the end of a decision process, and in fact, does not *require* the decision to be finalised. Instead, findings of perceptual CoM during action are in line with theories proposing that decision making and action selection operate in a parallel and integrated manner, rather than being discrete and serial processes (Cisek, 2007; Yoo & Hayden, 2018).

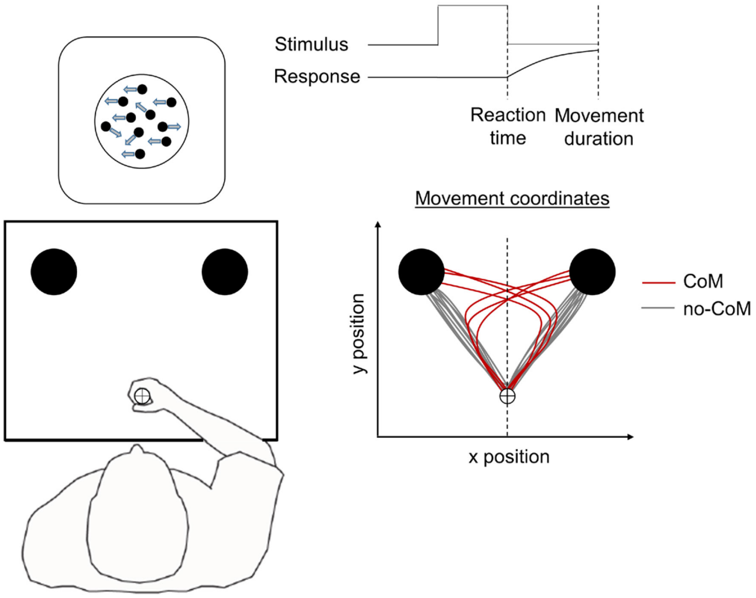

Figure 1.1. Changes of Mind in the random-dot motion task. Participants judge the net motion direction of the dots by reaching for the corresponding left/right target. Continuous movement trajectories occasionally indicate a Change of Mind, e.g., a switch from the left to the right target (red trajectories). Due to sensorimotor delays, Changes of Mind occur even when the stimulus disappears at response onset (adapted from Resulaj et al., 2009).

1.2.1 Factors influencing perceptual CoM

Variables that influence the frequency of CoM can provide further insights into the mechanisms that shape decisions as they evolve. In the RDM task, CoM is most frequent when the initial decision was erroneous or when response initiation was fast – and hence, when little evidence had been acquired by the time of the initial choice (Resulaj et al., 2009; Albantakis et al., 2012; van den Berg et al., 2016). Moreover, CoM is most likely when dot-motion coherence is relatively low (Resulaj et al., 2009). If motion coherence is high, CoM is rare because initial choices are usually correct and later sensory evidence further supports the initial choice. However, CoM does not necessarily increase monotonically with lower coherence since post-decision evidence may not be strong enough to drive a decision reversal when motion coherence is too low (Resulaj et al., 2009).

Together, these findings point to a strong link between CoM and processes involved in performance monitoring and error correction (Yeung & Summerfield, 2012). In fact, curved trajectories in the RDM task share characteristics with 'partial errors' – i.e., early activation of an incorrect motor response, which is later on overwritten by the correct response (Coles, Scheffers, & Fournier, 1995; Dshemuchadse, Scherbaum, & Goschke, 2013). Moreover, it has been proposed that CoM is closely linked to our *subjective* confidence that the initial decision was correct, given new post-decision information (Fleming, Putten, & Daw, 2018). In line with this, a study by van den Berg et al. (2016) showed that the very same sensory evidence that contributes to perceptual CoM also underlies changes in confidence about that decision. Hence, at least in the case of perceptual choice, CoM may largely reflect corrections of initial decisions that are erroneous, or that we do not feel confident about.

However, not all errors are corrected. One important reason for this is that decision reversals can be costly since a) one might erroneously switch from a correct to an incorrect decision if evidence in favour of a decision reversal is not sufficiently strong, and b) CoM can incur a temporal or effort cost. Consequently, CoM decisions are typically conservative in that they require more than simply a reversal of the direction of evidence (Resulaj et al., 2009). Additionally, the reversal criterion is modulated by the motor cost associated with CoM. More specifically, when response targets in the RDM task are far apart from each other, corrective movements are more costly, and hence, the frequency of CoM decreases (Burk et al., 2014; Moher & Song, 2014). The cost associated with CoM has been reported to affect decision-making processes at both early and late stages. That is, in the study by Burk et al. (2014), far targets caused participants to apply a more conservative CoM criterion, i.e., stronger post-decision evidence was required to drive decision reversals. Conversely, Moher & Song (2014) found that motor costs already affected decision making during earlier stages of the decision process. More specifically, in their study, participants' *initial* responses were slower when response targets were far, suggesting a more conservative speed-accuracy trade-off, which in turn reduced the risk of a costly decision reversal later on. The findings of the two studies are not mutually exclusive – presumably, motor costs are continuously evaluated throughout the decision process, just like sensory evidence. Consequently, it seems plausible that motor costs can affect decision making at several different stages, affecting both the initial decision as well as later decision reversals. More importantly, both studies provide converging evidence that the possibility to change one's mind (and the cost associated with that) affects the underlying decision-making process itself.

1.2.2 Models of perceptual CoM

All previous studies on CoM in perceptual decision making share the assumption that decision reversals are the result of continuous evaluation of information after an initial choice has already been made. However, the precise mechanism of this continuous process is debated. Two main types of computational models of CoM have been proposed: Bounded accumulator models (Resulaj et al., 2009; Burk et al., 2014; van den Berg et al., 2016) and attractor network models (Albantakis & Deco, 2011; Albantakis et al., 2012; Yan, Zhang, & Wang, 2016). Both models have been applied in several different domains of decision making and can accurately predict choice behaviour and response times across a large range of tasks (for an overview, see Deco, Rolls, Albantakis, & Romo, 2013). More recently, both models have been extended in order to account for decision reversals.

In accumulator models (**Figure 1.2A**), evidence for each choice option is accumulated over time until a decision boundary is reached (Smith & Vickers, 1988; Ratcliff & Rouder, 1998). Due to fluctuations in noisy perceptual stimuli, evidence accumulation sometimes initially crosses one boundary, but then reverses in favour of the alternative choice option causing a CoM (e.g., Resulaj et al., 2009). This model directly accounts for time-accuracy trade-offs that can explain the effect of several variables on the frequency of CoM. For example, Moher & Song (2014) proposed that reduced frequency of CoM under high cost can be explained by increasing the decision boundary in an accumulator model. High decision boundaries require more evidence to be obtained in order to reach a decision, and consequently, to reverse a decision. This reduces the likelihood that sufficient post-decision evidence is accumulated to cause a CoM. However, interestingly Resulaj et al. (2009) proposed that CoM decisions are subject to a different boundary that is separate from the initial decision boundary (B_{CoM}, **Figure 1.2A**). Reaching that second CoM boundary typically requires more evidence in favour of the alternative choice option than was needed for the initial decision (Resulaj et al., 2009; Burk et al., 2014; van den Berg et al., 2016). This is because CoM in the RDM task incurs motor costs due to longer path lengths of corrective movements. Accordingly, the further away the targets are from each other, the further away the CoM bound is shifted, explaining why far targets cause fewer CoMs than close targets (Burk et al., 2014).

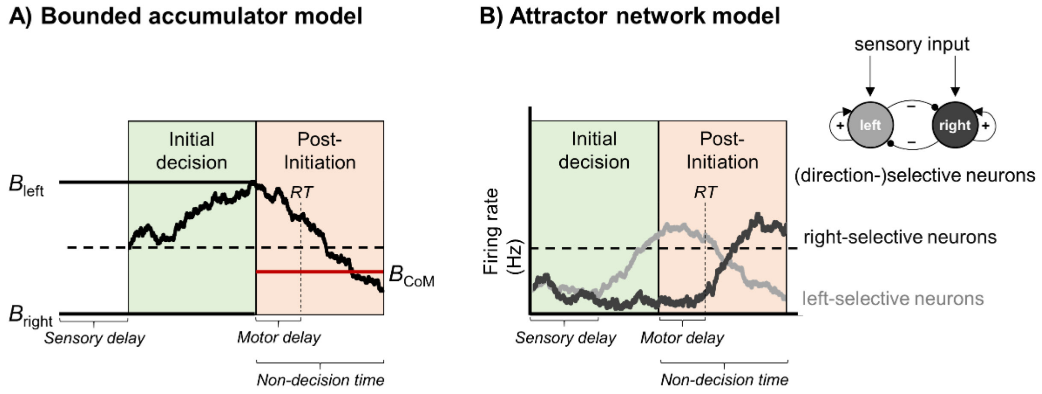

Figure 1.2. Computational models of CoM. A) Bounded accumulator (drift diffusion) model where relative evidence in favour of a choice option (e.g., left) is accumulated over time. After an initial bound has been reached, evidence continues to be accumulated due to sensorimotor delays (non-decision time). Occasionally, this causes the accumulator to reach a CoM boundary (red) after response initiation, indicating a decision reversal. B) Attractor network model with two nodes representing neural populations that selectively respond to left/right motion stimuli. Firing rates of each population are updated continuously based on the external input and excitatory/inhibitory connections. CoM occurs when one population of neurons reaches the firing threshold first, but later on, the alternative population wins the competition and reaches the threshold.

Similarly to accumulator models, attractor network models propose that a decision variable dynamically evolves over time until a decision threshold is reached (Wang, 2002, 2008). However, in attractor network models, the diffusion process occurs in a non-linear manner. Attractor networks typically consist of several nodes, which represent different neural populations that respond selectively to specific inputs (e.g., left vs. right dot motion; **Figure 1.2B**). The firing rate of each node encodes the decision variable and is updated continuously over time. Importantly, different nodes are connected through excitatory or inhibitory connections. Hence, the current state of a given node does not only depend on direct external inputs, but also on its inputs from other neural populations – or in case of auto-connections, on its own previous state. A response is made if one of the neuron pools reaches a fixed firing rate threshold. Due to self-sustaining dynamics, the network evolves into an 'attractor state' where firing rates remain relatively stable over time. However, crucially, when noise is high or when the system is perturbed, the network can switch from one attractor state to a different one later on, indicating a CoM (Moreno-Bote, Rinzel, & Rubin, 2007; Albantakis & Deco, 2011; Albantakis et al., 2012; Yan et al., 2016). That is, after an initial decision has been made, the firing rate of the alternative pool increases and reaches the threshold, causing the network to switch to a different attractor state (**Figure 1.2B**). The likelihood of attractor states to change varies with the degree of noise in the external input, but also depends on intrinsic fluctuations within the network, which in turn are a function of neural noise and the network's connectivity architecture (Albantakis & Deco, 2011; Yan et al., 2016). For example, strong self-excitatory connections can render attractor states more stable.

Both accumulator and attractor network models can account for commonly observed effects on CoM (e.g., Resulaj et al., 2009; Albantakis & Deco, 2011). For example, in both models, CoM is more frequent when the initial decision is erroneous because noise causes the wrong choice option to be reached first, but sufficient evidence in favour of the correct option is acquired over time due to the actual signal in the stimulus. Furthermore, both types of model predict that CoM occurs more frequently when the decision threshold is low, i.e., when only a small amount of evidence can drive a decision/decision reversal. Finally, in both types of models, decision reversals require relatively strong countermanding evidence after commitment to an initial choice. In accumulator models, this is implemented through a separate CoM boundary that is shifted away from the initial boundary. By contrast, attractor network models assume a fixed threshold for both initial decisions and subsequent decision reversals. However, due to inhibitory connections, the initially-chosen option suppresses competing choice alternatives, which consequently require more evidence to reach the firing threshold.

The differences and potential (dis-)advantages of accumulator vs. attractor network models have been debated extensively in the literature (e.g., Wang, 2008; Deco et al., 2013). For example, it has been proposed that attractor network models can easily be extended beyond 2-alternative choice tasks by simply adding more possible attractor states according to the number of choice options (Albantakis et al., 2012). By contrast, in some types of accumulator models, implementation of more than 2 choice options is less trivial, such as in drift diffusion models where the decision variable represents the *relative* evidence in favour of a given choice option (Tsetsos, Usher, & McClelland, 2011). However, other types of accumulator models (e.g., race models) assume independent accumulation for each choice option, and hence, can easily be extended to multiple-choice problems. Furthermore, it has been proposed that attractor networks are more biologically plausible than accumulator models due to their non-linear dynamics that are inspired by real neural circuits (Wang, 2008). However, biological plausibility is difficult to quantify and test directly. Moreover, some types of accumulator models share characteristics of networks. For example, in 'leaky competing accumulator models' (Usher & McClelland, 2001), evidence accumulation is imperfect due to leakage, or decay, over time. Additionally, in these models, alternative accumulators have mutual inhibitory connections, as in attractor networks. Hence, the two types of modelling approaches are not necessarily exclusive. Nevertheless, a main advantage of network models is that they can consist of several modules (or layers), and hence, allow for integration of a large range of decision variables that are encoded in different neural populations (Christopoulos, Bonaiuto, & Andersen, 2015). By contrast, traditional accumulator models only accumulate a single source of evidence (e.g., sensory evidence from an RDM stimulus), while other sources of information (e.g., motor costs) are modelled through their effects on a static decision threshold, rather than being treated as a decision variable per se (Burk et al., 2014; Moher & Song, 2014).

Hence, attractor network models might provide an appropriate approach to model CoM in voluntary action, where endogenous intentions need to be continuously integrated with sensory and value-based information. In **Chapter 3** of this thesis, a novel attractor network model will be proposed that consists of several nodes that continuously and dynamically integrate voluntary intentions, sensory evidence and motor costs in order to inform choices between several competing action alternatives.

1.2.3 Neural basis of perceptual CoM

While there is an extensive literature on the neural mechanisms underlying perceptual decisions (for a review, see Gold & Shadlen, 2007; or Hanks & Summerfield, 2017), only very few studies have specifically investigated the neural basis of CoM (Bollimunta, Totten, & Ditterich, 2012; Kiani, Cueva, Reppas, & Newsome, 2014; Fleming et al., 2018). With regard to perceptual choice in general, many previous studies have suggested that accumulation of sensory evidence may be encoded in posterior parietal cortex (Shadlen & Newsome, 2001; Kayser, Buchsbaum, Erickson, & D'Esposito, 2009; Bollimunta et al., 2012; O'Connell, Dockree, & Kelly, 2012), and frontal regions, including dorsolateral prefrontal cortex (Kim & Shadlen, 1999; Heekeren, Marrett, Bandettini, & Ungerleider, 2004) and motor areas involved in implementing perceptual decisions into actions (Gold & Shadlen, 2000; Donner, Siegel, Fries, & Engel, 2009). Yet, the role of these areas in driving perceptual CoM has only received attention more recently. This may largely be due to the fact that CoMs are usually rare, with a typical frequency of 5–10%, even under conditions that maximize the likelihood of decision reversals, e.g., high uncertainty and time pressure (Resulaj et al., 2009; Albantakis & Deco, 2011; Moher & Song, 2014). Furthermore, CoM usually occurs spontaneously, with little experimental control over whether or not a decision reversal occurs on an individual trial. This is particularly true for CoMs that result in overt reversals of behavioural responses. Hence, studies investigating the neural mechanisms of CoM have focused on *covert* decision reversals by measuring changes in neural activity in areas tracking perceptual evidence (Bollimunta et al., 2012; Kiani, Cueva, et al., 2014). For example, using an RDM task, Kiani et al. (2014) showed that neural activity in prefrontal cortex dynamically encodes the evolution of a decision variable within a given trial. This decision variable (i.e., neural activity patterns) occasionally reversed, indicating a CoM before the decision was implemented into overt behaviour. The authors verified that these CoMs observed on a neural level were behaviourally relevant, rather than reflecting pure noise. That is, the state of the internal decision variable accurately predicted overt behaviour in trials where responses were prompted early on in the trial. Furthermore, in line with previous studies, neural reversals were more likely when the perceptual decision was difficult and when the initial choice was erroneous. This suggests that neural activity patterns reliably tracked a perceptual decision variable in real time as decisions evolved, occasionally signalling changes in internal decision states based on new evidence. Hence, CoM may result directly from the neural processes that continuously evaluate perceptual evidence during decision formation.

Additionally, a recent fMRI study in humans investigated the brain areas involved in post-decision evaluation of sensory evidence and its effect on subjective ratings of confidence (Fleming et al., 2018). Given that both confidence and CoMs are, at least to some extent, driven by the strength of sensory evidence (van den Berg et al., 2016), confidence judgments can serve as a graded measure of processes that might be very closely linked to discrete CoM/no-CoM behaviour. In an RDM task, the authors manipulated the amount of perceptual evidence in favour of the correct choice, after participants had already committed to an initial decision. Participants were then asked to rate their confidence in the decision after having acquired the additional evidence. Posterior MFC tracked post-decision evidence – specifically, the probability that the initial decision was correct. Interestingly, activity in MFC showed a positive relation with post-decision evidence in errors, but a negative relation in correct responses. This indicates that this area may be specifically engaged when an erroneous action needs to be revised based on new evidence – in line with previous studies implicating posterior MFC in error monitoring and correction (Carter et al., 1998; Mars et al., 2005). Hence, MFC may contribute to perceptual CoM by informing error correction after an initial choice has already been made. Finally, Fleming et al.

(2018) found that a distinct area in the lateral anterior PFC mediated the effect of post-decision evidence on subjective confidence ratings, suggesting that this area transformed updates in decision variables into metacognitive judgments about one's own choices. However, this study did not explicitly investigate how exactly post-decision evidence tracked by MFC and subjective confidence represented in lateral anterior PFC contribute to, and possibly interact, in order to cause *overt* CoM.

1.3 CoM in value-based decision making

In addition to external sensory input, voluntary actions rely on value-based representations about the rewards and costs associated with an action. Similarly to CoM in perceptual choice, previous studies have shown that value-based decisions, for example between different food items, can change dynamically after an initial choice has already been made (Folke, Jacobsen, Fleming, & De Martino, 2016; Voigt, Murawski, & Bode, 2017). In analogy to the effects of confidence in perceptual decisions, Folke et al. (2016) showed that people change their mind more frequently when their confidence in an initial value-based decision is low, for example when choice values are highly similar for alternative options. Hence, in both perceptual and value-based choice, decision reversals are more likely when evidence in favour of the initial choice was relatively weak.

Updates in value-based decisions are particularly relevant when values of competing choice options are uncertain and/or change dynamically, for example, in probabilistic reversal learning (Izquierdo, Brigman, Radke, Rudebeck, & Holmes, 2017), or foraging in dynamic environments where agents commonly face decisions between exploitation of a previous choice vs. exploration of alternative choice options (Cohen, McClure, & Angela, 2007; Humphries, Khamassi, & Gurney, 2012; Rushworth, Kolling, Sallet, & Mars, 2012). Several brain areas have been shown to continuously track competing choice values in these scenarios, including posterior parietal cortex (Sugrue, Corrado, & Newsome, 2004), frontopolar cortex (Boorman, Behrens, Woolrich, & Rushworth, 2009), ventromedial frontal cortex (Tsuchida, Doll, & Fellows, 2010; Economides, Guitart-Masip, Kurth-Nelson, & Dolan, 2014; McGuire & Kable, 2015), and anterior cingulate cortex (Cohen et al., 2007; Camille, Tsuchida, & Fellows, 2011; Boorman, Rushworth, & Behrens, 2013; Kolling, Wittmann, & Rushworth, 2014; Kolling, Behrens, Wittmann, & Rushworth, 2016; Kolling, Wittmann, et al., 2016; Shenhav, Cohen, & Botvinick, 2016). Interestingly, patients with lesions in fronto-median areas are not typically impaired in learning a single choice value, but show a specific pattern of impairments in updating value representations when reward contingencies change dynamically, and hence, need to be updated continuously (Fellows & Farah, 2003).

However, most of these studies have investigated discrete actions, rather than CoM during ongoing movement. Moreover, choice reversals in these paradigms occur across several trials, or even blocks – and hence, are the result of relatively slow updates, e.g., during learning. However, choice values can be updated on a much faster time scale. For example, in a recent (unpublished) study, Voigt, Murawski, Speer, and Bode (2018; bioRxiv) proposed that choice values are dynamically updated while decisions are made. The authors measured choice-induced preference – i.e., the phenomenon by which choice behaviour can increase the subjective value of a chosen option, especially when the decision was generated endogenously (Festinger, 1957; Sharot, Velasquez, & Dolan, 2010). Choice-induced preference had previously been proposed to be driven by cognitive dissonance that causes a retrospective increase in value *after* a choice was made (Festinger, 1957). By contrast, Voigt et al. showed that choice values are already adjusted *while* choices are generated, suggesting that value-based information can be updated in a highly dynamic manner as decisions evolve. These online updates of values, and subsequent preference changes, could be predicted from activity in precuneus and dorsolateral prefrontal cortex. However, this was only true for choice items that were encoded in memory and were associated with hippocampal activity. Hence, value representations stored in memory may serve as internal cues guiding future behaviour, which may be particularly relevant for endogenous action selection (Voigt et al., 2018). Hence, there are dynamic reciprocal relations between endogenous actions and value-based representations, where actions can drive changes in subjective value, which then in turn inform future actions.

1.3.1 Temporal/effort costs

Finally, value-based decisions need to integrate both rewards and potential costs. Actions typically incur a cost in terms of effort and/or time associated with a given movement (Kurniawan et al., 2010; Shadmehr, de Xivry, Xu-Wilson, & Shih, 2010). As mentioned above, this can affect action selection in perceptual decision-making tasks (Burk et al., 2014; Moher & Song, 2014). However, costs also need to be weighed against potential rewards in value-based choice. It has been proposed that this is achieved through temporal/effort discounting, i.e., a decrease in the subjective value assigned to a reward as a function of its associated cost (Samuelson, 1937; Hartmann, Hager, Tobler, & Kaiser, 2013).

Effort may be a particularly interesting type of cost because deciding to invest physical effort to obtain a reward is directly linked to motivational aspects of behaviour. That is, overcoming effort costs not only requires hedonic ‘liking’ of a prospective reward, but an incentive ‘wanting’, which drives goal-directed behaviour (Berridge, Robinson, & Aldridge, 2009). Motivational deficits, such as apathy, are commonly observed in neurological and psychiatric conditions (Husain & Roiser, 2018), e.g., Parkinson’s disease (Starkstein et al., 1992; Chong et al., 2015), stroke (Starkstein, Fedoroff, Price, Leiguarda, & Robinson, 1993; Mayo, Fellows, Scott, Cameron, & Wood-Dauphinee, 2009; Caeiro, Ferro, & Costa, 2013), depression (Treadway, Bossaller, Shelton, & Zald, 2012), and schizophrenia (Hartmann et al., 2014).

Many previous studies on effort-based decision making measure participants' willingness to *initiate* an effortful action, e.g., squeezing a hand-held dynamometer with high force, in order to gain a reward (Hartmann et al., 2013; Chong et al., 2015). However, crucially, goal-directed behaviour often requires perseverance – i.e., the willingness to *maintain* an effortful action over long periods of time, instead of cancelling the action or changing to an easier, alternative course of action (Holroyd & Coles, 2002; Meyniel, Safra, & Pessiglione, 2014; Kolling, Wittmann, et al., 2016). It has been proposed that initiating vs. maintaining an effortful action are dissociable processes that rely on partially distinct mechanism (Holec, Pirot, & Euston, 2014; Meyniel et al., 2014). Specifically, deciding to initiate an action requires integration of *anticipated* effort and rewards, for example, based on external effort cues. Overestimation of prospective effort may underlie difficulties of action initiation observed in patients with depression or 'auto-activation deficit', causing an overall reduction in self-generated voluntary actions (Meyniel et al., 2014; Bonnelle et al., 2015). By contrast, maintaining an effortful action over time requires integration of *experienced* effort during action execution. This needs to be updated continuously as the action evolves. Meyniel et al. (2014) proposed an accumulator model, in which effort accumulates during ongoing action execution until a threshold is reached, causing the person to take a rest to refill resources. The higher the rate of effort accumulation, the earlier execution of an effortful action is stopped, and hence, this accumulator process can be directly linked to the decision about whether or not to maintain an ongoing effortful action. The rate of accumulation in turn depends on both the objective effort requirements that cause muscles to fatigue over time, but also the subjective experience of the exerted effort (Meyniel et al., 2014; Müller & Apps, 2018). Hence, effort-based decisions have to be updated continuously according to one's current bodily and motivational state. Disturbances of these processes, e.g., exaggeration of experienced effort in chronic fatigue (Nadarajah & Goh, 2015; Kuppuswamy, 2017), may cause difficulties in persistent voluntary action. In **Chapter 5** of this thesis, we report findings of reduced perseverance in voluntary goal pursuit in patients with post-stroke fatigue.

1.4 CoM in voluntary action

The studies reviewed above have focused on decision making in the context of perceptual or value-based choice. The aim of the current thesis is to extend the investigation of dynamic decision reversals to the field of voluntary action. As mentioned above, there are certain characteristics that may render voluntary action a particularly interesting field of investigation with regard to CoM: 1) *extended time spans*, providing many opportunities for decision reversals when new information is obtained, 2) *large number of affordances*, and hence, several alternative courses of action to switch to, 3) *counterfactual outcomes*, i.e., CoM can change the consequences of an action, 4) CoM may occur on *different hierarchical levels* of action, and hence, affect higher-order goal intentions or lower-level movements, and 5) voluntary actions need to integrate *multiple sources of information*, which may change dynamically over time. These characteristics may render voluntary actions particularly prone to decision reversals. Additionally, the fact that CoM can cause changes in action outcomes means that whether or not an agent changes an ongoing action can have important individual or social consequences (Gollwitzer & Oettingen, 2012; Goschke, 2014). Beyond such practical implications, there are important theoretical reasons for studying CoM in voluntary action.

1.4.1 Why study CoM in voluntary action?

First, by extending the investigation of CoM to voluntary action, we can gain new insights into the mechanisms driving decision reversals in other domains, beyond perceptual and value-based decision making. Previous studies on CoM have focused on a single source of evidence (e.g., perceptual or value-based information) that is continuously evaluated over time. By contrast, voluntary actions need to take into account a large variety of sources of information, including internally-generated intentions, value-based representations about rewards and costs of action alternatives, and external information about context. Consequently, studying CoM in voluntary action can provide new insights into how several different endogenous and exogenous sources of evidence interact over time to inform decision reversals.

Furthermore, we cannot assume that the findings from previous studies on perceptual CoM hold true for voluntary decisions. In fact, there are several reasons to assume that whether or not a decision was made endogenously may affect later decision updates. For example, as mentioned above, endogenous choice – but not externally-instructed choice – can increase subjective value, which can in turn strengthen commitment to an initial choice (Sharot et al., 2010; Voigt et al., 2017). In fact, traditional theories of volition consider the will to be a strong 'determining tendency' that can, for example, overwrite habitual responses (Ach, 1935). Hence, voluntary intentions may be strong and less susceptible to CoM. However, others have proposed that, compared to externally-instructed intentions, self-generated intentions are held more flexibly (Salvaris & Haggard, 2014), are associated with indecision and vacillation (Kaufman, Churchland, Ryu, & Shenoy, 2015), and can be updated more easily (Fleming, Mars, Gladwin, & Haggard, 2009). This may be related to the fact that voluntary decisions often do not have objectively correct or incorrect choice options. Hence, voluntary actions are relatively underdetermined by evidence, which may cause agents to 'keep their options open' in case more evidence informing action selection is obtained later on.

However, previous studies suggesting that voluntary intentions are flexible have focused on basic motor decisions about which one of two keys to press – with little to no consequences for participants. Yet, there are cases where intentions are of greater personal relevance, e.g., when choosing one's future career path, or similar 'goal intentions'. In these situations, self-generated intentions may be stronger, and hence, less prone to decision reversals. In other words, the degree to which intentions are reversible might depend on the strength of intention, which in turn may vary gradually. Hence, by studying *changes* in intentions, we can learn more about the conditions under which intentions are maintained vs. abandoned, which may provide important insights into what intentions are and how ‘determining’ they may be. Thus, measuring CoM may be a suitable approach to capture intentions as a continuous, gradual and reversible phenomenon. Similarly, other fields of psychology, e.g., memory research, have long-standing traditions of studying representations by investigating how and why they change over time (Atkinson & Shiffrin, 1968).

More generally, studying CoM in voluntary action cannot only shed light on the specific mechanisms underlying decision reversals, but might also provide novel insights into volition itself that might otherwise be difficult to gain. Previous studies have investigated endogenous action as a serial and discrete event (e.g., by measuring single keypresses), and hence, have taken single snapshots of voluntary action. However, in order to capture the evolution of actions, we need to apply continuous measures (Spivey, 2007; Song & Nakayama, 2009; Dshemuchadse et al., 2013; Gallivan & Chapman, 2014). The existing literature on CoM in perceptual and value-based decision making provides a good example of what can be gained by studying actions as continuous phenomena. For example, previous studies have shown how decision-relevant information is evaluated over time (Resulaj et al., 2009), how initially erroneous decisions are corrected during ongoing action execution (Dshemuchadse et al., 2013), and how decision criteria are flexibly adjusted in the face of motor costs (Burk et al., 2014; Moher & Song, 2014). As a consequence, these studies have been able to redefine and extend existing models of decision making and its underlying neural mechanisms. Hence, studying CoM cannot only provide insights into decision reversals themselves, but may also enable a better understanding of the more general mechanisms underlying voluntary action – e.g., how intentions are generated and transformed into actions, how they are re-evaluated after action onset, or how intentions (or *changes* in intentions) shape the subjective Sense of Agency over an action.

In summary, there are important practical and theoretical implications of studying CoM in voluntary action. Before addressing the specific questions this thesis aims to answer, we need to first specify in more detail what we mean by CoM in the context of voluntary action, and how exactly this can be measured. Given that voluntary actions require integration of multiple sources of information, and involve decisions about multiple action parameters (Brass & Haggard, 2008), there are many different ways in which agents may change their mind about a voluntary action. Hence, in the following, an important distinction between different types of CoM will be discussed before practical challenges of measuring CoM in voluntary action are addressed.

1.4.2 Hierarchical decision making: Goals vs. movements

Several theories propose that decisions about different aspects of action are organised in a hierarchical manner (Hebb, 1949; Mele, 1992; Cooper & Shallice, 2000; Botvinick, 2008; Pacherie, 2008; Kouneiher, Charron, & Koechlin, 2009; Cisek, 2012). Pacherie (2008) differentiates between distal (*D*), proximal (*P*) and motor (*M*) intentions (**Figure 1.3A**). Distal intentions refer to abstract, higher-order action goals, e.g., deciding to eat pizza for dinner. Proximal intentions are lower-level sub-goals, i.e., steps that are required to achieve higher-order goals, such as preparing pizza dough. Finally, motor intentions represent the precise motor actions that are necessary to achieve proximal and distal intentions, e.g., kneading pizza dough. Hence, while distal intentions refer to the goal of an action with respect to its outcome, proximal and motor intentions are the means of reaching that overarching goal. Specification of motor intentions is largely guided by contextual and sensorimotor information that is provided by exogenous input from the environment. For example, kneading the dough requires knowledge about the current location of the dough, its weight etc. By contrast, distal intentions are often generated based on one's own goals, preferences, and beliefs (Pacherie, 2008), and hence, may be endogenous. The translation of abstract endogenous goals into specific movements can be achieved through an internal inverse model that computes the motor commands required to reach a desired state (Kawato, 1999; Wolpert & Ghahramani, 2000; Pacherie, 2008).

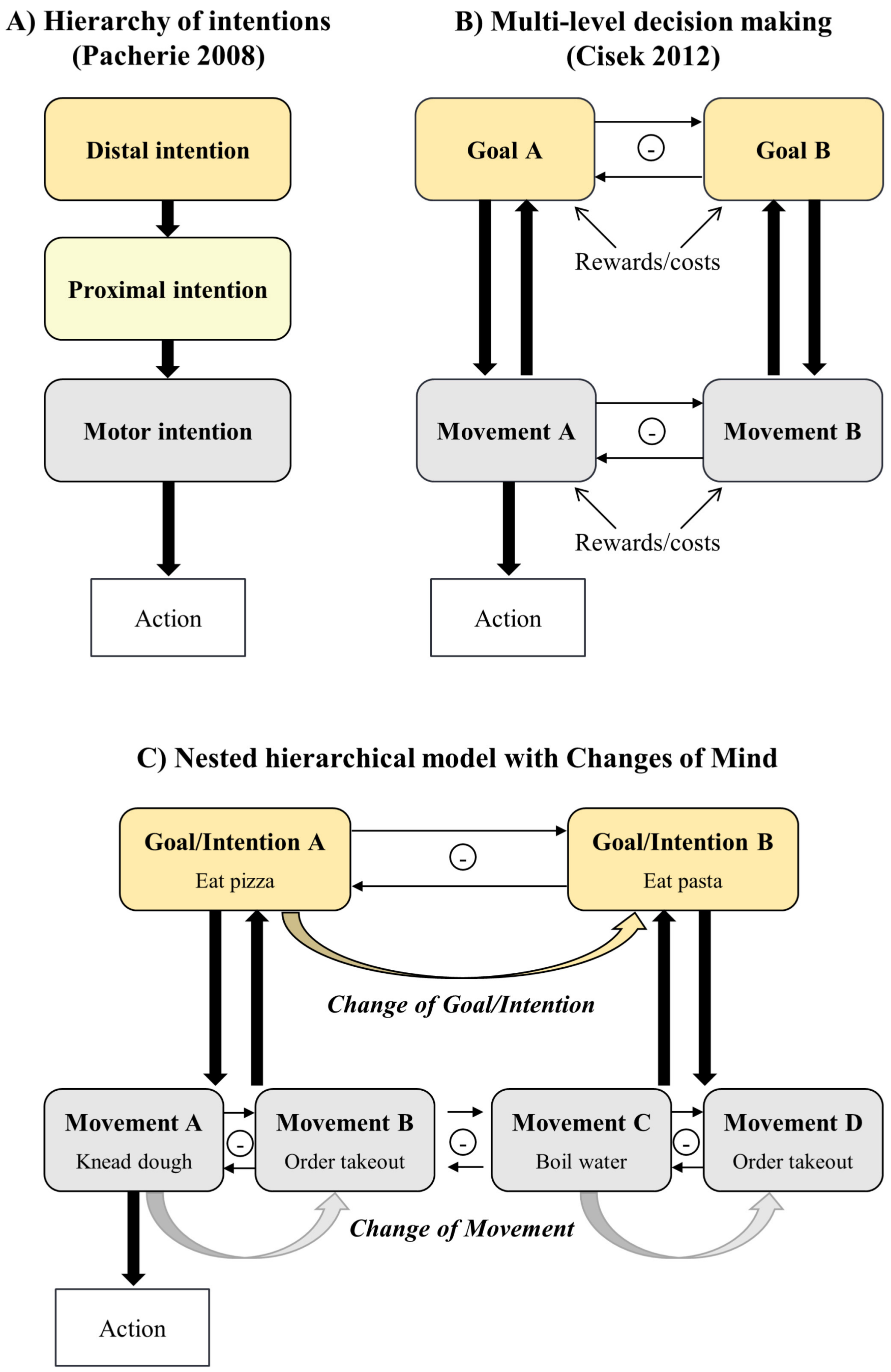

Figure 1.3. Hierarchical models of goals and movements. A) Pacherie's hierarchy of intentions. B) Cisek's model of multi-level decision making with parallel competition between higher-order goals and lower-level motor representations, and integration of information across both levels. C) Extended multi-level model where multiple movement alternatives are nested within each goal. Changes of Mind can occur on each hierarchical level, and hence, a distinction between Changes of Goals/Intentions and Changes of Movements can be made.

Similarly to Pacherie's hierarchical model of intentions, Cisek (2012) differentiates between higher-order abstract goals and lower-level motor representations, and proposes that action selection depends on parallel and integrated decision making on both levels of the hierarchy (**Figure 1.3B**). That is, different goal representations compete against each other, and at the same time, motor representations associated with each goal compete for execution. On each level, costs and rewards inform the competition between alternative goals/movements. Decisions are made through a 'distributed consensus', i.e., integration of information across both levels. That is, reciprocal connections allow information on one level of the hierarchy to bias the competition on the other level. Intuitively, the decision to select goal A biases the selection of the corresponding movement A. However, crucially, movement representations also inform higher-order goals. That is, the means of *how* to reach a goal might inform *what* goal to select, e.g., by providing information about the cost associated with each movement (Cos, Bélanger, & Cisek, 2011; Cisek, 2012; Christopoulos et al., 2015). For example, the effort associated with kneading pizza dough might be taken into account when deciding whether to make pizza, or instead, pursue a different goal that may be easier to achieve (e.g., cooking pasta). Hence, this model assumes that motor representations play an active part within the decision-making process. In line with this, it has been shown that multiple movement alternatives are already activated before a final decision between abstract goals has been made (Cisek & Kalaska, 2002, 2005; Gallivan & Wood, 2009; Chapman et al., 2010; Stewart, Gallivan, Baugh, & Flanagan, 2014; Gallivan, Barton, Chapman, Wolpert, & Flanagan, 2015), allowing motor representations to be integrated effectively into the decision-making process (Cisek, 2007, 2012).

Finally, in the model by Cisek, each goal is directly associated with a single movement. However, in many situations, a given goal may have multiple movement alternatives (**Figure 1.3C**). In fact, according to Hebb's principle of motor equivalence, several possible movements can result in the same outcome (Hebb, 1949). Hence, there are different ways of reaching a given goal, such as making pizza vs. ordering takeout from an Italian restaurant. Consequently, goals and movements may be organised in a nested hierarchical structure, where competition between higher-order goal intentions occurs in parallel to competition between multiple movement alternatives that are nested within each goal. Note that in the following, the words ‘intention’ and ‘goal’ are used interchangeably, and hence, within this thesis, intentions are referred to as higher-order goals, as opposed to lower-level motor intentions.

Importantly, CoMs can occur on each level of the hierarchy, and hence, can affect distal goal intentions or movements (**Figure 1.3C**). An agent might change a higher-order intention (e.g., eating pasta instead of pizza), but can also change the means required to implement that intention into action (e.g., ordering pizza delivery instead of making the pizza oneself). According to the principle of motor equivalence (Hebb, 1949), changing movements associated with the same intention does not change the outcome of an action (pizza). By contrast, when changing the intention, action outcomes change (pizza vs. pasta). Hence, CoM on a higher hierarchical level has different consequences from CoM on a lower level. Furthermore, CoM on each level may depend on different mechanisms and pieces of information. As mentioned above, lower-level movements may be strongly guided by sensorimotor information and motor costs associated with a given movement, whereas goals may more strongly depend on endogenous factors. Hence, a change in sensorimotor information (e.g., available kitchen equipment) can trigger a Change of Movement, whereas endogenous changes (e.g., change in food preferences) may trigger Changes of Intention. Crucially, however, due to reciprocal connections between goals and movements (Cisek, 2012), CoM on one level of the hierarchy might trigger changes on the other level. That is, if goals change, typically movements need to be changed (kneading dough for pizza vs. boiling water to cook pasta). More interestingly, new information obtained on the motor level may also inform changes in higher-order goals. In particular, costs associated with movements may drive changes in the goal itself. For example, if both means of obtaining pizza are costly (e.g., effort of kneading pizza dough vs. long delivery time for pizza), one might choose to cook pasta instead.

Hence, CoM about abstract goal intentions may not be completely independent from CoM about motor intentions and vice versa. Yet, movements vs. goals have traditionally been studied in separation. Research on movements has typically focused on very basic motor aspects of actions, such as movement kinematics and motor control in simple reaching tasks, without requiring decisions about higher-order goal intentions (e.g., Wolpert & Ghahramani, 2000). Conversely, research on goals has focused on abstract voluntary intentions with respect to personal health-related or professional goals, regardless of low-level motor aspects (e.g., Gollwitzer & Oettingen, 2012). In the following section, the two lines of research will be briefly reviewed with a specific focus on studies that have investigated changes on the level of movements or goals, respectively.

1.4.3 Changing movements

A large body of research suggests that the motor system is highly flexible, allowing for fast and efficient changes between alternative movement commands. This is typically measured using double-step reaching tasks (e.g., Goodale, Pélisson, & Prablanc, 1986; Buch, Mars, Boorman, & Rushworth, 2010) or cued switch paradigms (e.g., Nachev, Rees, Parton, Kennard, & Husain, 2005; Fleming et al., 2009; Obhi, Matkovich, & Chen, 2009). These paradigms have in common that participants initially prepare (or execute) one movement, but then receive an external cue that requires them to switch to an alternative movement. For example, in double-step tasks, participants have to reach for a target. After having initiated a movement towards a given target, the target occasionally changes its location, requiring participants to generate an updated motor command to change the ongoing movement. Hence, this is a sensorimotor change, which is in some way similar to CoM in the RDM task. That is, based on new sensory information (target location/dot-motion direction), a switch to an alternative motor command is required. However, double-step reaching tasks minimise perceptual decision-making demands and focus more strongly on aspects related to motor re-programming.

Changing movements requires updates of motor commands in primary motor cortex, which in turn relies on dynamic re-programming of motor plans in a network of areas including pre-SMA, premotor cortex, inferior frontal gyrus and basal ganglia (Wise & Mauritz, 1985; Leuthold & Jentzsch, 2002; Nachev et al., 2005; Buch et al., 2010; Neubert, Mars, Buch, Olivier, & Rushworth, 2010; Pastor-Bernier, Tremblay, & Cisek, 2012; Kaufman et al., 2015; Roberts & Husain, 2015; Saberi-Moghadam, Ferrari-Toniolo, Ferraina, Caminiti, & Battaglia-Mayer, 2016). The mechanisms through which these areas drive changes in motor output involve both 1) inhibitory activity that cancels an initial motor plan and 2) excitatory activity that initiates the new motor plan (Mars, Piekema, Coles, Hulstijn, & Toni, 2007; Buch et al., 2010). Interestingly, it has been shown that the very same neural circuits in premotor cortex that programmed an initial response during motor planning are also involved in changing motor plans later on – when target locations change before movement onset (Wise & Mauritz, 1985), or even during ongoing movement execution when online changes are necessary (Pastor-Bernier et al., 2012; Kaufman et al., 2015). This indicates a remarkable continuity of the processes that shape movements as they evolve.

Reprogramming of movements incurs a cost, resulting in response slowing and larger P3 amplitudes in the EEG when a switch from one motor plan to another one is necessary (Fleming et al., 2009; Orban de Xivry & Lefèvre, 2016). However, the motor system has several mechanisms in place that make motor switches as efficient as possible. For example, under target uncertainty, labile motor plans are generated, which can be reprogrammed more flexibly to accommodate new motor commands (Gallivan, Bowman, Chapman, Wolpert, & Flanagan, 2016). Similarly, when motor intentions are generated endogenously, they are kept more flexible than when they are instructed, further facilitating switching (Fleming et al., 2009). Additionally, the motor system operates in a highly parallel manner where alternative movement representations can be activated simultaneously (Jentzsch, Leuthold, & Ridderinkhof, 2004; Cisek, 2007; Stewart et al., 2014; Gallivan et al., 2015). Such parallel motor representations have been observed in dorsal premotor cortex (Cisek & Kalaska, 2002, 2005; Pastor-Bernier & Cisek, 2011), posterior parietal cortex (Baldauf, Cui, & Andersen, 2008; Cui & Andersen, 2011) and anterior intraparietal area (Baumann, Fluet, & Scherberger, 2009; Gallivan & Wood, 2009). Once a movement has been initiated, alternative movement representations remain activated, even when the action alternative is not available anymore in the external environment (Filevich & Haggard, 2013). This suggests that the motor system does not only represent a single movement that is currently selected for execution, but instead, maintains representations of counterfactual motor actions that are available in a current context. This in turn can facilitate switches between different movements after action onset (Fleming et al., 2009).

1.4.4 Changing goal intentions

In paradigms measuring changes of movement, action goals are typically relatively basic (e.g., reaching the target) and remain constant throughout the task. Hence, these studies have not addressed why, when and how people change higher-order abstract goals. Instead, goal representations have often been studied in the context of social and motivational psychology, where distal intentions are assumed to be of high personal or social relevance (Gollwitzer & Oettingen, 2012). For example, people may intend to quit smoking, or pursue a certain career. The stability of such distal goals may directly depend on the strength of the intention to reach a given goal (Ajzen, 1991). However, as Ajzen's 'theory of planned behaviour' states: People do not always act according to their own goals – even when they have strong intentions – because they may experience a lack of perceived control over their behaviour, or they can encounter "intervening events [that] may produce changes in intentions" (Ajzen, 1991, p. 185).

Indeed, successfully pursuing a distal intention over time requires ‘shielding’ that goal from alternative competing goals and other factors that may hinder goal attainment, such as distracting stimuli or temptations (Mischel, 1974; Gollwitzer & Oettingen, 2012). Gollwitzer (1999) proposed that goal shielding can be achieved through ‘implementation intentions’, i.e., specification of concrete if-then plans. Implementation intentions are conceptually similar to proximal/motor intentions – that is, they formulate specific actions that are required to reach a given goal. Importantly, Gollwitzer suggested that planning these actions in advance facilitates goal-directed responses when encountering a critical situation. For example, the goal to quit drinking alcohol is more likely to be achieved when having pre-planned what to order at the bar or how to respond when being offered a drink. This idea has been supported by a large range of experimental evidence showing that implementation intentions can help to reduce alcohol consumption (Armitage, Rowe, Arden, & Harris, 2014), promote healthy and sustainable eating habits (Adriaanse, Vinkers, De Ridder, Hox, & De Wit, 2011; Loy, Wieber, Gollwitzer, & Oettingen, 2016), increase physical activity (Bélanger-Gravel, Godin, & Amireault, 2013), break unwanted habits (Webb, Sheeran, & Luszczynska, 2009) or reach other long-term behavioural goals (for a review, see Wieber, Thürmer, & Gollwitzer, 2015). Importantly, this supports the idea of reciprocal interactions between decisions about *what* to do and *how* to do it (**Figure 1.3B–C**), in that early specification of lower-level plans can affect higher-order abstract goals.

Research on goal attainment usually focuses on scenarios where goal pursuit is the optimal behaviour. In fact, changing or ‘giving up’ on a goal in these scenarios is viewed as a failure of self-control (Mischel, 1974; Steimke et al., 2016) or ‘weakness of the will’ (Gollwitzer, 2014). However, adaptive behaviour requires a balance between stability and flexibility of intentions, where abandoning an initial goal can sometimes be advantageous, for example, to prevent escalation of commitment to a costly course of action (Staw, 1981). Additionally, failure to deactivate goals upon completion can cause interference with new goals (Anderson & Einstein, 2017; Walser, Goschke, Möschl, & Fischer, 2017).

Hence, the ability to disengage from one's own goals may indicate flexibility, rather than weakness, of the will. Accordingly, 'goal-shifting' may be related to more general mechanisms underlying flexible cognitive control, such as in task-switching, mental set-shifting, or belief updating (Miyake et al., 2000). For example, in task-switching paradigms, participants have to switch forth and back between two concurrent task goals, such as adding vs. subtracting two numbers. Similarly to switching between alternative motor commands, switching between tasks causes performance costs, including slower RTs and higher error rates on switch compared to non-switch trials (Allport, Styles, & Hsieh, 1994; Kiesel et al., 2010). While changes in movements largely rely on brain areas closely connected to motor areas, task switching additionally recruits brain areas involved in abstract task and rule representations, such as dorsolateral and medial prefrontal cortex (Gu et al., 2007; Hyafil, Summerfield, & Koechlin, 2009; Schuck et al., 2015).

Many psychiatric and neurological conditions are associated with imbalances in goal flexibility vs. stability (Goschke, 2014). For example, ruminative tendencies typically observed in depression are associated with reduced flexibility in goal-shifting tasks, but improved performance in tasks that require goal maintenance (Altamirano, Miyake, & Whitmer, 2010). Similarly, obsessive compulsive disorder (OCD) is associated with a high degree of rigidity, as indicated by repetitive and persistent thoughts and behaviour (Gu et al., 2007; Meiran, Diamond, Toder, & Nemets, 2011). In both depression and OCD, rigidity in task-switching paradigms is correlated with reduced engagement of anterior PFC (Remijnse et al., 2013). By contrast impulsivity is associated with a tendency to act before sufficient evidence for a given action has been accrued (Frank, Samanta, Moustafa, & Sherman, 2007), which may also increase the likelihood to switch to an alternative action when new stimuli are encountered. For example, impulsivity in attention deficit hyperactivity disorder (ADHD) or Parkinson's disease, is related to increased behavioural variability (Hauser, Fiore, Moutoussis, & Dolan, 2016), reduced long-term goal pursuit and 'distractibility', which can be improved through implementation intentions (Gawrilow, Gollwitzer, & Oettingen, 2011). Furthermore, in Parkinson's disease, administration of dopaminergic medication increases cognitive flexibility, but at the same time, increases impulsivity (Cools, Barker, Sahakian, & Robbins, 2003), suggesting that cognitive and behavioural flexibility are subject to a common underlying neural mechanisms that may rely on the dopaminergic system (Durstewitz & Seamans, 2008). Hence, by studying the mechanisms underlying changes in goals, important insights can be gained that are relevant with regard to disturbances of the mechanisms that govern the balance between flexibility vs. stability, and can cause impairments in several mental disorders.

1.4.5 Challenges of studying CoM in voluntary action

According to the hierarchical models reviewed above, the distinction between different types of CoM in voluntary action seems essential. Hence, when measuring CoM, we need to carefully specify what type of CoM is captured – i.e., changes of motor intentions and/or changes of distal intentions. Most previous studies have exclusively focused on either sensorimotor changes, or changes about higher-order goal intentions, respectively. By contrast, less is known about how exactly information is integrated across both levels of the hierarchy, and how dynamic changes on one level affect changes on the other level. In **Chapter 2** of this thesis, a new paradigm will be introduced that allows us to dissociate sensorimotor action updates from changes in higher-order distal intentions, and investigate their reciprocal relations.

In addition to defining *what* CoM is measured, we need to consider *how* a given CoM is triggered: Endogenously or exogenously. By definition, voluntary actions involve an endogenous decision component. It has been proposed that endogenous decisions are the result of accumulation of ‘internal’ evidence, similar to accumulation of sensory evidence in perceptual choice (Schurger et al., 2012; Bode et al., 2014; Khalighinejad, Schurger, Desantis, Zmigrod, & Haggard, 2018). Consequently, CoM about endogenous decisions may be driven by changes in accumulated internal evidence. However, we have little to no experimental control over such internal signals. While in RDM tasks, experimenters can manipulate precisely how much evidence the decision maker gets in favour of each choice alternative, this is not possible for endogenous decisions. In fact, voluntary actions are sometimes described as being ‘spontaneous’ or ‘freely capricious’ (Libet et al., 1983). To solve this, previous studies investigating changes of voluntary intentions have largely focused on tasks in which behavioural switches were instructed by external cues – allowing for direct experimental control over switch rates (Fleming et al., 2009; Obhi, Matkovich, & Chen, 2009). However, externally-instructed CoM requires changing from an internal to an external mode of action selection. Hence, in these situations the final action is exogenous rather than endogenous. While these studies are an important step towards a better understanding of the flexibility of actions, we also need to consider scenarios in which the decision to reverse or pursue an initial intention is itself endogenous. In this thesis, a new approach will be introduced in order to provide new insights into the continuous nature of voluntary actions where both the initial action selection as well as later action updates are endogenous. More specifically, in all experiments reported in this thesis, decision reversals are induced by noisy or changing external information after participants have made an initial voluntary decision. Crucially, in contrast to previous studies, these external changes do not contain an explicit instruction about whether to stay or to switch. Instead, changes in external information can provide a new context triggering re-evaluation of an initial decision, which may or may not cause a CoM. In that sense, CoM can be seen as a matter of updating intentions and actions based on new contextual information.

1.5 Summary & thesis overview

In summary, systematic investigation of CoM is relatively sparse, and to date, has exclusively focused on either perceptual or value-based decisions. While previous studies have provided important evidence showing that people constantly evaluate information and can adjust their actions accordingly, endogenous components of action selection have often been neglected. Hence, there are several open questions about the continuous processes that shape voluntary action, and studying Changes of Mind may provide a unique opportunity to answer some of these questions. In particular, we propose that investigating how intentions are modified can provide important insights into what intentions are and how they shape voluntary actions.

This thesis introduces several innovations in method, and reports novel findings that advance the scientific understanding of the dynamic processes underlying volition. In **Chapter 2** of this thesis, a new behavioural paradigm will be proposed that allows us to measure when people change a voluntary intention, and/or change the movements required to implement the intention into action. Our results show that the need to change an ongoing movement can sometimes trigger a change in the intention itself, and these dynamic updates in turn depend on the strength of the initial intention and trade-offs with its associated motor costs. In **Chapter 3**, an attractor network model will be introduced that can capture these different types of CoM by dynamically integrating multiple action-relevant sources of information that can either cause a Change of Movement or a Change of Intention. In **Chapter 4**, an fMRI study will be reported that measured the neural dynamics through which endogenous intentions are integrated with changing external information. This study revealed dynamic neural codes in a fronto-parietal network, which enables flexible updates in higher-order voluntary intentions. Finally, in **Chapter 5**, pursuit of voluntary intentions was studied in patients with post-stroke fatigue, providing evidence for reduced perseverance in these patients when goal pursuit required continuous investment of effort.

Chapter 2.

Two ways to change your mind – Effect of intentional strength and motor costs on Changes of Intention

2.1 Introduction

The aim of the current chapter is to investigate the dynamic mechanisms underlying changes in a) higher-order goal intentions vs. b) lower-level movements. As mentioned in the general introduction, voluntary actions require abstract goals to be translated into specific movements. In many scenarios, multiple goals may be available and each goal can be associated with several movement alternatives, requiring decision-making processes on each level of the hierarchy to select an appropriate action (Cisek, 2012). Movement selection largely relies on external sensory information (e.g., location of goal object), whereas goal intentions may be more strongly guided by endogenous decisions. On each level, information can change dynamically, suggesting two dissociable types of CoM during voluntary action (**Figure 1.3C**): 1) Changes of Movement that represent changes in *how* a goal is implemented into action without changes in the goal itself, and/or 2) Changes of Intention that correspond to changes in *what* goal is selected.

Changes of Movement may occur when new sensory information from the environment is obtained, requiring the inverse model to compute a new motor command (Kawato, 1999; Wolpert & Ghahramani, 2000). This is similar to CoMs that have previously been reported in the RDM task (Resulaj et al., 2009; Moher & Song, 2014; van den Berg et al., 2016). That is, when dot-motion coherence is low (sensory evidence is weak and noisy), participants occasionally initiate a movement towards one target, but later on redirect the ongoing movement towards the other target. This is a sensorimotor change, suggesting that low-level aspects of action selection are updated continuously and dynamically. Furthermore, it has been shown that when the motor costs of corrective movements are high (e.g., far target distance), these CoMs occur less frequently (Burk et al., 2014; Moher & Song, 2014). Hence, Changes of Movement are directly informed by sensory information and cost information associated with a given movement.

However, previous studies have not captured changes in higher-order voluntary goal intentions – henceforth referred to as Changes of Intention. Such changes regarding higher-level voluntary intentions should directly depend on the strength of the initial intention (Ajzen, 1991; Sheeran, Webb, & Gollwitzer, 2005; Fleming et al., 2009). That is, the stronger the initial intention is, the less likely a person should be to reverse the intention later on. Intentional strength in turn might depend on choice values (Rushworth, 2008), such as a strong preference for one goal over another, or confidence regarding the internal decision (Folke et al., 2016). Yet, few goals are worth pursuing at *any* cost. Specifically, achieving a goal often involves effort- or time-related motor costs (e.g., Treadway, Buckholtz, Schwartzman, Lambert, & Zald, 2009; Shadmehr et al., 2010) that may induce Changes of Intention. Finally, the probability of pursuing a distal intention may depend on the extent to which the intention has been translated into specific action plans (‘implementation intentions’, Gollwitzer, 1999; Achtziger, Gollwitzer, & Sheeran, 2008). That is, intentions might be less likely to be changed once they have been translated into precise motor commands by the inverse model. Importantly, effects of motor costs and motor planning on Changes of Intention would suggest that movement-related information is continuously integrated with higher-order intentions to inform dynamic decision reversals across both levels of the hierarchy.

Finally, while previous studies have captured *objective* changes in actions induced by decision reversals (e.g., changing movement trajectories), effects of CoM on our *subjective* Sense of Agency (SoA) have not previously been measured. Changing an ongoing movement could reduce SoA by making actions feel ‘dysfluent’ (Wenke, Fleming, & Haggard, 2010; Sidarus & Haggard, 2016). Whether changing an endogenous, higher-order intention would affect SoA is less clear. Previous research suggests that distal action goals boost SoA (Metcalfe, Eich, & Miele, 2013; Vinding, Pedersen, & Overgaard, 2013). Consequently, deviations from initial intentions might decrease SoA. However, on an alternative view, changing an intention might require additional voluntary control, or a stronger exertion of will (Ach, 1935), and thus, people may experience stronger SoA when going against, or ‘vetoing’ an initial intention (Libet, 1999). Finally, reconstructive theories view conscious intentions as mere retrospective confabulations (Wegner, 2002). People appear to experience actions as intentional, even when they were not part of an initial plan, or are not even their own (Wegner et al., 2004; Aarts et al., 2005). This view would predict that reversals of endogenous intentions should not affect SoA at all. Hence, the link between Changes of Intention and SoA can provide important new insights into the role of voluntary intentions in shaping our actions and the conscious experience of control we perceive over them.

In the current study, participants performed a novel version of the RDM task in which they had to integrate the perceptual decision about dot-motion direction (left/right) with an endogenous intention about which colour to paint the dots. Based on previous studies, we expected to observe perceptual CoM regarding the dot-motion direction (e.g., Resulaj et al., 2009). Importantly, the current paradigm allowed us to differentiate between trials in which perceptual updates only resulted in updates of the movement (Change of Movement), or additionally, an update of the initial colour intention (Change of Movement + Intention). In two experiments, we tested the hypotheses that the frequency of Changes of Intention is higher when initial intentions are weak (Exp. 1), when the motor cost of intention pursuit is high (Exp. 2) and when advance motor preparation is not possible (Exp. 1 and 2). Additionally, in both experiments, subjective reports of SoA were obtained to investigate the effect of CoM on the phenomenology of action.

2.2 Experiment 1

2.2.1 Methods

2.2.1.1 Participants

The study was approved by the UCL Research Ethics Committee. Participants provided written informed consent prior to the study. Based on pilot data (*N* = 13), a power calculation was conducted to determine the sample size required to obtain a percentage of CoM that is significantly greater than zero across participants. With an observed effect size of *d* = 0.67, α = .05, and β = .8, the analysis resulted in *N* = 16. In anticipation of attrition, 21 right-handed participants were recruited through the ICN subject database. One participant did not reach the performance criterion in the training session (see below) and another participant withdrew after training. Two further participants were excluded, one due to technical issues during data collection and one due to strategic decision delay in the task (see below). The final sample consisted of 17 participants (13 female, age: *M* = 22.6 yr, *SD* = 3.1). Participants received £7.50/hour and a performance-based reward.

2.2.1.2 Apparatus and stimuli

The experiment was programmed in Matlab R2014a and the Psychophysics Toolbox (Brainard, 1997). RDM stimuli were generated using the Variable Coherence RDM code (https://shadlenlab.columbia.edu/resources/VCRDM.html). At each video frame, 7 dots were presented and displaced 3 frames later at a screen refresh rate of 60 Hz. The percentage of dots that were displaced in the same direction determined the motion coherence. The RDM stimuli were presented in a central, square aperture (4.5° x 4.5°) and motion direction (left/right) was assigned randomly for each trial. Target circles of 1.8° diameter were located at a distance of 9.6° from the centre of the screen (x = 6.0°, y = 7.5°). Target colours were blue/green/pink/orange of comparable perceived luminance. Participants were seated approximately 60 cm from a computer screen and moved a cursor to the targets using a Wacom Intuos Pro pen tablet. Movement trajectories were recorded at a sampling frequency of 125 Hz.

2.2.1.3 Colour RDM task

Participants performed an adapted version of the RDM task (**Figure 2.1**). At the beginning of each trial, participants freely chose between two colours (random pair of blue/green/orange/pink). Participants were instructed to say the chosen colour in their head, and on 10% of trials, they were prompted to say their choice out loud. Once they had chosen a colour, they clicked on a central fixation cross and after a random delay of 700–1000 ms, the RDM stimulus and 4 targets, 2 of each colour, appeared. Using the touch pad, participants then had to move the cursor to the target that matched both the perceived dot-motion direction and their endogenous colour choice (e.g., left blue target). In most trials, targets of the same colour were arranged diagonally – e.g., the top-right and bottom-left targets were blue while the top-left and bottom-right targets were green, or vice versa (randomly assigned).

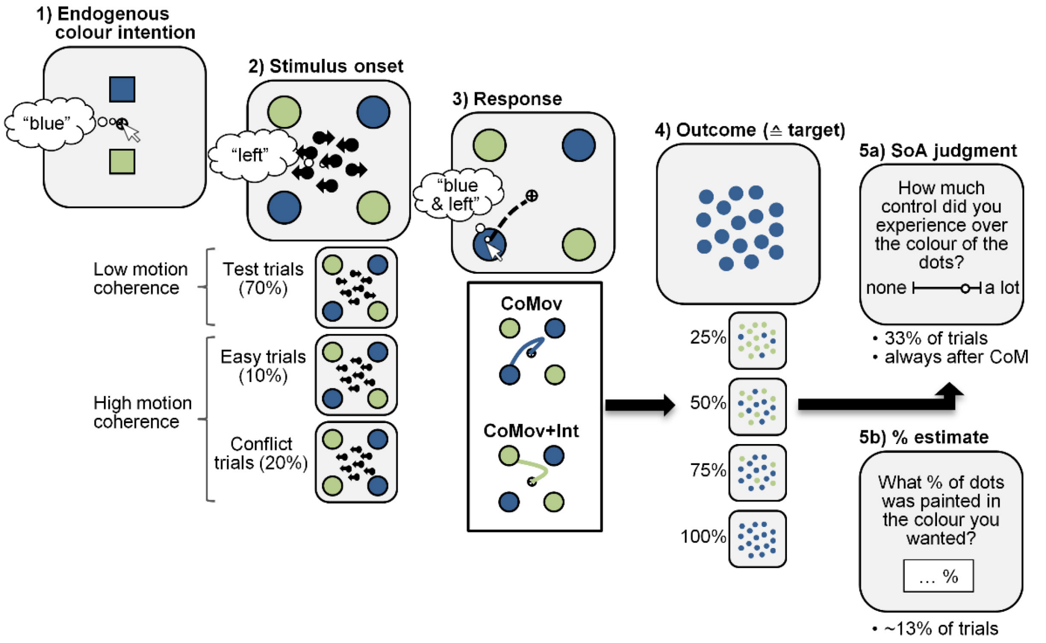

Figure 2.1. Colour RDM task. Participants generated an endogenous colour intention (1) that had to be integrated with the sensory input of the RDM stimulus (2). Responses were indicated by moving the cursor to the target that matched both the colour intention and dot-motion direction (3). Continuous movement trajectories were measured during response execution allowing for online classification of 'Changes of Movement' (CoMov) and 'Change of Movement + Intention' (CoMov+Int). Once participants reached the target, 25/50/75/100% of the dots were painted in the colour of the hit target (4). On some trials, participants were asked to provide SoA judgements (5a) or to estimate the percentage of dots that matched their initial colour intention (5b).

In analogy to the original RDM task, CoM was defined as a decision reversal regarding the dot-motion direction (e.g., an initial response towards a target on the right followed by a switch to a left target). Importantly, the current paradigm allowed us to differentiate between trials in which perceptual CoM only resulted in 1) a Change of Movement while the initial colour intention was pursued (*CoMov*; e.g., switch from right-blue to left-blue target), or 2) a Change of Movement that *additionally* involved a Change of Intention (*CoMov+Int*; e.g., switch from right-blue to left-green target). These two types of CoM were discriminated online based on movement trajectories: If the cursor position exceeded 10% of both the x- and y-distance towards a given target, but then ended in the diagonally opposite target (of the same colour), the trial was classified as CoMov. If it ended in the horizontally neighbouring target (of different colour), it was classified as a CoMov+Int. Due to the diagonal target arrangement, intention pursuit (CoMov) was associated with longer movement paths than switching to the neighbouring target of different colour (CoMov+Int). Hence, when participants changed their mind about the dot-motion direction, they could save motor costs by switching to the target that did not match their initial colour choice.

Importantly, while participants were instructed to generate colour intentions at trial start, they were not explicitly told that they had to *maintain* their initial colour choice throughout the trial. In particular, participants did not receive any instructions as to whether they should stick with their initial colour intention when they changed their mind about the dot-motion direction. Instead, in trials with perceptual CoM, the decision between a) switching to the other target of the same colour or b) switching to the nearby target of different colour was endogenous. This enabled us to capture spontaneous Changes of Intention. Furthermore, the importance of pursuing colour choices was ambiguous on purpose to allow us to capture inter-individual differences in intentional strength – that is, the importance, or weight, a given participant assigned to the colour choice relative to the perceptual choice. For example, a participant who considered colour choices to have little task relevance, would generate weaker intentions, and should be less likely to stick with an initial colour choice when facing the higher cost of colour pursuit in CoM trials. By contrast, a participant who considered perceptual and colour choices to be of equal importance would be more likely to pursue an initial colour choice when updating an ongoing movement based on a perceptual decision reversal. Finally, note that there was no reason for participants to switch to another colour unless they had changed their mind about the dot-motion direction, and hence, switched between left/right targets. Consequently, switches between the two targets of different colour on the *same side* of the screen (i.e., vertical switches) were not considered real Changes of Intention within the context of the current task.

500 ms after participants reached a target, 25/50/75/100% of the dots from the last 3 video frames were presented in the colour of the hit target (1 sec). The remaining dots were shown in the other colour option of that particular trial. In 33% of trials and after every CoM, participants were then asked "How much control did you experience over the colour of the dots?" (SoA judgment), which they replied to on a visual analogue scale ranging from "none" to "a lot". In 20% of the remaining trials (i.e., ~13%), they were asked "What percentage of dots was painted in the colour you chose?". The outcome judgments were included to motivate participants to pay attention to the action outcomes, and hence, render colour choices more meaningful within the context of the task. However, given that outcome judgments never appeared after CoM (which was always followed by SoA ratings), we did not further analyse them. Importantly, after CoM, the percentage of dots painted in the chosen colour was always 50% to avoid that differences in action outcome confound effects of CoM on SoA.

Trials varied according to three conditions differing in coherence of the RDM stimulus and/or the target arrangement. In *test trials* (70%), motion coherence was low, with the precise value being determined individually prior to the experiment to ensure around 60% perceptual choice accuracy. Furthermore, in these trials, targets of the same colour were presented in diagonally-opposite corners to induce higher motor costs for CoMov (intention pursuit) compared to CoMov+Int (Change of Intention) when a perceptual CoM occurred. In *easy trials* (10%), targets were also arranged diagonally, but motion coherence was high (80% coherence) rendering the perceptual decision very easy. Finally, in *conflict trials* (20%), motion coherence was as high as in easy trials (80%), but both targets of the same colour were on the same side of the screen. Consequently, in roughly half of the conflict trials, there was a conflict between intentional colour choice and dot-motion direction (e.g., a participant had chosen blue, both blue targets appeared on the right side, but the dots moved to the left). In this case, participants were instructed to respond according to the dot motion, and hence, move to a target that did not match their own colour choice. Thus, perceptual choices took priority over colour intentions.

As mentioned above, in 90% of trials, participants were *not* asked to verbalise their colour choice at trial start, and colour choices were inferred from movement trajectories instead (e.g., if the movement was initiated towards a green target, a choice for green was inferred). This minimised demand characteristics that might discourage participants from changing their initial colour choice when having to say it out loud. Yet, this raises the question whether participants indeed chose a colour at trial start (frame 1, **Figure 2.1**), or instead, delayed their decision to stimulus onset (frame 2, **Figure 2.1**). The conflict trials allowed us to address this question: If participants generated initial colour intentions, colour-motion mismatches would induce response conflict. Consequently, RTs and error rates would, on average, be higher in conflict than easy trials even though the perceptual decision was equally easy in both conditions. These performance costs would be driven by trials in which conflict occurred. However, the inference is based on mean performance, and does not require explicitly identifying which specific trials involved conflict and which did not. Note that no response costs would be observed if participants did not make colour choices at trial start since, in that case, participants would simply respond based on dot motion direction without any conflict induced by colour choices. Thus, the average performance cost in conflict relative to easy trials served as an indicator of 1) whether, overall, participants generated initial colour intentions and 2) how strong colour intentions were for each individual as indicated by the degree of their performance cost in conflict compared to easy trials.

In 50% of trials within each condition, targets were presented immediately after colour choice (early targets). In the other 50%, they appeared simultaneously with the dots, i.e., 700–1000 ms after colour choice. Early targets allowed for advance motor preparation, i.e., participants could pre-activate the motor commands associated with the two targets corresponding to their chosen colour. For example, if a participant chose blue, and the blue targets appeared in the top-right and bottom-left locations, movements towards these targets could be prepared before dot-motion onset. This was not possible for late targets, in which no information about target locations was available before dot onset.

After a short practice block, participants were given 1h to complete as many trials as possible (*M* = 358.2, *SD* = 37.5). To motivate participants to be fast and accurate, they won 1 p for every correct perceptual choice. After each block of 30 trials, participants received feedback about their perceptual choice accuracy. There was no trial-by-trial error feedback, but a "too slow!" message was shown if response initiation exceeded a certain deadline or if the target was not reached within 3 sec after response initiation. In order to induce fast response initiation, the response deadline was initially 1000 ms, but decreased by 50 ms after every block if a participant had less than 10% trials with CoM and less than 15% misses. Reaction times (RTs) were defined as the point in time at which the cursor left a central circle of 1.1° diameter, at which point the RDM stimulus disappeared. Previous studies showed that, due to sensorimotor delays, CoM occurs even when the external stimulus is removed at action onset (Resulaj et al., 2009).

2.2.1.4 Training session

Participants had to pass a training session the day before the actual experiment. They were trained on the original 2-choice RDM task until they reached 70% accuracy in trials with 35% motion coherence. One participant failed to reach the criterion and was not invited for the experimental session. All other participants performed 160 additional trials with randomly varying motion strength (5–65% coherence) in order to obtain stable performance. Finally, an alternating staircase procedure was administered (see Moher & Song, 2014 for details) to determine the motion coherence at which a participant’s accuracy was ~60% (coherence: *M* = 11.8% *SD* =

4.1%). This level was chosen to maximize the frequency of perceptual CoM (Resulaj et al., 2009). During training, trial-by-trial error feedback (red dots) was provided.

In both the training and test session, participants were instructed to fixate the central cross throughout each trial. Electrooculography was used to monitor eye movements and, whenever necessary, participants were reminded to keep fixation.

2.2.1.5 Data analysis

Movement trajectories were analysed in Matlab R2014b. All trials that had been classified as CoM during the task were inspected individually. Trials with double CoM (0.56%) or initial movement trajectories that were not clearly directed towards one of the targets (e.g., circular trajectories or vertical movement initiation; 0.13% of trials) were excluded from all analyses.

Furthermore, velocity profiles were analysed. Note that participants might have initiated a response in any direction in order to comply with the short response deadline, subsequently choosing a target only after having left the home position. In that case, curvature away from the initial trajectory would not be a CoM, as the initial trajectory would not reflect commitment to a specific target. Completely excluding any element of strategic delay for individual trials is difficult. However, frequent stopping shortly after movement initiation even in trials with straight trajectories would clearly indicate strategic decision delay. One participant stopped in 28.6% of straight trajectories, with an average stop duration of 351.2 ms and was therefore excluded from all analyses. Such stopping was rare in all other participants (stop frequency: $M = 7.4\%$[1], $SD = 5.2\%$; stop duration: $M = 157.9$ ms, $SD = 40.8$ ms).

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[1] Note that this percentage is highly comparable to the percentage of trials with CoM, and hence, can be attributed to decision uncertainty and vacillation, rather than strategic decision delay.

Given the small percentage of trials with CoM, mixed-effects logistic regression (MELR) models were used for analyses of CoM frequency (Bagiella, Sloan, & Heitjan, 2000). Model fitting was performed using Maximum-likelihood estimation with the lme4 package (Bates, Maechler, Bolker, & Walker, 2014) in R (R Development Core Team, 2015). Binomial models with a logit link were specified. To investigate CoM, two types of binary outcome variables were analysed: Either no-CoM (0) vs. CoM (1) for analyses of overall frequency of perceptual CoM (regardless of type of CoM), or CoMov (0) vs. CoMov+Int (1) for analyses of different types of Change of Mind within CoM trials. Participants were modelled as random intercepts. Including random slopes in addition to random intercepts did not change any of the results and only one of the models performed significantly better when random slopes were added. Hence, all models reported contain random intercepts only. Parameter estimates *b* and 95% profile confidence intervals are reported in log-odds space, and odds ratios (OR) are reported to facilitate interpretation. Statistical inference was performed by comparing models with vs. without a given fixed effect using likelihood-ratio tests. Satterthwaite approximation for degrees of freedom was used (Kuznetsova, Brockhoff, & Christensen, 2015). All other analyses (comparison of means with ANOVAs/*t* tests) were performed in IBM SPSS Statistics for Windows, version 21 (Corp, Released 2012). For RT analyses, only correct trials within +/- 3 SD of the individual's average RT in each condition were included.

2.2.2 Results

2.2.2.1 Task performance

In test trials, perceptual choice accuracy was 56.6% (*SD* = 9.1%), which did not differ significantly from the target accuracy of 60% ($t(16) = 1.54$, $p = .144$, Cohen's $d = 0.37$). Crucially, perceptual choice accuracy was significantly worse in test trials than in easy trials ($M = 93.4\%$, $SD = 7.0\%$, $t(16) = 20.13$, $p < .001$, $d = 4.88$) and RTs were significantly slower in test ($M = 570.5$

ms, *SD* = 58.3 ms) than in easy trials (*M* = 534.2 ms, *SD* = 41.5 ms, $t(16) = 3.99$, $p = .001$, $d = 0.97$).

2.2.2.2 Changes of Mind

In order to investigate how difficulty of the perceptual decision affected CoM, we first analysed the effect of trial condition (easy/test) on the overall frequency of perceptual CoM (no-CoM/CoM), regardless of whether it was a CoMov or CoMov+Int. An MELR model with trial condition as a fixed effect (dummy-coded with easy trials serving as baseline) showed that trial condition had a significant effect ($\chi^2(1) = 45.69$, $p < .001$), with the likelihood of CoM being higher in test compared to easy trials ($b = 1.84$, 95% CI [1.19, 2.63], OR = 6.27).

Crucially, within CoM trials, two different types of CoM can be distinguished: A switch between diagonally opposite targets (of the same colour) indicates CoMov, whereas a switch between horizontally neighbouring targets (of different colour) represents CoMov+Int. **Figure 2.2** shows single-trial movement trajectories in test trials of an individual participant. The average frequency of CoMov and CoMov+Int in test and easy trials is illustrated in **Figure 2.3A**.

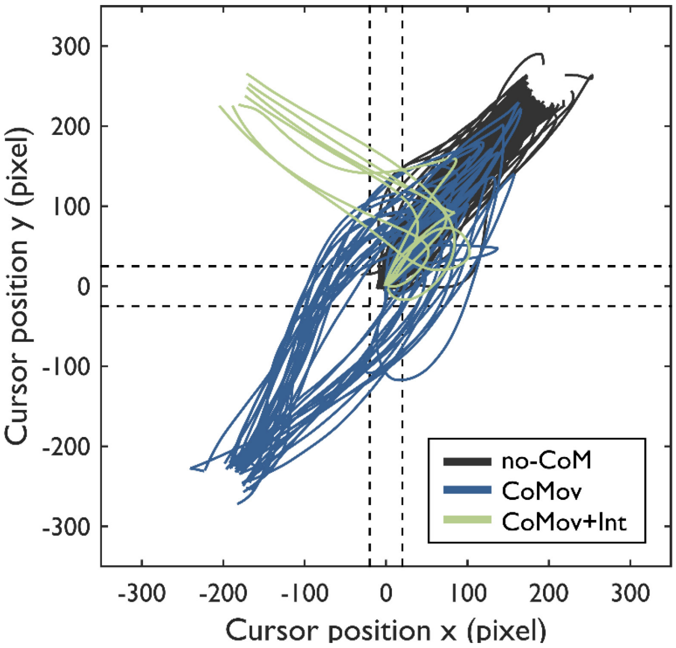

Figure 2.2. Single-trial movement trajectories in test trials. Movement trajectories of one participant are shown. For illustration purposes, trajectories were mirrored such that the initial movement was always directed towards the upper right target, but ended in a different target depending on the class of movement trajectory (black: no Change of Mind; blue: Change of Movement; green: Change of Movement + Intention). Dashed lines indicate the coordinates that were used as criteria for CoM classification.

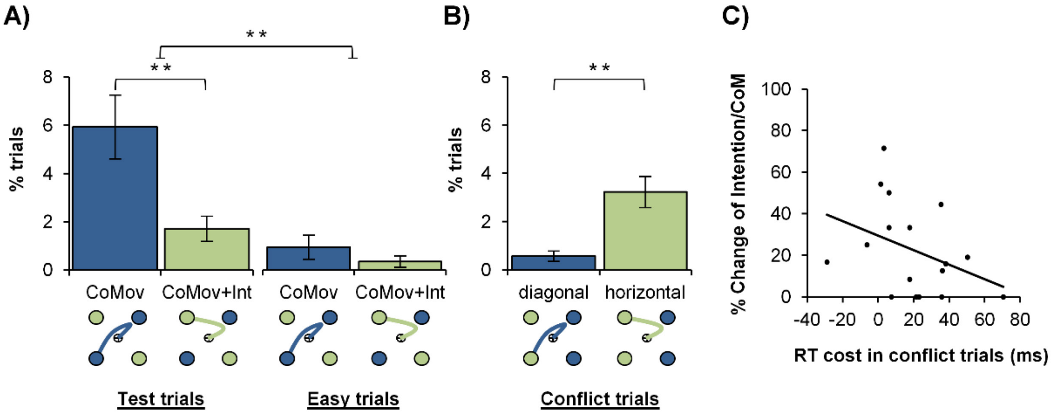

Figure 2.3. Changes of Mind in the colour RDM task. A) Percentage of trials classified as 'Changes of Movement' (CoMov) and 'Change of Movement + Intention' (CoMov+Int) in test and easy trials. B) Percentage of conflict trials with diagonal and horizontal movement corrections of partial errors that were induced by mismatches between colour intentions and dot-motion direction (mean +/- 1 SEM; ** $p < .01$, $N = 17$). C) Correlation across participants between RT costs in conflict trials and frequency of Changes of Intention (relative to overall percentage of CoM).

In order to investigate the relative frequency of CoMov vs. CoMov+Int, only trials with CoM were included in an MELR, with CoMov (0) vs. CoMov+Int (1) as outcome variable and trial condition (easy/test) as a fixed effect. The effect of trial condition was not significant (b = -0.13, 95% CI [-1.93, 1.67], OR = 0.88, $\chi^2(1) = 0.02$, p = .890), suggesting that perceptual uncertainty only affected whether or not a perceptual CoM occurred, but did not affect whether participants changed their mind about their colour intention. Interestingly, in test trials, CoMov was more frequent (M = 5.9%, SD = 5.5%) than CoMov+Int (M = 1.7%, SD = 2.2%), as indicated by an intercept that was significantly lower than 0 (b_0 = -1.56, 95% CI [-2.47, -0.89], OR = 0.2, z = -4.42, p < .001). Hence, when changing a movement based on new sensory evidence, participants pursued their colour intention more often than switching to the target of different colour, despite the extra motor costs of diagonal compared to horizontal movement adjustments. A similar trend was observed in easy trials, although overall CoM frequency was low in this condition and the intercept was not significantly different from 0 (b_0 = -1.43, 95% CI [-3.30, 0.43], OR = 0.24, z = -1.50, p = .132).

2.2.2.3 Did participants generate initial colour intentions?

The fact that, overall, participants were reluctant to giving up their colour intentions suggests that they assigned a relatively high importance to colour choices in the task. Additionally, we analysed conflict trials to further investigate whether participants indeed generated colour intentions at trial start, even on trials where they did not have to verbalise their choice. In conflict trials, perceptual choice accuracy was descriptively lower (M = 90.5%, SD = 7.2%) and RTs were significantly slower (M = 549.7 ms, SD = 45.8 ms) than in easy trials (accuracy: M = 94.1%, SD = 6.8%, $t(16)$ = 2.11, p = .051, d = 0.51; RTs: M = 534.2 ms, SD = 41.5 ms, $t(16)$ = 2.51, p = .023, d = 0.61). These response costs were present even when only trials with early target onset were analysed (accuracy: M_Δ = 3.63%, SD_Δ = 7.27, $t(16)$ = 2.06, p = .056, d = 0.50; RTs: M_Δ = 29.7 ms, SD_Δ = 32.7 ms, $t(16)$ = 3.74, p = .002, d = 0.91), suggesting that the effects were not simply driven by participants being surprised about the uncommon target configuration in conflict trials. Instead, response costs in conflict trials showed that, overall, participants generated initial colour intentions, which on some conflict trials did not match the RDM direction, hence inducing response costs. Moreover, movement trajectories in conflict trials indicated that participants occasionally initiated a response towards one target, but then adjusted the movement to end in another target, similar to CoM in test/easy trials (**Figure 2.3B**). In conflict trials, movement adjustments presumably reflect partial errors in colour-motion mismatch trials. That is, participants initiated responses towards their chosen colour, but then corrected themselves to respond according to the dot motion as instructed. In line with this, an MELR, with no-CoM vs. CoM as outcome variable and trial condition (easy/conflict) as a fixed effect showed that corrective movements in conflict trials occurred significantly more often than perceptual CoM in easy trials, despite dot-motion coherence being matched in both conditions (b = 1.09, 95% CI [0.39, 1.92], OR = 2.97, $\chi^2(1) = 9.93$, p = .002). This confirms that corrections in conflict trials were not merely induced by perceptual noise, but instead, can only be explained by conflict induced by mismatches between colour intention and perceptual input.

Note that, in conflict trials, participants could adjust movements in two ways (**Figure 2.3B**) by either switching to the diagonally opposite target (similar to CoMov in test trials) or the horizontally neighbouring target (as in CoMov+Int). In an MELR with trial condition as a predictor (easy/conflict, with conflict trials as a reference level) and diagonal (0) vs. horizontal (1) movement corrections as outcome variable revealed a significantly positive intercept (b_0 = 1.74, 95% CI [0.97, 3.24], OR = 5.71, z = 3.46, p < .001), indicating an overall preference for horizontal over diagonal movement corrections in these trials. This suggests that participants were sensitive to the higher motor costs of diagonal movement corrections and preferred less costly horizontal corrections. The fact that, in test trials, participants preferred diagonal (CoMov) over horizontal (CoMov+Int) movements showed that participants were generally willing to overcome these motor costs to pursue their colour intentions when possible. However, the relative frequency of CoMov relative to CoMov+Int in test trials varied across participants (*M* = 77.4%, *SD* = 22.1%). Thus, participants may have differed in how much weight they assigned to the colour choice relative to the perceptual task, and hence, how strong their colour intentions were.

2.2.2.4 Effect of intentional strength on Changes of Intention

We tested whether participants with stronger colour intentions showed fewer Changes of Intention out of all test trials with CoM. Individuals' average response costs in conflict compared to easy trials served as an indicator of the strength of colour intention, with higher response costs indicating stronger intentions. Since only 9/17 participants made errors in conflict trials, we focused on RT costs as an indicator of the strength of colour intention. The difference in RTs in conflict–easy trials was correlated with the relative frequency of Changes of Intention out of all CoM ($\frac{\% \, CoMov+Int}{\% \, CoM}$) in test trials. As predicted, we found that, across participants, higher RT costs in conflict trials (i.e., stronger colour intentions) were associated with fewer Changes of Intention in test trials (Spearman's $\rho(15) = -.50$, $p = .043$, 95% CI [-.07, -.76]; **Figure 2.3C**).

2.2.2.5 Effect of advance motor preparation

In order to check whether the frequency of either type of CoM was affected by target onset, and hence, the time participants had to implement colour intentions into motor commands, an MELR analysis was conducted for test trials only. Including target-onset time as a fixed effect (early/late, dummy-coded with early targets as reference level) did not significantly improve model performance compared to a model with random effects only. This was true for both a model with no-CoM vs. CoM as outcome variable ($b = 0.10$, 95% CI [-0.14, 0.33], OR = 1.10, $\chi^2(1) = 0.62$, $p = .432$), as well as for a model with CoMov vs. CoMov+Int as outcome variable ($b = 0.40$, 95% CI [-0.21, 1.02], OR = 1.48, $\chi^2(1) = 1.62$, $p = .203$). This suggests that the opportunity to plan movements prior to dot motion onset did not have an effect on whether or not people changed their mind about the dot-motion direction, nor on the type of CoM they showed when changing their mind.

2.2.2.6 *Potential effect of target confusion*

One potential alternative interpretation of trials classified as CoMov+Int needs to be addressed. It is possible that participants switched to a target of different colour because their initial movement was erroneously directed towards a target that did not match their colour choice due to difficulties in target detection. In that case, curved trajectories would not represent a genuine Change of Intention, but rather a correction of an initial colour error. However, a significant number of CoMov+Int was observed across participants even in test trials with early target onset ($M = 1.37\%$, $SD = 1.85\%$, $t(16) = 3.06$, $p = .008$, $d = 0.74$), even though participants had 700–1000 ms to identify target-colour locations in these trials. Moreover, participants were rewarded based on perceptual choice only, and hence, switching between horizontal targets merely based on colour would result in a potential monetary loss. Instead, if target confusion occurred, participants should switch to the target of different colour on the *same* side of the screen (rather than to the horizontally neighbouring target). In this case the trajectory was *not* classified as CoMov+Int[2]. These vertical movement corrections were indeed observed on 3.24% of test trials ($SD = 2.56\%$) and occurred significantly more often in late- than early-onset test trials ($b = 1.18$, 95% CI [0.79, 1.59], OR = 3.25, $\chi^2(1) = 38.76$, $p < .001$). This suggests that, when participants confused target colours due to difficulties in target detection, they switched to the target of different colour that was on the same side of the screen. By contrast, switches to the horizontally

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[2] Trials with vertical movement corrections (between targets on the same side of the screen) were considered as no-CoM trials in all analyses. Excluding these trials does not change any of the results.

neighbouring target (CoMov+Int) presumably represent genuine Changes of Intention that were caused by an initial CoM about the dot-motion direction, rather than target confusion.

2.2.2.7 Effect of CoM on SoA

Trial numbers for CoM were generally low, in particular for CoMov+Int, which only occurred on ~2% of trials. Additionally, 5 participants did not show any CoMov+Int. Hence, in order to have a sufficiently large sample, the effect of CoM on SoA was analysed across Experiments 1 and 2 (see section 2.3.2.4), rather than for each experiment separately.

2.2.3 Discussion Experiment 1

In a novel paradigm, two types of CoM in voluntary action were dissociated based on movement trajectories: 1) ‘Changes of Movement’ in which participants changed decisions about exogenous stimuli, requiring them to update motor commands while still pursuing their initial endogenous intention and 2) ‘Changes of Movement + Intention’ where movement updates did not only reflect decision reversals about exogenous stimuli, but additionally, a change of the initial endogenous intention. Although the frequency of CoM was generally very low, we observed 7.6% CoM in test trials, which is clearly comparable with previous studies reporting 2–15% CoM in trials with comparable motion coherence (Resulaj et al., 2009; Moher & Song, 2014; van den Berg et al., 2016). Further, several areas of cognitive theory, e.g., memory research, rely strongly on data from infrequent errors – no doubt because errors are highly informative about the processes generating performance (Loftus, 2005). Finally, the frequency of CoM varied systematically across trial conditions. Specifically, in line with previous studies on perceptual decision reversals, we found that CoM was more frequent when sensory noise was high, and hence, when initial responses were initiated based on weak sensory evidence. Crucially, we found that the need to update an ongoing movement based on new sensory information occasionally induced a change in the higher-order goal intention, suggesting that movement reprogramming triggered a re-evaluation of the initial goal itself.

Our results further showed that the frequency of Changes of Intention was inversely related to the strength of participants' initial intentions. More specifically, some participants generated stronger colour intentions as indicated by a high performance cost under endogenous-exogenous conflict. These participants were more likely to pursue their initial intention when adjusting an ongoing movement. Inter-individual differences in intentional strength reflected the importance, or weight, participants assigned to colour choices in the task, relative to the dot-motion judgment. These differences in turn were presumably caused by differences in demand characteristics based on individuals' interpretation of the instructions (Orne, 1962), or the subjective value participants assigned to the colours (Rushworth, 2008), e.g., based on preferences for certain colours. Note that our design did not allow us to capture variability in intentional strength on a trial-by-trial basis, but rather, the strength of the colour choices throughout the task. However, intentions can vary in strength within people, and it is likely that this would affect the likelihood of a person changing an intention in a given situation (Fleming et al., 2009; Salvaris & Haggard, 2014).

In a second experiment, we manipulated the trade-off between intentions and their associated motor costs on a trial-by-trial basis by varying target distances within participants. We hypothesised that the frequency of Changes of Intention increases when the cost of pursuing the initial intention is high relative to changing the intention. This would provide more direct evidence that intention reversals can be caused by high motor costs associated with intention pursuit. Furthermore, it would establish a means to experimentally induce a higher frequency of Changes of Intention.

2.3 Experiment 2

2.3.1 Methods

2.3.1.1 Participants

Based on the same power calculation as for Experiment 1, we aimed for a sample size of 16 participants in Experiment 2. Twenty-one right-handed participants were initially invited for the experiment. Three participants did not reach the performance criterion during training and two further participants were excluded due to poor performance in the test session (> 15% errors or misses in easy trials), resulting in a final sample of 16 participants (11 female, age: *M* = 23.2 yr, *SD* = 2.9).

2.3.1.2 Task

The task was identical to Experiment 1 with the following exceptions (**Figure 2.4**): Target distance varied on a trial-by-trial basis within participants in order to manipulate the relative motor cost of intention pursuit after a perceptual CoM (**Figure 2.4A**). In 50% of trials of each condition, the targets of different colour were far (18°; i.e., far horizontal distance), whereas in the other 50% of trials, the targets of different colour were close (6°; i.e., close horizontal distance). To eliminate visual differences in target detection, the distance of targets from the centre was constant across conditions, i.e., for close horizontal targets, vertical distance was far and vice versa. Importantly, in the far-target condition, path lengths for CoMov and CoMov+Int were roughly equal, whereas in the close-target condition, path length was shorter for CoMov+Int while it was the same as in the far-target condition for CoMov (**Figure 2.4B**). Hence, in the close-target condition, switching to the target of different colour allowed participants to save motor costs, rendering intention pursuit *relatively* more costly than in the far-target condition. This should increase the frequency of Changes of Intention in the close- compared to the far-target condition, in which CoMov and

CoMov+Int were equally costly (**Figure 2.4C**). In order to enhance the differences in motor costs between target-distance conditions, the cursor speed was 1.8 times slower than in Experiment 1, increasing overall travel distance of movements.

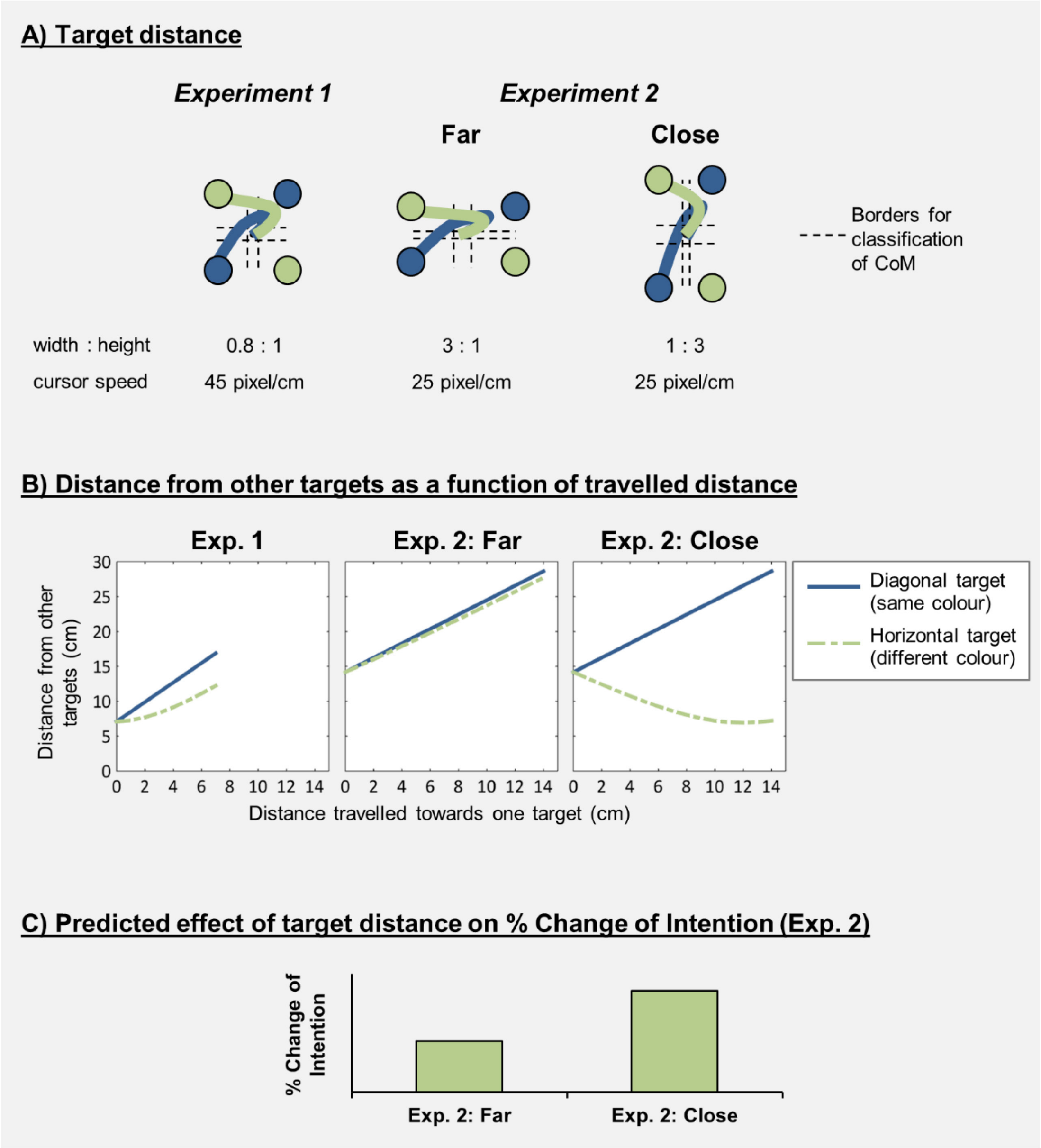

Figure 2.4. Design of Experiment 2. Manipulation of horizontal target distance. A) Target locations in Experiment 1 and 2. B) Distance from the diagonal/horizontal target as a function of travelled distance (assuming straight movement trajectories towards targets). In the far-target condition, costs associated with each target were roughly equal, whereas in the close-target condition, the target of different colour was closer, hence rendering intention pursuit *relatively* more costly. C) Predicted effect of target distance on frequency of Changes of Intention in Experiment 2.

As in Experiment 1, CoM was classified online when movement trajectories exceeded 10% of both the x- and y- distance from one target, but then ended in another target. Due to the different target locations, the absolute coordinates that had to be exceeded differed between target distance conditions (**Figure 2.4A**). This ensured that CoM classification was not biased by differences in movement angles across target distance conditions.

In addition to target locations, target onset times were changed in Experiment 2. In 80% of test trials, targets were presented early (700–1000 ms before dot motion onset). This ensured a large percentage of test trials in which participants had enough time to identify the target colours. If participants switch to a target of different colour in this condition, the switch is unlikely due to target confusion, but rather represents a Change of Intention. In the remaining 20% of test trials, target onset was late (i.e., simultaneous with dot onset), which enabled us to investigate if the frequency of Changes of Intention was higher when participants were *not* able to prepare movements associated with the chosen colour prior to dot motion onset.

After a training session (see Experiment 1), participants were invited for two identical experimental sessions of 1.15h each, in which they completed an average of 815.6 trials in total (*SD* = 57.2). The duration of Experiment 2 was increased compared to Experiment 1 in order to obtain a sufficient number of CoMov and CoMov+Int for each target distance condition.

2.3.1.3 Data analysis

Movement trajectories that were classified as CoM were visually inspected, and trials with double CoM (0.83%), or trajectories that were not clearly initiated towards one target (0.47%) were excluded from all analyses. Movement velocities indicated that none of the participants showed strategic decision delay.

2.3.2 Results

2.3.2.1 Task performance

As in Experiment 1, accuracy of the perceptual choice was significantly lower in test trials (*M* = 58.5%, *SD* = 5.2%) compared to easy trials (*M* = 96.2%, *SD* = 3.4%, *t*(15) = 26.54, *p* < .001, *d* = 6.64), and perceptual CoM occurred more frequently in test (*M* = 10.3%, *SD* = 9.9%) than easy trials (*M* = 3.3%, *SD* = 4.1%, *t*(15) = 3.15, *p* = .007, *d* = 0.79). Furthermore, in trials where participants did not have to verbalise their colour choice, accuracy showed a trend towards being lower in conflict (*M* = 93.1%, *SD* = 5.7%) than easy trials (*M* = 95.7%, *SD* = 3.5%; *t*(15) = 1.89, *p* = .078, *d* = 0.47). In contrast to Experiment 1, no difference in RTs was observed between conflict trials (*M* = 560.8 ms, *SD* = 47.5 ms) and easy trials (*M* = 563.0 ms, *SD* = 48.5 ms, *t*(15) = 0.38, *p* = .712, *d* = 0.09). However, the rate of misses (i.e., trials in which movement initiation exceeded the response deadline) was numerically increased in conflict trials (*M* = 3.3%, *SD* = 3.3%; easy trials: *M* = 2.0%, *SD* = 3.1%; *t*(15) = 1.29, *p* = .216, *d* = 0.32). Additionally, there were significantly more corrective movements in conflict trials (*M* = 5.5%, *SD* = 6.3%) than there were CoM in easy trials (*M* = 3.4%, *SD* = 5.5%, *t*(15) = 3.51, *p* = .003, *d* = 0.88) suggesting that, as in Experiment 1, participants generated initial colour intentions that resulted in response costs when external information did not match the endogenous intention.

2.3.2.2 Effect of motor costs on Changes of Intention

In order to investigate the effect of target distance on the likelihood of CoMov vs. CoMov+Int, an MELR model with target distance as a fixed effect (far/close, dummy-coded with far distance as reference level) was conducted for test trials. It revealed a significant effect of target distance ($\chi^2(1) = 15.47$, *p* < .001), with CoMov+Int occurring more often in the close- than far-target condition (*b* = 0.76, 95% CI [0.38, 1.16], OR = 2.15). Interestingly, target distance did not have a significant effect in a model with no-CoM vs. CoM as outcome variable (*b* = 0.06, 95%

CI [-0.08, 0.20], OR = 1.06, $\chi^2(1) = 0.70$, *p* = .404). Hence, target distance did not affect whether or not participants changed their mind about the dot-motion direction, but affected whether or not participants pursued their initial colour choice when a perceptual CoM occurred.

2.3.2.3 *Effect of advance motor preparation*

In order to investigate the effect of advance motor preparation on CoMov vs. CoMov+Int, target-onset time was included as a fixed effect (early/late, with early onset as reference level) in addition to target distance (**Figure 2.5**). This model revealed no significant main effect of target onset (*b* = -0.05, 95% CI [-0.82, 0.67], OR = 0.95, $\chi^2(1) = 0.02$, *p* = .902). However, there was a trend for an interaction between target distance and target-onset time (*b* = 0.78, 95% CI [-0.14, 1.74], OR = 2.19, $\chi^2(1) = 2.75$, *p* = .097). In order to further investigate this interaction, the effect of target distance on CoMov+Int and CoMov was investigated separately for trials with early and late target onset. Relative to no-CoM trials, the likelihood of CoMov+Int increased significantly for close compared to far targets in both the early-target condition (*b* = 0.48, 95% CI [0.12, 0.84], OR = 1.61) , $\chi^2(1) = 6.95$, *p* = .008) and late-target condition (*b* = 0.96, 95% CI [0.33, 1.65], OR = 2.60 , $\chi^2(1) = 9.10$, *p* = .002), with the effect being descriptively stronger in the late-target condition. Additionally, in the late-onset condition, CoMov significantly *decreased* (relative to no-CoM) for close compared to far targets (*b* = -0.46, 95% CI [-0.83, -0.09], OR = 0.63 , $\chi^2(1) = 5.94$, *p* = .015), which was not the case in early-onset trials (*b* = 0.02, 95% CI [-0.16, 0.19], OR = 1.02 , $\chi^2(1) = 0.04$, *p* = .836). Consequently, the *relative* frequency of Changes of Intention out of all CoM tended to increase more strongly with close targets in the late-target condition than in the early-target condition.

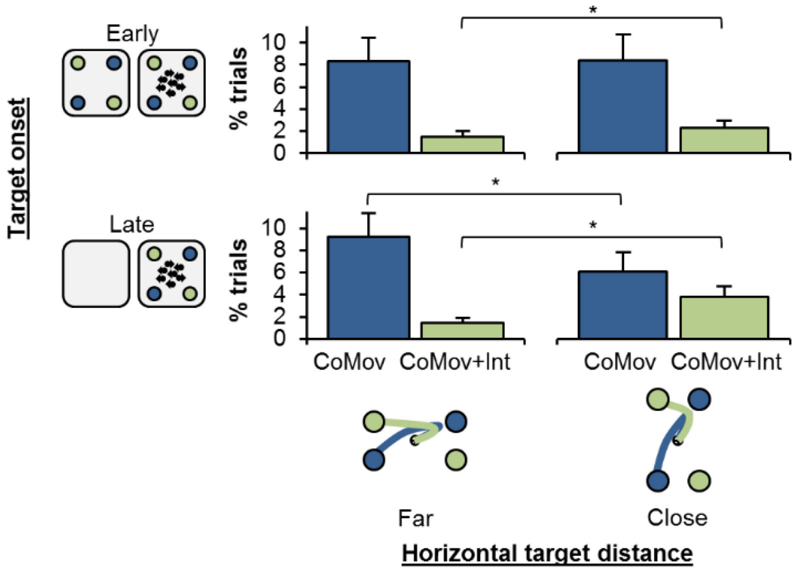

Figure 2.5. Results of Experiment 2. Percentage of trials with CoMov and CoMov+Int, separated by target distance and target-onset time (mean +/- 1 SE; * $p < .05$, $N = 16$).

2.3.2.4 SoA judgments (Exp. 1 & 2)

To analyse SoA judgments, the data were collapsed across both experiments to increase power ($N = 33$). SoA ratings were rescaled to reflect the position on the scale as a percentage. In test trials without CoM, SoA ratings increased linearly with the percentage of dots matching the colour of the hit target (linear contrast: $F(1, 32) = 164.91$, $p < .001$, $\eta_p^2 = .837$). When including experiment as a factor, no significant main effect of experiment, nor any interaction were observed (both $F < 1$). Hence, in both experiments, SoA ratings were sensitive to action outcomes showing that participants made appropriate use of the rating scale.

2.3.2.5 Effects of CoM on SoA

Next, we investigated if SoA ratings were affected by CoM in test trials. Action outcomes were always 50% in trials with CoM. Hence, for no-CoM, only 50% outcome trials were included to analyse the effect of CoM on SoA regardless of action outcomes.

Variability in trial numbers with CoM was high across participants [*n* CoMov: *M* = 29.8, *SD* = 37.5, range: 1–159; *n* CoMov+Int: *M* = 7.3, *SD* = 9.0, range: 0–43] and 5/33 participants did not show any CoMov+Int. Therefore, linear mixed-effect models were used since they are recommended for analysing unbalanced and missing data (Bagiella et al., 2000). Furthermore, they allowed us to include continuous predictors that varied on a trial-by-trial level, e.g., movement times. Participants were modelled as random intercepts.

A model was specified that included CoM as a fixed effect (no-CoM/CoMov/CoMov+Int; dummy coded with no-CoM trials serving as baseline) and SoA ratings as a continuous outcome variable. This model performed significantly better than a model without CoM as a predictor ($\chi(2) = 13.75$, $p = .001$). Post-hoc pairwise comparisons with a Bonferroni-corrected α-level of .05/3 = .017 revealed that the effect of CoM on SoA ratings was driven by a significant decrease of SoA in CoMov (**Figure 2.6A**; *M* = 43.8%, *SD* = 9.6%) compared to no-CoM (*M* = 47.1%, *SD* = 8.1%; $b = -3.02$, 95% CI [-4.62, -1.42], $t(2169.9) = 3.70$, $p < .001$), whereas CoMov+Int (*M* = 44.1%, *SD* = 11.0%) did not differ significantly from no-CoM trials ($b = -1.10$, 95% CI [-3.49, 1.29], $t(2161.2) = 0.91$, $p = .366$). The difference between CoMov and CoMov+Int was not significant ($b = 1.92$, 95% CI [-0.48, 1.42], $t(2162.2) = 1.57$, $p = .118$). When adding experiment as a predictor, no main effect of experiment ($\chi(1) < .01$, $p = .924$), nor an interaction with CoM ($\chi(2) = 0.33$, $p = .847$) was found, suggesting that the effect of CoM on SoA was comparable across both experiments.

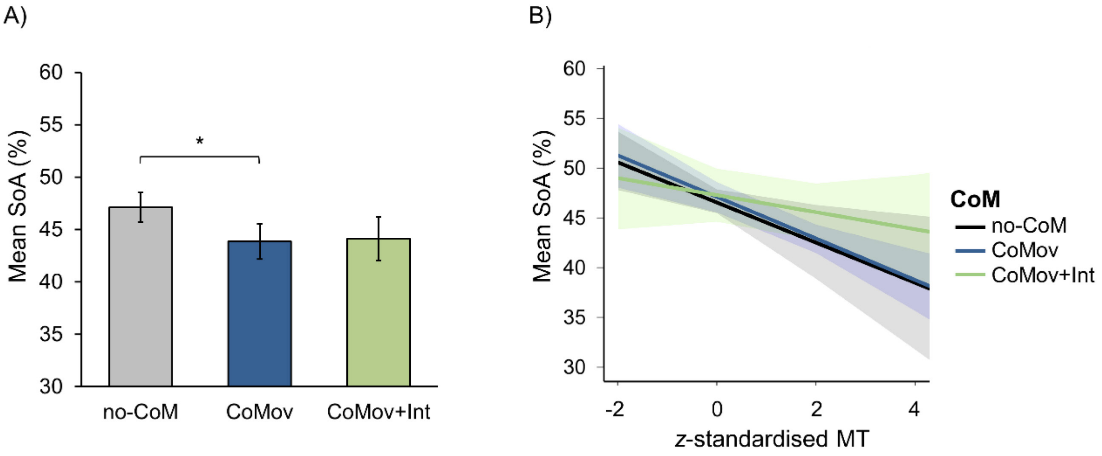

Figure 2.6. Effect of CoM on SoA. A) Mean SoA ratings for each type of CoM. B) Predicted SoA ratings (marginal effects) for a mixed-effects model including movement times as a predictor (± 1SE, *N* = 33).

As CoM was classified based on movement trajectories, trials differed in terms of pure motor aspects. More specifically, movement times (MTs; i.e., time between response initiation and target hit) were shorter in no-CoM trials (*M* = 480.3 ms, *SD* = 246.8 ms) than in trials with CoMov+Int (*M* = 975.8 ms, *SD* = 365.6 ms, *t*(27) = 10.19, *p* < .001, *d* = 1.93) and CoMov (*M* = 1089.5 ms, *SD* = 354.9 ms, *t*(32) = 18.92, *p* < .001, *d* = 3.29). To investigate if differences in MTs accounted for differences in SoA ratings, individuals' *z*-standardised MTs were included as a covariate in the model (**Figure 2.6B**). This revealed a significant main effect of MTs ($\chi(1) = 24.32$, *p* < .001) driven by lower SoA ratings for longer MTs (*b* = -1.81, 95% CI [-2.58, -1.14]). Furthermore, the effect of CoM on SoA disappeared ($\chi(2) = 1.51$, *p* = .470), and the decrease of SoA ratings in CoMov compared to no-CoM trials was not significant in the model including MTs

($t(2160.0) = 0.04$, $p = .970$). This suggests that the effect of CoMov on SoA was accounted for by differences in MTs. Again, no difference in SoA rating was observed in CoMov+Int compared to no-CoM trials in the model including MTs ($b = 1.44$, 95% CI [-2.20, 3.42], $t(2168.6) = 1.10$, $p = .273$). Finally, there was no significant interaction between CoM and MTs ($\chi(2) = 2.22$, $p = .330$). In fact, longer MTs significantly reduced SoA judgments even when only trials without CoM were considered ($b = -2.15$, 95% CI [-3.58, -0.72], $\chi(1) = 8.65$, $p = .003$), suggesting that MTs affected SoA judgments regardless of whether or not CoM occurred.

2.3.3 Discussion Experiment 2

In Experiment 2, the relative motor cost associated with intention pursuit was manipulated by varying target distances. When the distance to the alternative target colour was short compared to the initially-chosen colour, movement costs for CoMov+Int were low relative to CoMov. This caused an increased frequency of Changes of Intention compared to a condition where targets of both colours were roughly equally distant. Hence, motor costs influenced whether perceptual CoM caused a change in the movement required to realise an intention, or additionally, a change in the intention itself. This effect was particularly strong when target onset was late, i.e., when participants were not able to pre-select motor plans associated with their colour intentions. Thus, when intentions were translated into movement plans only later in the trial, the initial intention was more susceptible to cost-induced updates, compared to when participants could plan movements in advance.

Interestingly, advance motor planning did not seem to strengthen the intention itself as this would have predicted an overall lower frequency of Changes of Intention in early compared to late targets. Instead, the observed interaction between target-onset time and target distance suggests that early implementation of intentions into potential motor commands modulates the effect of other influencing factors, e.g., costs, on intention updates. Hence, motor planning seems to ‘shield’ intentions (Veling & Van Knippenberg, 2006; Achtziger et al., 2008) from cost-induced updates. That is, once people have had adequate time to plan ahead, they seem relatively inured to increases in costs of realising their intention. Thus, time since action planning appears to be a key factor in how information about movement-related costs is integrated with higher-order intentions. Finally, the fact that action costs had a greater effect when targets were presented late, compared to when they were presented early, suggests that integration of motor costs occurred rapidly and dynamically. That is, even when participants could *not* anticipate action costs before dot-motion onset (late targets), motor costs affected decision making, and in fact, had a stronger effect than when targets were presented early. Hence, it seems plausible that motor costs do not simply shift a fixed decision threshold prior to action onset (Moher & Song, 2014), but instead, are dynamically integrated with other decision-relevant variables as actions evolve.

Finally, in contrast to previous studies (Burk et al., 2014; Moher & Song, 2014), we did not observe an overall increase in perceptual CoM in close compared to far targets. Hence, in our study, motor costs did not affect whether or not participants changed an ongoing action, but instead, affected *which* aspects of action selection were changed (goals vs. movements). It is possible that in the current study, participants were willing to correct their perceptual choices regardless of motor costs, given that they obtained additional monetary rewards for correct perceptual choices. Hence, motor costs may have not been sufficiently strong to overwrite perceptual decisions. By contrast, voluntary decisions were not associated with monetary incentives, and hence, differences in motor costs may have had a stronger impact on intention reversals than perceptual CoM per se. More generally, endogenous decisions often do not have an objectively ‘correct’ or ‘wrong’ choice options, and hence, participants may have used information about motor costs to break the symmetry between equal-appearing voluntary goals (Bode et al., 2013).

2.4 General discussion

While previous studies of CoM have focused on exogenous action (e.g., Resulaj et al., 2009; Albantakis et al., 2012), the current study investigated changes of voluntary action decisions. In Experiment 1, we showed that the frequency of Changes of Intention was inversely related to the strength of participants' initial intentions. In Experiment 2, we found that higher motor costs associated with intention pursuit induced more Changes of Intention, especially when participants could not implement intentions into precise motor commands prior to dot-motion onset.

Our results provide evidence for a striking flexibility of intentions in voluntary action. We show that agents can adjust motor intentions (Goodale et al., 1986; Fleming et al., 2009; Obhi, Matkovich, & Gilbert, 2009), but can also dynamically change endogenous, distal intentions during action. On the one hand, this flexibility is highly advantageous in that it allows people to flexibly adjust their behaviour to the current context. On the other hand, an important concept of the voluntary control of behaviour is the need for intention pursuit over a long period of time – e.g., when intending to quit smoking or lose weight. People may give up on these intentions because of new stimuli that can trigger decision reversals. For example, addiction relapse is often caused by exposure to drug-related external stimuli, in particular in individuals with high sensitivity to incentive cues (Robinson, Robinson, & Berridge, 2013). Our results support the assumption that the strength of an endogenous intention (e.g., to quit smoking) is an important factor for successful pursuit of intentions. Furthermore, goal achievement may be facilitated by low costs (e.g., easily-accessible healthy food options) and pre-planning of actions (e.g., "when I go to a bar, I will order orange juice"). Our study provides a quantitative laboratory model for measurement of these processes, which will facilitate future investigation of the neurocognitive mechanisms underlying intention pursuit. In particular, by capturing intentions as a gradual and continuous quantity, our paradigm offers a novel approach to investigate the factors that render voluntary intentions more flexible vs. stable.

2.4.1 Changes of Mind and Sense of Agency

In both experiments, reduced SoA was observed after Changes of Movement. However, this effect was statistically accounted for by differences in movement times between trials with vs. without CoMov. Participants may have used movement times as a proxy of (in)efficient motor performance or difficulty of action selection, which reduces SoA (Wenke et al., 2010; Sidarus, Chambon, & Haggard, 2013; Sidarus & Haggard, 2016). Importantly, our results suggest that SoA is not only informed by how efficient the *initial* action selection was, but additionally takes into account the 'fluency' of continuous movement execution after initial onset. While previous studies have investigated SoA in continuous actions (Wen, Yamashita, & Asama, 2015b; Oishi, Tanaka, & Watanabe, 2018), these studies have focused on aspects of performance related to action outcomes, e.g., by perturbing sensorimotor feedback. By contrast, the current results suggest that SoA is modulated even in the absence of such external perturbations, and takes into account subtle indicators of how 'fluent' or easy execution of a continuous movement was. Additionally, slower movement times may have contributed to a reduction in SoA by prolonging the delay between action initiation and action outcomes (Sato & Yasuda, 2005; Wen, Yamashita, & Asama, 2015a), hence weakening the perceived causal link between one's own actions and their sensory consequences.

Interestingly, SoA was not modulated by Changes of Intention. That is, deviating from an initial action goal neither decreased (Metcalfe et al., 2013; Vinding et al., 2013), nor increased SoA (Ach, 1935; Libet, 1999). Hence, our findings are broadly in line with reconstructive accounts of conscious intention, which state that SoA is independent of the actual initial intention and instead relies on retrospective inference (Wegner, 2002; Wegner et al., 2004; Aarts et al., 2005). As a consequence, SoA does not change when intentions are reversed. Indeed, as action goals are updated, predictions about action outcomes may be rapidly adjusted during action (Synofzik, Thier, & Lindner, 2006) without any consequences for subsequent inferences informing SoA.

However, the absence of any significant effect of Changes of Intention on SoA in our study should be interpreted with caution since it is a null result based on low trial numbers. In particular, we cannot rule out that strong and sustained intentions may contribute to SoA.

2.4.2 Conclusion

Voluntary actions are shaped by continuous decision-making processes that integrate external information with endogenous intentions. By investigating this integration process, our novel experimental design shed some light on the nature of intentions themselves. Specifically, we suggest that endogenous intentions come by degrees, are continuously re-evaluated, and can sometimes be changed. The flexible nature of action selection allows agents to dynamically decide *which* intention to pursue and *how* to pursue it. Insights into the factors that influence behavioural flexibility vs. persistence are highly relevant to our understanding of the mechanisms underlying goal pursuit and its disturbances, with important social and personal implications.

Chapter 3.

An attractor network model of CoM in voluntary action

3.1 Introduction

In **Chapter 2** of this thesis, we introduced an adapted RDM task in which participants reached for one of four possible targets that matched both their endogenous intention regarding target colour and a perceptual decision about dot-motion direction. Continuous movement trajectories were measured in order to identify when participants changed their mind about the dot-motion direction, which either resulted in a Change of Movement to another target of the same colour, or a Change of Movement + Intention that additionally involved a switch to a nearby target of different colour. In the current chapter, a new attractor network model will be introduced in order to gain more insights into the putative mechanisms underlying CoM in voluntary action. Specifically, this model captures how higher-order voluntary intentions, i.e., distal goals of an action, are integrated with sensory information from the environment, and also with the costs associated with a given movement. Crucially, this integration is dynamic and continuous, which can cause a CoM during ongoing action execution.

As mentioned in the general introduction (**Chapter 1**), attractor network models might provide an appropriate approach to capture such dynamic integration of different decision variables. These models are dynamical systems of interconnected neurons whose firing rates are updated continuously (P. Miller, 2016). Activity patterns evolve into attractor states that typically remain relatively stable over time, however, changes in states can occur due to changes in external inputs and/or intrinsic dynamics of the network (Moreno-Bote et al., 2007; Albantakis & Deco, 2011; Albantakis et al., 2012; Yan et al., 2016). In addition to the dynamic nature of attractor networks, these models allow for integration of various decision variables through excitatory/inhibitory connections between different neural populations (Lo & Wang, 2006; Cisek, 2012; Christopoulos et al., 2015).

Another important class of models in computational neuroscience are bounded accumulator models (Smith & Vickers, 1988; Ratcliff & Rouder, 1998), which have been applied to a range of choice scenarios (Deco et al., 2013) and can capture CoM in perceptual decision making (Resulaj et al., 2009; Burk et al., 2014; van den Berg et al., 2016). These types of model typically only take into account a single source of evidence (e.g., sensory input). Other decision-relevant variables (e.g., motor costs) have previously been implemented through changes in static variables, such as decision thresholds (Burk et al., 2014). Hence, it is not clear how accumulator models can account for multiple sources of information that change dynamically over time. In particular, motor costs may need to be evaluated continuously, for example, when costs cannot be fully anticipated in advance, or when the current state of an ongoing movement affects its associated cost. Hence, for some scenarios, it is unlikely that motor costs simply affect a fixed decision threshold prior to action onset. Therefore, in the current model, continuous changes in motor costs were modelled as a decision variable that was integrated dynamically into the decision-making process. This was achieved by explicitly modelling motor outcomes of the decision process (i.e., continuous movement trajectories), which then informed updates in motor costs depending on the current location, and hence, distance to each of the choice targets.

Previous attractor network models of CoM have exclusively focused on decisions about perceptual stimuli (Albantakis & Deco, 2011; Albantakis et al., 2012; Yan et al., 2016), even though network approaches readily allow for integration of multiple sources of information (Christopoulos et al., 2015). Specifically, in previous models, neural network nodes responded selectively to left/right dot-motion direction. By contrast, in the task introduced in **Chapter 2**, participants made choices between 4 targets based on an endogenous colour intention and dot-motion direction of an RDM stimulus. Furthermore, behavioural results suggested that participants took into account information about motor costs when implementing their decisions into action. Hence, three main sources of information were integrated: 1) the endogenous intention about colour (blue/green), 2) external sensory input (left/right dot-motion direction) and 3) motor costs associated with each action alternative. Hence, in this chapter, an extended attractor network model is proposed that consists of different types of neural populations representing different modalities of information (**Figure 3.1**): 1) neural populations encoding the voluntary colour intention (I_1 and I_2), 2) neurons that selectively respond to sensory information about left/right dot-motion (S_1 and S_2), and 3) neurons that calculate the movement cost according to the distance to each of the 4 target locations (C_1, C_2, C_3, C_4). Information from these neural populations is combined by action nodes (A_1, A_2, A_3, A_4) that integrate all sources of information and specify the motor output, i.e., initiation of a movement towards the chosen target location. For example, action A_1 is selected for execution if the intention is blue (I_1 fires at a high rate), if the dots move left (S_1 fires at a high rate), and if the cost of moving to the left-blue target is relatively low (C_1 fires at a low rate). In other words, the firing rate of each action node reflects the strength of evidence in favour of a given action based on the combined information encoded in a distributed network of neurons.

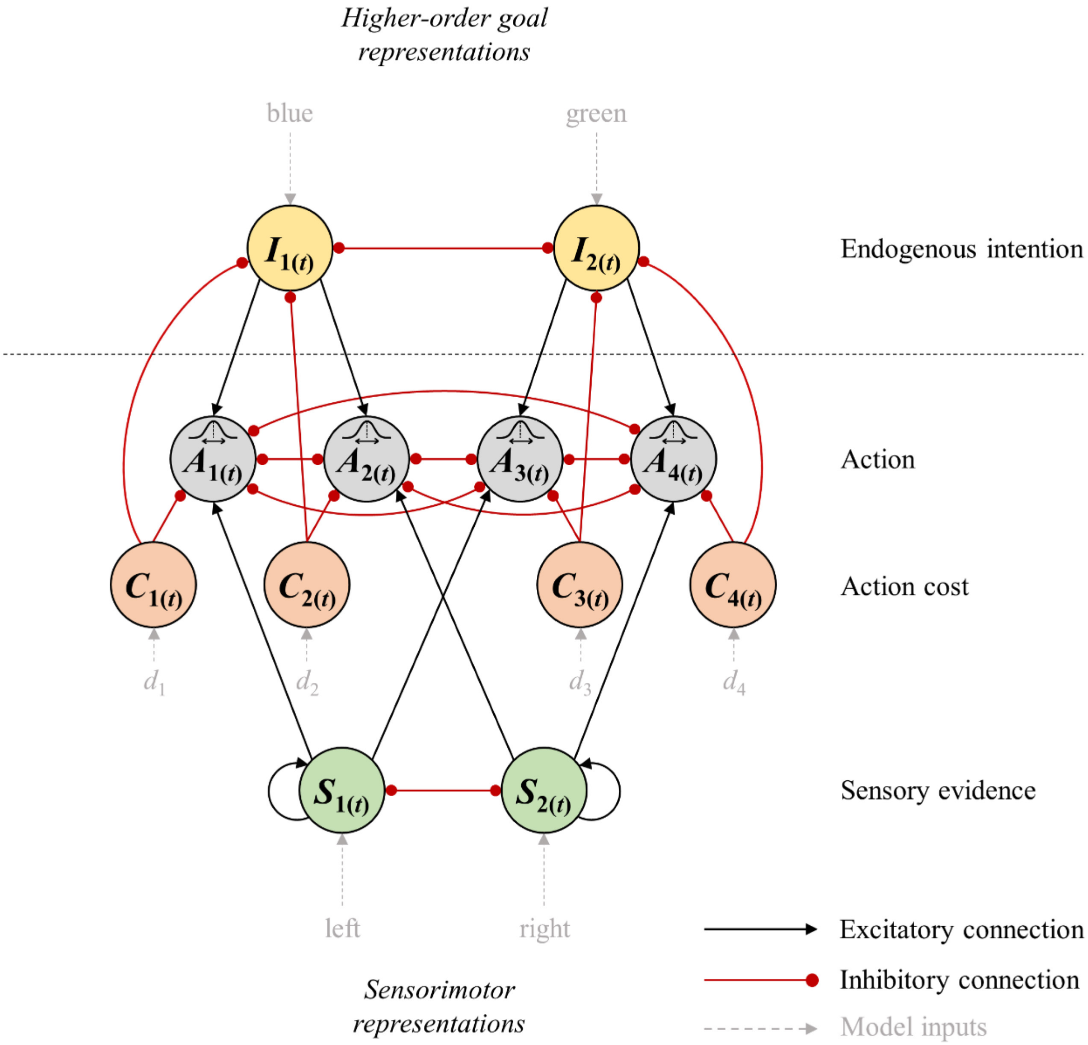

Figure 3.1. Hierarchical attractor network model of CoM. The network consists of 12 neural nodes that encode different pieces of information. Nodes are connected through excitatory (black) or inhibitory (red) connections. The action nodes A_1 to A_4 compete against each other to determine which one of the 4 choice targets is selected. This competition takes into account information about 1) voluntary intentions (blue/green represented by nodes I_1 and I_2), 2) sensory information (left/right encoded by sensory nodes S_1 and S_2) and action costs (C_1 to C_4) that depend on the distance d to each target location. Intention nodes are represented on a hierarchically higher level than sensorimotor nodes, allowing for top-down regulation of the degree of variability in firing rates of the action nodes. All firing rates are updated continuously and can change dynamically. Hence, CoM can occur when one action node crosses the threshold for movement execution first, but later on, another action wins the competition. Different types of CoM can be dissociated based on which action the network switches to when a decision reversal occurs (e.g., Change of Movement: $A_1 \rightarrow A_2$, or Change of Movement + Intention: $A_1 \rightarrow A_4$).

Furthermore, in contrast to previous models of CoM, the model introduced here has a hierarchical structure that was inspired by theories of intention hierarchy (Pacherie, 2008) and multi-level decision making (Cisek, 2012). More specifically, in the current model, colour intentions are represented on a hierarchically higher level than sensorimotor information. That is, in line with the behavioural task, colour intentions reflect abstract, distal action goals with respect to the action outcome (coloured dots). By contrast, sensorimotor information about perceptual inputs (dot-motion stimulus) and movement-related costs inform *how* that goal can be achieved. Hence, hierarchy in the current model corresponds to the distinction between *what* goal to pursue vs. *how* to pursue it, and hence, the distinction between distal vs. motor intentions (Pacherie, 2008). Hierarchy was implemented as top-down noise regulation in action selection through the intention nodes I_1 and I_2. Specifically, stronger intentions caused a decrease in noise, and hence, decreased variability in firing rates of the action nodes A_1 to A_4. This is in line with previous studies showing that voluntary intentions are associated with noise reduction in motor-related neural activity (Khalighinejad et al., 2018). Additionally, the implementation of hierarchy through noise regulation was inspired by Hierarchical Gaussian Filters, where the degree of noise (or 'volatility') of a hierarchically-lower variable can change over time, depending on the current state of a hierarchically-higher variable (Mathys, Daunizeau, Friston, & Stephan, 2011; Mathys et al., 2014).

Within each level of the hierarchy, neural populations that encode the same modality of decision evidence (i.e., intention nodes I_1 and I_2, and sensory nodes S_1 and S_2) compete against each other through lateral inhibition. At the same time, the 4 action nodes compete against each other, and hence, determine the final behavioural outcome through a winner-take-all mechanism (Cisek, 2007) – or 'untangling' of decision inputs into action (Yoo & Hayden, 2018). Additionally, connectivity across the two hierarchical levels allows for exchange of information. That is, higher-order intentions bias the competition between lower-level action representations, but additionally, motor representations also guide intentions. Specifically, in line with the behavioural findings, motor costs associated with each action have inhibitory effects on colour intentions. Hence, in the current model, decisions are made through a distributed consensus across different hierarchically-organised neural populations (Cisek, 2012).

Crucially, firing rates are updated continuously and change dynamically. This can cause CoM, which may either reflect a change in *what* intention is pursued and/or a change in *how* a given intention is implemented into motor action based on sensory evidence. For example, the network can switch from action A_1 to action A_2, reflecting a Change of Movement (CoMov), i.e., a switch between actions that correspond to different sensory states ($S_1 \rightarrow S_2$) but the same colour intention ($I_1 \rightarrow I_1$). Alternatively, the network might switch from A_1 to A_4, reflecting a Change of Movement + Intention (CoMov+Int), and hence, a change in both the sensory state ($S_1 \rightarrow S_2$) as well as the colour intention ($I_1 \rightarrow I_2$). Finally, a Change of Intention (CoInt) can occur between actions associated with different intentions but the same sensory state (e.g., $A_1 \rightarrow A_3$). Note that these types of CoM were not considered in the behavioural task as we assumed that these (vertical) switches reflected colour errors where participants erroneously initiated a movement towards a target that did not correspond to their actual initial colour intention (e.g., due to difficulty in target detection). This assumption can be tested in the current model. That is, by defining the 'true' colour intention on a given trial, simulations can be used to analyse whether switches between different intentions reflect correction of an initial colour error, or instead, a reversal of an intention, e.g., due to cost-induced intention updates when an ongoing movement needs to be changed.

The main aim of this chapter is to test whether the proposed computational model can account for the behavioural findings reported in **Chapter 2**. More specifically, systematic simulations were performed in order to test the effects of different variables (e.g., strength of sensory evidence, colour intention, or motor cost) on the rate of CoMov and CoMov+Int, respectively. Hence, our approach can be described as a sensitivity analysis of model outcomes to changes in a given parameter of interest. No formal model fitting was performed, and instead, model parameters were defined based on previous models, conceptual/mathematical reasons, and consideration of parsimony. Consequently, the precise model parameters and quantitative outcomes should be interpreted with caution. Instead, the conceptual validity of the model was evaluated qualitatively based on its ability to reproduce the overall pattern of behaviour and the different types of CoM observed in the experiments, regardless of the precise quantitative accuracy of predictions.

3.2 Methods

3.2.1 Model implementation

The model was implemented in Matlab R2016b. All model code is available on the Open Science Framework (https://osf.io/4f895/?view_only=c4e1b3ab60974ce39e7103585dfea97f).

3.2.2 Network architecture

The attractor network model consists of 12 neural nodes that are grouped into different modules according to the source of information they represent (**Figure 3.1**):

1) Two ***intention nodes*** (I_1, I_2) that encode the voluntary intention (blue/green)
2) Two ***sensory nodes*** (S_1, S_2) that selectively respond to dot-motion direction (left/right)
3) Four ***cost nodes*** (C_1, C_2, C_3, C_4) that calculate the cost associated with each action based on distance to each target location
4) Four ***action nodes*** (A_1, A_2, A_3, A_4) that correspond to the 4 possible action alternatives, and hence, location of the choice targets (left/right top/bottom)

Each node represents a population of neurons whose firing rates change dynamically over time. The firing rates of intention nodes (I_1, I_2) and sensory nodes (S_1, S_2) depended on model inputs whose intensities corresponded to the strength of intention and strength of sensory evidence (i.e., motion coherence), respectively. Firing rates of cost nodes (*C*1 to *C*4) depend on the distance *d* to each target location. Hence, intention, sensory and cost nodes are 'input nodes' that receive direct model inputs. Action nodes did not receive any direct external inputs, but instead, integrated information from all other network nodes in order to determine the behavioural outcome (i.e., movement trajectory towards one of the 4 targets). Integration of information is achieved through neural connectivity. Colour intentions and sensory inputs have excitatory effects on action nodes, whereas costs have inhibitory effects. Furthermore, neurons that encode the same modality of information, e.g., S_1 and S_2, but respond selectively to a specific input (e.g., left vs. right dot motion) inhibit each other. This mutual inhibition between horizontal nodes (lateral inhibition) represents neural competition, which ensures that over time, a single choice option is selected through a winner-take-all mechanism that supresses competing choice alternatives.

The precise strength of connections is to some extent arbitrary and was defined by informally exploring different values in order to ensure that one of the action nodes reaches a fixed firing rate threshold within a certain time frame (e.g., RTs < 1000 ms). More importantly, the *relative* strength of each connection was chosen based on conceptual reasons and parsimony considerations. For example, to reduce the number of free parameters, connections were assumed to be symmetric, and hence, I_1 and I_2 had equally strong connections of +1 onto their corresponding action nodes. Similarly, each cost node had inhibitory effects of strength -1 on action nodes. Sensory nodes S_1 and S_2 had slightly stronger connections of +1.5 onto action nodes, given that perceptual decisions took priority in the task (see **Chapter 2**). Furthermore, inhibitory competition within each modality was set to -0.5, with the exception of lateral inhibition between neighbouring action nodes A_1 and A_2 (and A_3 and A_4), which inhibited each other with a strength of -1.0. This was because these actions corresponded to diagonally-opposite targets, respectively, and hence, movements in either direction were mutually exclusive (i.e., competition is stronger). Finally, sensory nodes had self-excitatory connections of +0.25, representing temporal integration of sensory evidence from the dot-motion stimulus (Wong & Wang, 2006; Albantakis & Deco, 2011). Note that intention nodes did not have self-excitatory connections because in the task, initial colour choices had already been made at trial start. Hence, at the point in time when the dot stimulus was presented, colour intentions did not require accumulation of new endogenous information about colour per se. Instead, intention updates were assumed to depend on the cost associated with pursuing the colour choice over time. Hence, cost information was updated continuously and had inhibitory (-0.5) effects on intentions. **Figure A1** in Appendix A illustrates the attractor network including the weight associated with each connection.

3.2.3 Modelling firing rates

In order to compute the firing rates of each neural node over time, a mean-field approach was used (Wong & Wang, 2006; Yan et al., 2016). That is, instead of modelling individual spiking neurons, the overall firing rate of a given neural population (node) was calculated for each point in time. Firing rates of each node were updated in time steps of 1 ms and depended on 1) how strongly a given node was stimulated (based on external model inputs and excitatory/inhibitory inputs from other nodes), 2) the node's firing rate on the previous time step, and 3) neural noise. Hence, the following equations were used to determine the firing rate *r* of a given node *i* at time point *t*.

First, the total stimulation that each node received at time *t* was calculated (**Equation 3.1**) based on direct external inputs into that node (if any), plus the sum of neural inputs from all other nodes (and itself in case of auto-connections). The neural input that node *i* received from node *j* depended on the firing rate of *j* at the previous time step weighted by its connectivity to *i* as defined by the weight matrix *W*:

$$stim_{i,t} = in_{i,t} + \sum_{j=1}^{12} r_{j,t-1} W_{i,j} \tag{3.1}$$

Updates in firing rates were then computed (**Equation 3.2**) as a function of the node's previous firing rate, the current stimulation $stim_{i,t}$ it received, and a base time constant τ of 100 ms (Wong & Wang, 2006; Yan et al., 2016) indicating how fast neurons changed their firing rates in response to changes in inputs. Hence, using the Euler-Maruyama approximation for differential equations (P. Miller, 2016; Hahne et al., 2017), the firing rate of node *i* at time *t* was calculated as follows:

$$r_{i,t} = r_{i,t-1} + (stim_{i,t} - r_{i,t-1})\tau^{-1} \qquad (3.2)$$

Finally random Gaussian noise *s* was added to the firing rate of each node:

$$r_{i,t} = r_{i,t} + s_{i,t} \quad \text{with } s_{i,t} \sim N\left(0, \sigma_{i,t}^2\right) \text{ and } \sigma_{i,t}^2 \geq 0 \qquad (3.3)$$

The degree of neural noise varied according to σ^2, which was initially set to 2 Hz for all nodes. However, according to the assumption of top-down noise regulation through higher-order intentions, σ^2 of each action node A_1 to A_4 varied as a function of the state of intention nodes I_1 and I_2 (**Equation 3.4**). Specifically, higher firing rates of I_1 caused a reduction of noise in its associated action nodes A_1 and A_2. For example, if I_1 fired at 50% of its maximum firing rate, noise in A_1 and A_2 was reduced by 50%:

$$\sigma^2{}_{A1,t/A2,t} = \sigma_0^2 - \frac{r_{I1,t-1}}{100}\sigma_0^2 \quad \text{and} \quad \sigma^2{}_{A3,t/A4,t} = \sigma_0^2 - \frac{r_{I2,t-1}}{100}\sigma_0^2 \qquad (3.4)$$

Firing rates were restricted to a range of 0–100 Hz. All neurons started with a background firing rate of 10 Hz. Once one of the action nodes reached a fixed firing rate threshold of θ = 40 Hz (and surpassed all other action nodes by at least 10 Hz to ensure a single winning action), a movement was initiated with a motor delay of 180 ms. Movement direction corresponded to the chosen target location and movement speed was constant at 0.7 pixels/ms, resulting in a movement duration of ~450 ms for straight movement trajectories, in line with movement times measured in Experiment 1 of **Chapter 2**. Movement execution towards a chosen target continued even if the action node dropped below the threshold, unless another action node reached the firing rate threshold, in which case the movement was redirected towards the new target choice. Firing rates continued to be updated for 380 ms after initial threshold crossing due to a non-decision time consisting of sensory delays of 200 ms and motor delays of 180 ms (Albantakis & Deco, 2011). This caused decisions to be updated even after initial action onset (Resulaj et al., 2009; Albantakis & Deco, 2011). After the non-decision time, firing rate updates were stopped and the movement was completed according to the final target choice.

3.2.4 Model inputs

External model inputs were simulated at a rate of f_{in} = 60 Hz. Inputs into sensory nodes were presented after the sensory delay of 200 ms. The respective strength of inputs into S_1 and S_2 corresponded to the strength of sensory evidence, i.e., dot-motion coherence, and was calculated as:

$$in_{S1,S2} = f_{in}\,(1 \pm \frac{coh}{100}), \qquad (3.5)$$

with *coh* corresponding to the % coherence and +/– indicating whether or not motion direction corresponded to the neurons' preferred motion direction. By analogy, inputs into intention nodes depended on the strength of the endogenous colour intention *col*, i.e., the relative 'endogenous evidence' in favour of a given colour:

$$in_{I1,I2} = f_{in}(1 \pm \frac{col}{100}) \qquad (3.6)$$

Equations 3.5 and **3.6** ensured that model inputs were normalised, and hence, that the total input into the network was constant across different levels of sensory/endogenous strength. Similarly, the input into cost nodes was set to an equal value of 60 Hz at trial start. Once a movement was initiated, costs were updated relative to changes in Euclidean distance between the current position and each target location. Consequently, the total external inputs from all three sources of information (sensory, endogenous, costs) were balanced, and thus, only the *relative* strength of evidence from each source affected action selection.

3.2.5 Simulations

Systematic simulations were performed in order to test how changes in a given model parameter affected model outcomes. Each simulation consisted of 30 runs of 1000 trials each. In a given simulation, a single model parameter was varied, whereas all other model parameters were kept constant. In particular, unless stated otherwise, the model parameters introduced above were fixed (e.g., the connections between nodes and their respective weights). By contrast, the strength of evidence from each source of input was manipulated, i.e., the strength of sensory evidence from the RDM stimulus (*coh*), the strength of colour intention (*col*) and the target distance (*d*) in order to 1) test the sensitivity of model outcomes to changes in these input parameters, and 2) test whether the model produced patterns of behaviour that were comparable to our findings reported in **Chapter 2**. Furthermore, the effect of different degrees of neural noise was investigated. Specifically, the effect of hierarchical noise reduction through voluntary intentions was analysed by comparing models with different degrees of hierarchical control. Model performance was largely evaluated based on the following behavioural outcomes:

1) <u>*RTs*</u>: Point in time of initial response initiation, defined as the time t at which an action node first crossed the threshold, plus the motor delay of 180 ms. Trials in which action thresholds were crossed before stimulus onset (early responses, ~1%) or more than 1000

ms after stimulus onset (misses, ~3%) were excluded. Note that RTs were generally slightly faster for erroneous trials, but the patterns of changes in RTs was the same for correct/error trials. Hence, reported RTs include both correct and erroneous choices.

2) _Mean % errors_: Errors in initial/final target selection. In all simulations, the true correct choice was A_1 (left-blue). Two different types of errors can be differentiated:
    a) Perceptual errors (i.e., true dot-motion direction is left, but right target is chosen)
    b) Colour errors (i.e., true colour intention is blue, but green target is chosen)
3) _Mean % CoM_: Different types of CoM can be differentiated,
    a) Change of Movement (CoMov) where the perceptual decision is changed without a change in colour intention (e.g., $A_1 \rightarrow A_2$, switch from left-blue to right-blue)
    b) Change of Movement + Intention (CoMov+Int) where both the perceptual decision and colour intention are changed (e.g., $A_1 \rightarrow A_4$, switch from left-blue to right-green)
    c) Change of Intention (CoInt) where the intention changes without a change in the perceptual decision (e.g., $A_1 \rightarrow A_3$, switch from left-blue to left-green).

    Note that, although all types of CoM technically involve changes in an ongoing movement, for the sake of consistency with the terms used in **Chapter 2**, 'Change of Movement' refers to changes involving a perceptual CoM with regard to the dot-motion direction (i.e., switch from left to right or v.v.). By contrast, Change of Intention here does not involve a perceptual change, but instead corresponds to vertical changes between targets of different colour on the same side of the screen.
4) _CoM time_: Point in time of CoM relative to first threshold crossing.
5) _% corrective CoM_: CoM may reflect corrections of initial errors, either
    a) correcting perceptual error: Both CoMov and CoMov+Int involve perceptual switches, and hence, may reflect corrections of perceptual errors
    b) correcting colour error: CoInt and CoMov+Int involve colour switches, and hence, may reflect corrections of initial colour errors.

3.3 Results

3.3.1 Overall performance & CoM

First, in order to validate that the model was able to produce different types of CoM, simulations with a default set of fixed parameters were run. The parameters were obtained by exploring values of motion coherence (*coh*) and intentional strength (*col*) in a range from 0%[3], 3.2% 6.4% 12.8% 25.6% and 51.2% in line with previous models (Resulaj et al., 2009; Albantakis & Deco, 2011). Parameters that best matched participants' overall performance were selected (see below). Hence, dot-motion coherence was set to a low value of *coh* = 3.2% in line with the high difficulty of perceptual decisions in the task. The strength of colour intention was set to a high value of *col* = 51.2%, according to relatively strong colour intentions observed in participants as indicated by lower frequencies of CoMov+Int than CoMov. Finally, target distances from the centre were set to $x = 200$ and $y = 250$ according to the target locations used in Experiment 1 of **Chapter 2**.

Figure 3.2 illustrates model inputs and outputs of an individual simulated trial without CoM. Across all simulated trials, the model produced realistic choice behaviour with mean RTs of 626.0 ms (*SD* = 3.7 ms), perceptual errors in 38.3% of trials (*SD* = 1.7%) and colour errors in 4.0% of trials (*SD* = 0.6%). Note that the perceptual error rate is highly comparable with participants' performance in test trials (~40%). Hence, although the motion coherence chosen here was lower than the actual coherence levels used in the task, it was selected to approximate participants' overall task performance, rather than the actual dot-motion coherence of the task.

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[3] Note that for 0% coherence/intentional strength, correct choice options were assigned randomly.

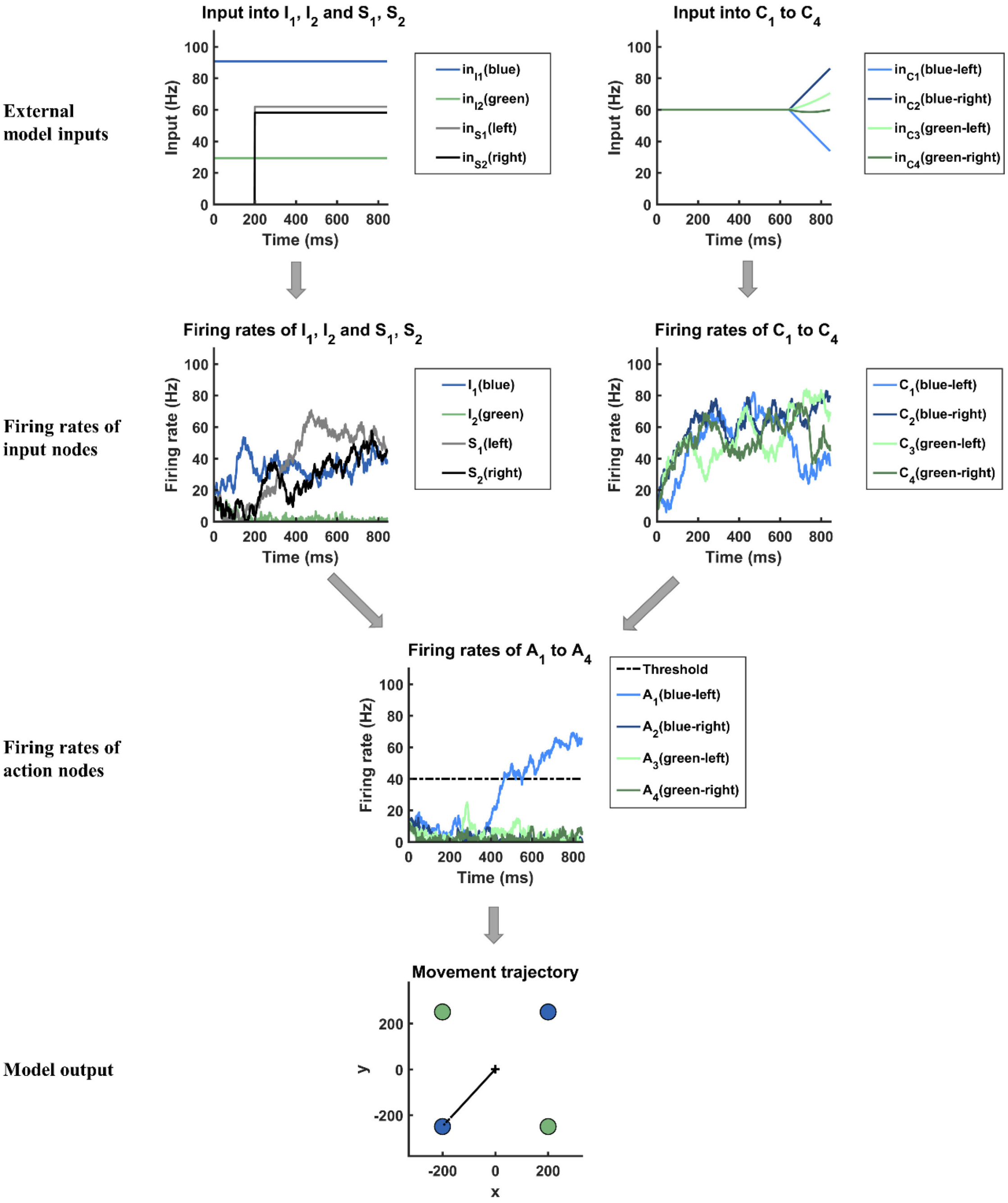

Figure 3.2. Simulation of a single trial without CoM. External model inputs (top row) are applied to intention, sensory and cost nodes (second row). Information is then combined by action nodes (third row) that determine the resulting movement trajectory (bottom row). In this example, the model correctly selects the left-blue target. After threshold crossing, the corresponding movement is initiated with a motor delay of 180 ms, and firing rates continue to be updated for a total non-decision time of 380 ms. Furthermore, inputs into cost nodes change after action initiation, according to the distance of the current cursor position to each target. Note that updates in cost nodes lag behind updates in action nodes due to the motor delay (i.e., costs only start changing 180 ms after a given action node has crossed the threshold).

Importantly, the model was able to capture CoM. Trials with double-CoM (*M* = 2.5%, *SD* = 0.5%) were excluded to simplify interpretation. The remaining CoM trials (*M* = 14.5%, *SD* = 1.0%) could be classified into CoMov, CoMov+Int, and CoInt. **Figure 3.3** illustrates examples of individual trials for each type of CoM (**Figures A2–A4** in Appendix A illustrate the same example trials including the firing rates of input nodes). As in the behavioural experiments, CoMov was more frequent (model: *M* = 9.7%, *SD* = 0.9%; Exp. 1 **Chapter 2**: *M* = 5.9%, *SD* = 5.5%) than CoMov+Int (model: *M* = 1.5%, *SD* = 0.4%; Exp. 1 **Chapter 2**: *M* = 1.7%, *SD* = 2.2%). Hence, when a perceptual CoM occurred, the model was more likely to switch to another action that corresponded to the same colour intention, instead of an action associated with the alternative colour intention. Furthermore, CoInt occurred in 3.4% of trials (*SD* = 0.6%), which is comparable to the frequency of vertical movement corrections observed in Experiment 1 (*M* = 3.2%, *SD* = 2.6%). As expected, the majority of CoInt trials (*M* = 75.0%, *SD* = 6.3%) reflected corrections of initial colour errors. By contrast, only 28.3% (*SD* = 13.3%) of CoMov+Int involved initial colour errors, whereas 64.5% (*SD* = 13.0%) of CoMov+Int reflected corrections of *perceptual* errors, which additionally involved a switch to the alternative colour. Similarly, 65.3% (SD = 4.5%) of CoMov reflected corrections of initial perceptual errors. Hence, as expected, CoMov and CoMov+Int were to a similar extent driven by an initially erroneous perceptual choice that was subsequently corrected by changing to a target associated with the alternative sensory state (e.g., right → left). Whether perceptual CoM resulted in CoMov or CoMov+Int was assumed to be driven by factors other than perceptual evidence, such as the cost associated with pursuing the initial colour (see section on target distance below). For example, **Figure A3** in Appendix A illustrates an example where the model initially selects the right-blue action, reflecting a perceptual error, which is subsequently corrected by switching to a left target. Instead of switching to the left-blue action according to the initial colour intention, the model switches to left-green, given that this action is associated with lower costs.

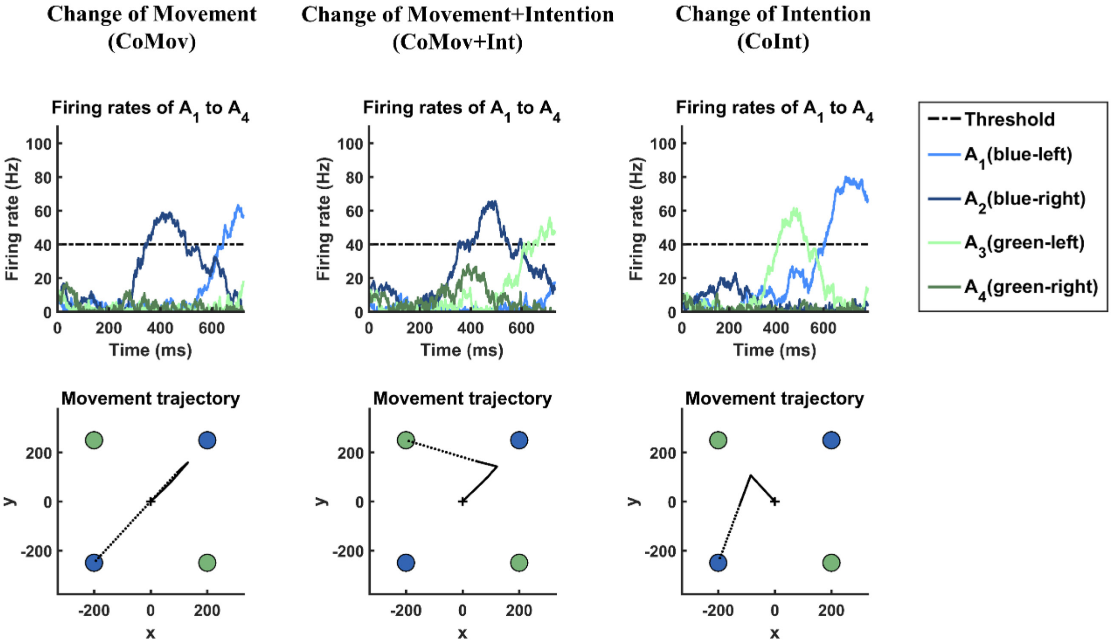

Figure 3.3. Model outputs of individual trials with CoM. Firing rates of action nodes (top row) and resulting movement trajectories (bottom row) are shown for trials with CoMov (left), CoMov+Int (centre) and CoInt (right). Dotted lines in movement trajectories indicate completion of movements after firing rates ceased to be updated (i.e., after non-decision time).

Note that CoM could only occur within a time window of 380 ms after initial threshold crossing based on the non-decision time. On average, CoM occurred 215.1 ms (*SD* = 6.4 ms) after initial decisions, which varied across the different types of CoM: CoInt occurred earlier (*M* = 169.2 ms, *SD* = 16.4 ms) than CoMov (*M* = 234.1 ms, *SD* = 10.3 ms) and CoMov+Int (*M* = 279.0 ms, *SD* = 23.2 ms), presumably due to the relatively high strength of colour intentions and the fact that intentions were activated prior to sensory inputs, causing colour errors to be corrected early on. More interestingly, CoMov+Int occurred slightly later than CoMov, which was expected given that differences in motor costs are larger towards the end of the movement (see **Figure 3.2**, top-right), and hence, motor costs should be more likely to cause intention reversals the later the CoM occurs. Note that this was also predicted for behavioural results in **Chapter 2** (see **Figure 2.4**). However, in **Chapter 2**, we did not find that CoMov+Int occurred later than CoMov (results not reported), possibly because the point in time at which decision reversals occurred is difficult to estimate in real movement trajectories. In addition to the small trial numbers with CoM, we may not have had sufficient power to detect such subtle differences in the timing of decision reversals. Hence, compared to purely behavioural measures, the current computational model might enable more detailed insights into the precise time course of decision updates and their implementation into motor action.

3.3.2 Effect of sensory evidence

In order to test how the strength of sensory evidence affected model outcomes, simulations were run with varying levels of dot-motion coherence of *coh* = 0%, 3.2%, 6.4%, 12.8%, 25.6%, or 51.2%, while the other parameters were kept constant (*col* = 51.2%, target locations: *x* = 200, *y* = 250). In line with previous studies (e.g., Resulaj et al., 2009; Albantakis & Deco, 2011) and the findings reported in **Chapter 2**, higher dot-motion coherence was associated with faster RTs and fewer perceptual (but not colour) errors (**Figure 3.4A–B**). Furthermore, higher dot-motion coherence caused a lower frequency of perceptual CoM, i.e., fewer CoMov and CoMov+Int (**Figure 3.4C**). Interestingly, higher dot-motion coherence caused a slight increase in colour errors and CoInt – presumably because stronger sensory evidence meant that neural noise more strongly affected colour selection. Finally, higher dot-motion coherence caused CoMov and CoMov+Int to occur earlier (**Figure 3.4D**) and more likely to correct an initial perceptual error (**Figure 3.4E**). This is because sensory evidence in favour of the correct choice option was stronger, and hence, was obtained faster and was more likely to result in a correct final choice. Hence, temporal integration of strong sensory post-decision evidence informed decision reversals in favour of the correct perceptual choice, and as a result, improved performance.

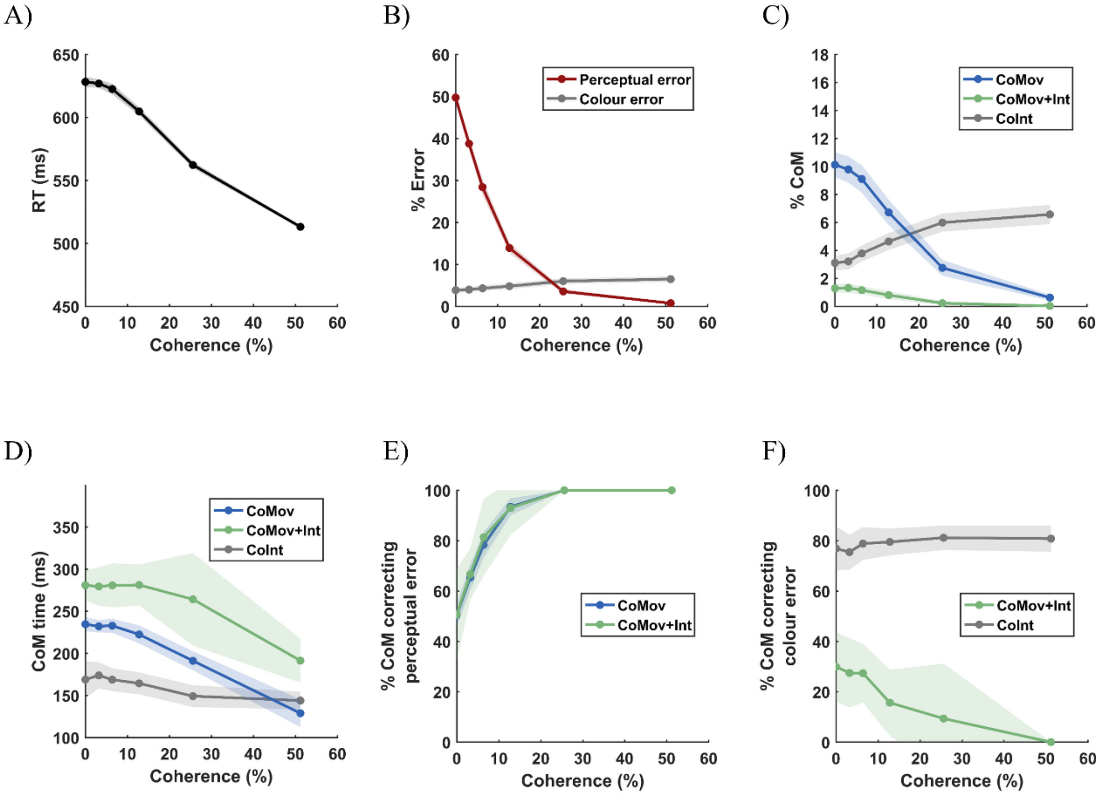

Figure 3.4. Effect of sensory evidence on model outcomes. Effect of dot-motion coherence (*coh*) on reaction times (A), % errors with regard to perceptual choice and colour choice (B), % of trials with different types of CoM (C), time point at which CoM occurred (D), % of CoM involving perceptual switch that corrected an initial perceptual error (E), and % of CoM involving colour switch that corrected an initial colour error (F) [*M* ± 1 *SD*].

3.3.3 Effect of strength of colour intention

In Experiment 1 of **Chapter 2**, participants varied in the relative frequency of CoMov+Int and participants with stronger colour intentions were less likely to switch colours when changing their movements. In order to check whether the model could reproduce this finding, simulations with different degrees of intentional strength *col* = 0%, 3.2%, 6.4%, 12.8%, 25.6% and 51.2%

were performed, while the other parameters were kept constant (*coh* = 3.2%, target locations: x = 200, y = 250). Note that changes in the strength of intention should have different effects than changes in the strength of sensory evidence, not only because they are conceptually different (i.e., they are associated with different action alternatives), but also, because of mathematical reasons. Specifically, compared to sensory nodes, intention nodes had a) slightly weaker connections to action nodes (because of dot-motion priority in the task), b) did not have self-excitatory connections and c) exerted top-down control over noise in action selection (see section 3.5 below).

As predicted from our behavioural findings, stronger colour intentions were associated with a decrease in CoMov+Int and an increase in CoMov (**Figure 3.5C**). Hence, the relative frequency of CoMov+Int out of all perceptual CoM decreased with stronger intentions. Note that stronger colour intentions also caused fewer colour errors (**Figure 3.5B**). However, even when trials with colour errors were excluded, CoMov+Int decreased relative to CoMov. This was due to the fact that stronger colour intentions shifted the percentage of colour errors that were corrected disproportionally towards CoInt, whereas CoMov+Int correcting colour errors were less frequent for stronger intentions (**Figure 3.5C**). Hence, stronger colour intentions did not reduce CoMov+Int by reducing the number of colour errors that had to be corrected. Instead, our modelling results suggest that, when a perceptual CoM occurred, stronger colour intentions caused the model to favour the original colour intention, rather than switching to the alternative colour, hence reducing the frequency of CoMov+Int relative to CoMov. Interestingly, strength of intention only had a weak effect on the point in time of CoInt, in that CoInt only occurred slightly faster for very strong intentions compared to weak intentions (**Figure 3.5D**). This is presumably due to the fact that colour corrections generally occurred very early due to the head start of intentions (in both the model and the task), causing a floor effect in the timing of CoInt.

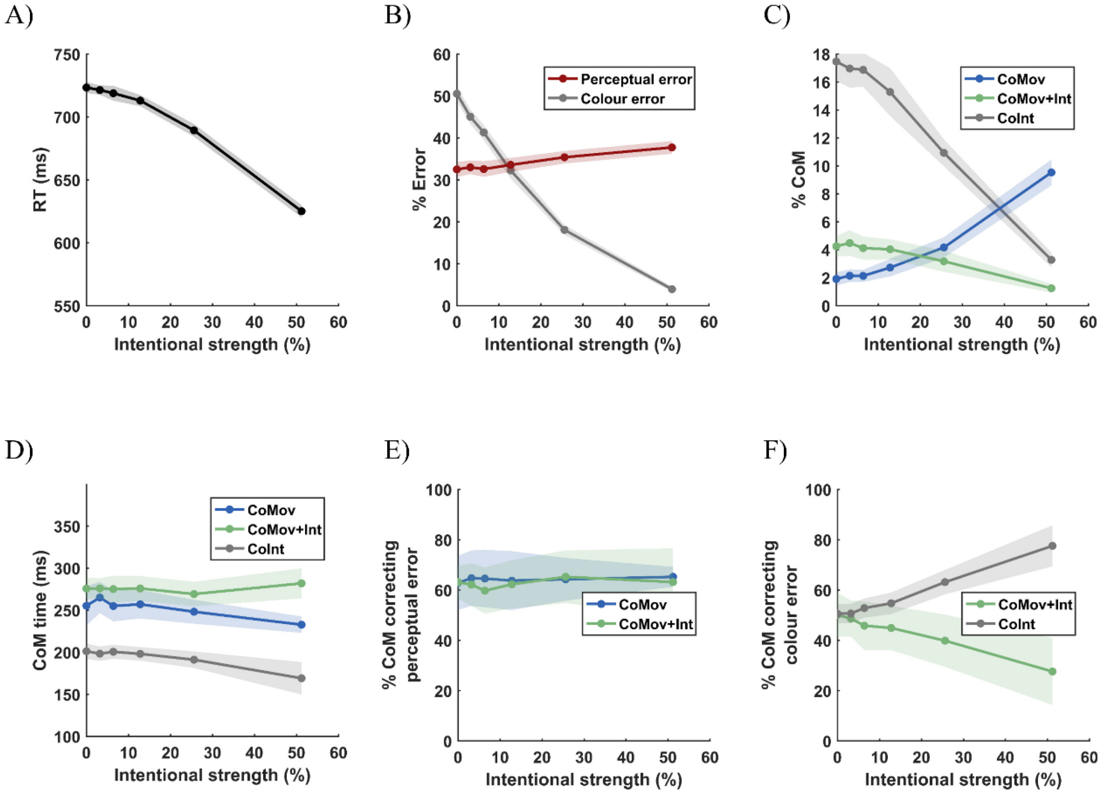

Figure 3.5. Effect of intentional strength on model outcomes. Effect of strength of intention (*col*) on reaction times (A), % errors with regard to perceptual choice and colour choice (B), % of trials with different types of CoM (C), time point at which CoM occurred (D), % of CoM involving perceptual switch that corrected an initial perceptual error (E), and % of CoM involving colour switch that corrected an initial colour error (F) [*M* ± 1 *SD*].

Importantly, the model could also reproduce reaction time costs observed in conflict trials in which both targets of the same colour were located on the same side of the screen (**Figure 2.1**, **Chapter 2**). In line with the task, motion coherence was set to a high value (*coh* = 51.2%) to simulate conflict trials. Furthermore, the model was changed such that intention nodes mapped onto actions corresponding to targets associated with the same dot-motion direction (i.e., blue →

both left actions A_1 and A_3; green → both right actions A_2 and A_4). The true colour intention of a given trial was selected randomly in order to induce a mismatch between colour intention and perceptual input on ~50% of trials (e.g., intention = green and both green targets are on the right side, but dot-motion direction = left). This caused an overall increase in RTs for trials with correct perceptual choices ($M = 540.9$ ms, $SD = 1.4$ ms) compared to the model without any conflict trials ($M = 513.0$ ms, $SD = 1.5$ ms). Additionally, RT costs in conflict trials were larger for strong colour intentions ($col = 51.2\%$: $\Delta RT = 27.9$ ms) compared to weak intentions ($col = 3.2\%$: $\Delta RT = 4.3$ ms). Hence, stronger colour intentions caused higher reaction time costs in conflict trials, and at the same time, caused fewer Changes of Intention in test trials. Thus, in line with our assumption in **Chapter 2**, inter-individual differences in the strength of colour intentions may have been the underlying mechanism causing the observed correlation between RT costs in conflict trials and the frequency of CoMov+Int in test trials (**Figure 2.3C**, **Chapter 2**).

3.3.4 Effect of motor costs

In Experiment 2 of **Chapter 2**, target distance was manipulated in order to investigate the effect of motor costs on CoM. When horizontal target distance was short (close targets), switching to the target of different colour when a perceptual CoM occurred allowed participants to save costs in terms of time and/or effort. As a result, CoMov+Int was more frequent when horizontal target distance was close compared to when it was far, while the overall frequency of CoM was not affected by target distance. Hence, motor costs did not affect whether or not a decision reversal occurred, but instead, affected which type of CoM occurred. By analogy, simulations with different target locations were run where horizontal target distance was either close ($x = 100$, $y = 300$) or far ($x = 300$, $y = 100$), while keeping the other parameters constant ($coh = 3.2\%$, $col = 51.2\%$). Note that target distance from the centre was equal for all targets, and hence, initial costs were constant across simulations. Instead, the relative change in costs after action onset varied as a function of the target locations. As predicted, the model could reproduce the behavioural finding, showing an increase in CoMov+Int for close compared to far targets, whereas CoMov was slightly reduced in close compared to far targets (**Figure 3.6**). Hence, the relative frequency of CoMov+Int out of all perceptual CoM increased with close targets.

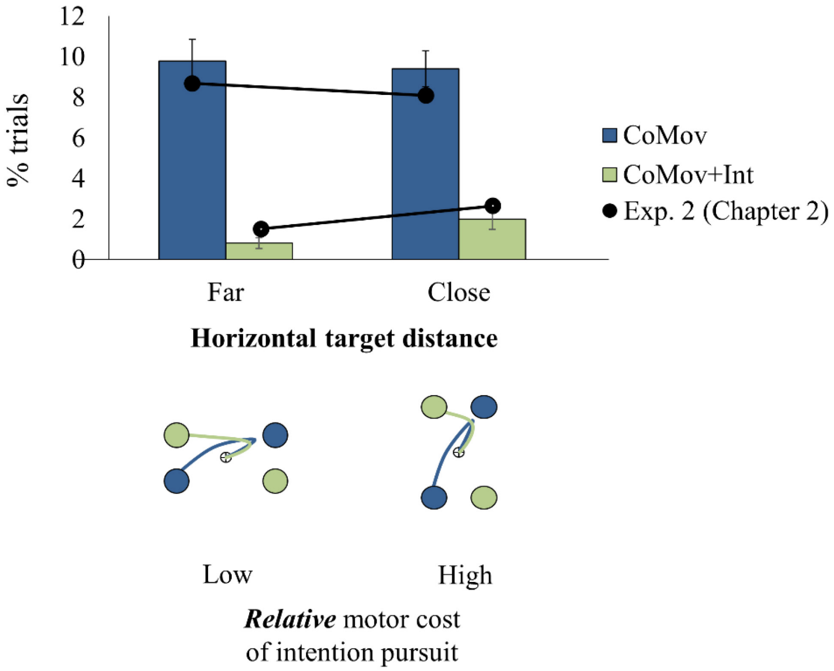

Figure 3.6. Effect of motor costs on CoM. Effect of relative motor costs (target distance) on frequency of CoMov (blue) and CoMov+Int (green) [*M* ± 1 *SD*]. Black data points represent behavioural results observed in Exp. 2 in **Chapter 2**.

Importantly, target distance did not affect the rate of perceptual errors (close: *M* = 38.3%, *SD* = 1.7%; far: *M* = 38.8%, *SD* = 1.9%), nor the rate of colour errors (close: *M* = 3.9%, *SD* = 0.6%; far: *M* = 3.8%, *SD* = 0.7%). Hence, the same effect of target distance on CoMov+Int was observed when trials with colour errors were excluded (results not shown), suggesting that higher frequencies of CoMov+Int for close targets cannot be attributed to a potential increase in colour errors. Furthermore, RTs were highly comparable across target distance conditions (close: *M* = 626.0 ms, *SD* = 3.7 ms; far: *M* = 626.1 ms, *SD* = 3.8 ms). This suggests that target distance (i.e., motor costs) directly affected continuous updates of colour intentions after action onset, rather than inducing changes in initial action selection.

Finally, in the behavioural task, the effect of target distance was stronger for trials with late compared to early target-onset time (**Figure 2.5**). Given that the current model did not explicitly model target onset, we were not able to directly implement this manipulation in the model. Possibly, pre-activation of action nodes corresponding to the chosen colour prior to stimulus onset could be used to mimic advance motor planning that presumably occurred in trials with early target onset. However, preliminary results indicated that this did not have any effect on the difference in CoMov or CoMov+Int in far vs. close targets (results not shown).

3.3.5 Effects of neural noise

In all simulations reported above, only parameters concerning external model inputs were varied in order to test whether the model produced patterns of results that resembled the behavioural findings. However, parameters of the network itself can provide further insights into how differences in network properties can affect behavioural outcomes. Of particular interest here is the role of neural noise, and more specifically, the assumed role of voluntary intentions in regulating the degree of noise in action selection.

First, the degree of neural noise was varied with σ^2 ranging from 0 to 3 Hz (**Figure 3.7**). Higher neural noise decreased RTs at the cost of higher error rates (**Figure 3.7A–B**). Furthermore, as expected, all types of CoM were more frequent for higher levels of noise (**Figure 3.7C**). Hence, neural noise changed the global dynamics of the network, rendering attractor states less stable overall. Additionally, higher noise reduced the frequency of corrective CoMs. That is, with higher degrees of noise, perceptual CoM was less likely to reflect correction of an initial perceptual error (**Figure 3.7E**) and CoInt was less likely to reflect colour correction, which instead was more strongly reflected in CoMov+Int (**Figure 3.7F**). Hence, the effect of CoM on improving performance was smaller the stronger noise fluctuations were within the network.

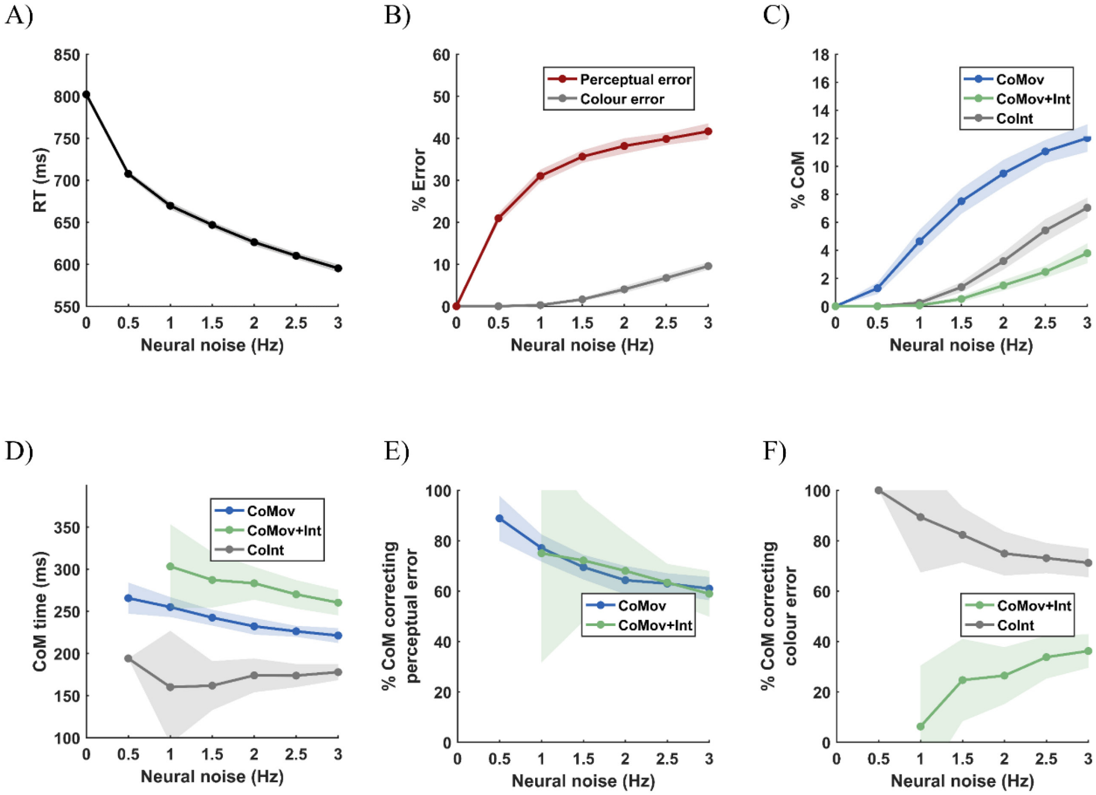

Figure 3.7. Effect of neural noise on model outcomes. Effect of level of neural noise (σ^2) on reaction times (A), % errors with regard to perceptual choice and colour choice (B), % of trials with different types of CoM (C), time point at which CoM occurred (D), % of CoM involving perceptual switch that corrected an initial perceptual error (E), and % of CoM involving colour switch that corrected an initial colour error (F) [*M* ± 1 *SD*].

More interestingly, the degree of noise in the current model was not constant throughout a given trial. Instead, the degree of noise in action nodes depended on the state of their associated higher-order intentions. In order to investigate whether and how hierarchical noise modulation affected model behaviour, simulations with varying degrees of hierarchical control were compared. This was implemented by adding a coefficient h to **Equation 3.4**, indicating the degree to which noise in A_1 to A_4 was reduced as a function of the firing rates of intention nodes:

$$\sigma^2{}_{A1,t/A2,t} = \sigma_0^2 - h\frac{r_{I1,t-1}}{100}\sigma_0^2 \quad \text{and} \quad \sigma^2{}_{A3,t/A4,t} = \sigma_0^2 - h\frac{r_{I2,t-1}}{100}\sigma_0^2 \qquad (3.7)$$

Simulations with varying degrees of hierarchical control (h = 0, 0.25, 0.5, 0.75, 1, 1.5, 2, 3) were conducted, where $h = 0$ corresponds to a model without hierarchy and $h = 3$ corresponds to strong hierarchical control. All other model parameters were kept at their default values (*coh* = 3.2%, *col* = 51.2%, $x = 200$, $y = 250$, initial $\sigma^2 = 2$ Hz).

Stronger hierarchical control slowed down responses and slightly increased perceptual choice accuracy (**Figure 3.8A–B**). This is in line with the role of noise reported above. That is, noise-induced responses tend to be fast and erroneous, and hence, noise reduction through hierarchical control reverses this effect. More interestingly, however, the strongest effect of hierarchical control was observed for the rate of CoMov, which decreased with higher levels of noise reduction (**Figure 3.8C**). Furthermore, CoMov tended to occur slightly later with stronger hierarchical control. By contrast, the other types of CoM were not affected by hierarchy, nor was the percentage of corrective CoMs. Reduction in CoMov was largely driven by the fact that perceptual error rate was reduced, hence decreasing the need to correct perceptual errors later on. However, even when excluding perceptual errors, CoMov was reduced in a model with strong hierarchy of $h = 3$ (*M* = 1.6%, *SD* = 0.6%) compared to a model with no hierarchy (*M* = 4.5%, *SD* = 0.6%). Together, these results suggest that hierarchical control reduced variability in movement selection, and hence, in how a given intention was implemented into motor action, without affecting selection of the intention itself. Note that the degree of these effects varied with intentional strength. As expected, for weaker intentions, hierarchical control had weaker effects on variability in movement selection, and hence, on reduction of CoMov. The opposite effect was observed when varying the level of dot-motion coherence. That is, higher coherence caused hierarchical control to have a weaker effect on variability in movement selection (which generally had low variability when dot-motion coherence was high).

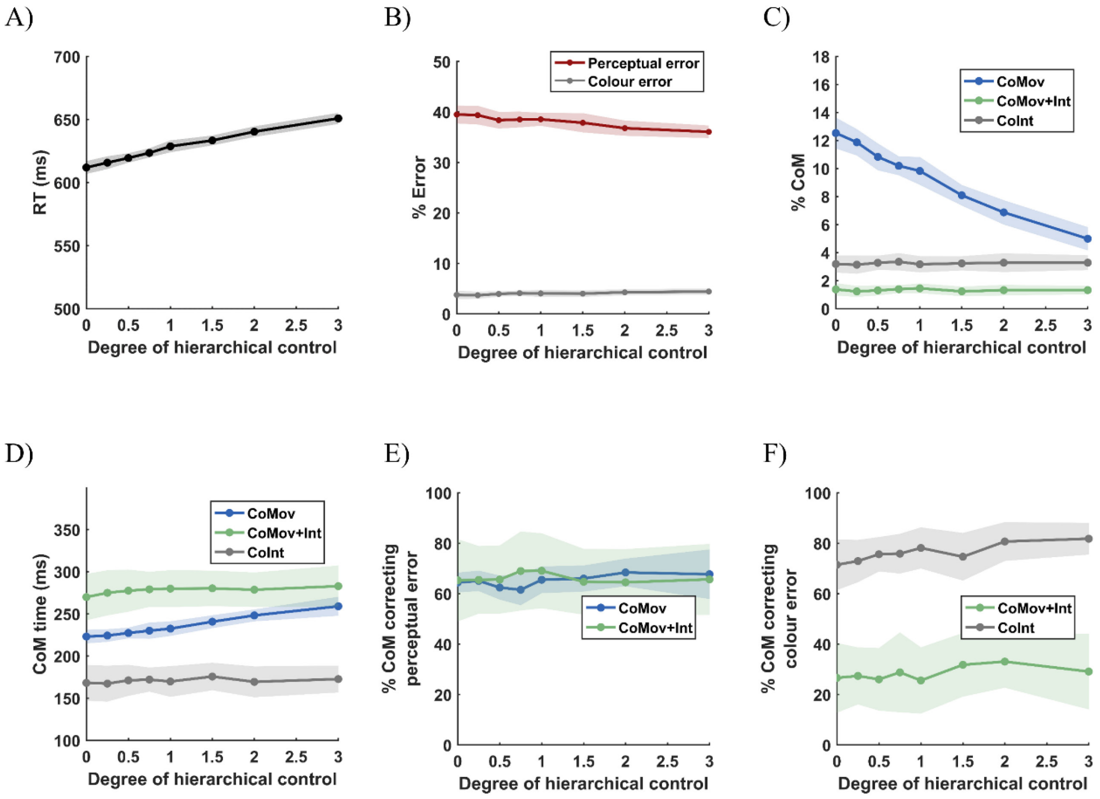

Figure 3.8. Effect of hierarchical control on model outcomes. Effect of degree of hierarchical control (*h*) on reaction times (A), % errors with regard to perceptual choice and colour choice (B), % of trials with different types of CoM (C), time point at which CoM occurred (D), % of CoM involving perceptual switch that corrected an initial perceptual error (E), and % of CoM involving colour switch that corrected an initial colour error (F) [*M* ± 1 *SD*].

3.3.6 Summary of results

Table 3.1 provides an overview of the main findings with regard to CoMov and CoMov+Int obtained with the current modelling approach. Higher dot-motion coherence decreased the frequency of both types of CoM. Stronger intentions reduced the frequency of CoMov+Int, but increased the frequency of CoMov. Higher relative costs of intention pursuit had the opposite effect, in line with the assumption that intention pursuit depends on a trade-off between voluntary intentions and their associated costs. Finally, higher levels of neural noise increased the frequency of both types of CoM, and noise reduction through higher-order intentions specifically reduced the frequency of CoMov, but did not affect CoMov+Int.

Table 3.1. Summary of model results.

Model parameter	***% CoMov***	***% CoMov+Int***
↑ dot-motion coherence (*coh*)	↓	↓
↑ intentional strength (*col*)	↑	↓
↑ relative cost of intention pursuit (*d*)	↓	↑
↑ neural noise (σ^2)	↑	↑
↑ hierarchical noise reduction (*h*)	↓	=

3.4 Discussion

While previous computational models of CoM have exclusively focused on perceptual choice (Resulaj et al., 2009; Albantakis & Deco, 2011), the attractor network model introduced here captures the dynamic integration of different sources of information that can drive different types of CoM in voluntary action. Specifically, the model continuously integrates higher-order endogenous intentions with lower-level sensorimotor information in order to guide decisions between multiple available courses of action. Dynamic fluctuations can cause changes in attractor states, i.e., transitions from one action alternative to a different one during ongoing movement execution. These changes can either reflect reversals about perceptual decisions requiring a change in *how* to implement an intention into action, and/or a change in *what* intention to implement. Which type of CoM occurs depends on the combined neural activity in a network of neurons whose respective firing rates encode endogenous intentions, perceptual inputs, motor costs, and action representations. Interconnectivity between neural populations allows for decision making through a distributed consensus where various pieces of relevant information are integrated in a dynamic manner in order to guide action selection (Cisek, 2012; Yoo & Hayden, 2018).

Systematic simulations showed that the model could qualitatively reproduce the pattern of behavioural results reported in **Chapter 2**. More specifically, we tested how sensitive multiple features of model outcomes were to variations in parameters. The model accurately predicted that high noise in sensory evidence increases the overall likelihood of perceptual CoM, whereas the strength of intention and its trade-off with associated motor costs determines whether that change results in a Change of Movement or a Change of Movement + Intention. The model also produced Changes of Intention that did not involve a perceptual CoM – in line with the vertical movement corrections observed in **Chapter 2**. As expected, these types of changes were largely driven by initial colour errors, which may have occurred due to difficulty in target detection in the task. By contrast, Changes of Movement + Intention largely reflected a deviation from the original (correctly-selected) colour target when an ongoing action had to be changed based on new sensory evidence from the RDM stimulus. Whether or not perceptual CoM resulted in a change in the colour intention depended on motor costs. That is, in line with the behavioural findings, the model predicted more intention reversals when the cost of intention pursuit was high relative to the cost associated with switching to a nearby target of different colour.

Hence, the model proposed here provides a valid framework for the continuous and dynamic integration of multiple sources of information that guide voluntary action. Furthermore, neural networks may be a biologically plausible account of the non-linear dynamics underlying action selection in the brain (Christopoulos et al., 2015). Neural populations in the current model may broadly correspond to functionally-specialised anatomical brain regions. Specifically, the sensory nodes S_1 and S_2 are analogous to neural populations in posterior parietal cortex (e.g., lateral intraparietal cortex) that accumulate sensory evidence based on inputs from direction-sensitive neurons in the middle temporal visual area MT/V5 (Newsome, Britten, & Movshon, 1989; Shadlen & Newsome, 1996; Gold & Shadlen, 2007). The current model captured this process of sensory evidence accumulation in a biologically realistic manner through recurrent self-excitatory connections allowing for integration of perceptual information over time (Wong & Wang, 2006; Cain, Barreiro, Shadlen, & Shea-Brown, 2013). The network nodes encoding voluntary colour intentions may reflect regions in MFC and precuneus that have been shown to generate endogenous ‘what’ decisions and guide action selection through a medial action pathway (Passingham, 1987; Brass & Haggard, 2008; Soon et al., 2013; Zapparoli et al., 2018). Finally, action nodes correspond to areas in pre-motor cortex, which generate motor commands that are then sent to primary motor cortex to initiate a movement – or change an ongoing movement when new information is obtained (Wise & Mauritz, 1985; Buch et al., 2010; Pastor-Bernier et al., 2012).

3.4.1 Role of action representations

Importantly, action nodes in the current model were not simply a mere ‘output’ system of higher-order decision-making areas, but instead, were actively involved in the decision process itself by competing against each other taking into account combined information from other neural populations. Hence, action nodes served as a neural hub that integrated different sources of decision-relevant information and determined which action was selected for execution through a winner-take-all competition. In line with previous studies, multiple action representations evolved in parallel, in a dynamic and gradual manner depending on the current state of evidence in favour of each action (Cisek & Kalaska, 2005; Cisek, 2007; Pastor-Bernier & Cisek, 2011; Selen, Shadlen, & Wolpert, 2012; Thura & Cisek, 2014; Yoo & Hayden, 2018).

Additionally, action nodes had direct access to information about motor costs associated with a given movement. Cost representations may be directly encoded within an ‘action space’ in dorsomedial frontal brain areas (Walton, Bannerman, & Rushworth, 2002; Rudebeck, Walton, Smyth, Bannerman, & Rushworth, 2006; Prévost, Pessiglione, Météreau, Cléry-Melin, & Dreher, 2010), allowing for efficient and rapid integration of motor costs during ongoing action selection (Cisek, 2007). Such efficient encoding of costs in brain regions that are also involved in action implementation may be particularly relevant when costs change dynamically, e.g., during continuous motor actions where costs can change constantly according to the current position. In our task in **Chapter 2**, participants may in principle have been able to fully anticipate future action costs since target locations were revealed at the same time as sensory evidence. Hence, it is possible that participants simply changed their decision strategies prior to action onset, for example, by applying a more conservative threshold when targets were far (Moher & Song, 2014). Indeed, people anticipate motor costs of future courses of action in advance in order to optimise movement selection and planning (Cos et al., 2011). However, this may not be efficient in cases where a high number of action alternatives co-exist, or when action costs can change dynamically as a function of online updates during execution. In particular, in the current paradigm, the relative cost of each of the four action alternatives varied as a function of the state of the action (current location). Hence, rather than fully anticipating all potential future action states and their associated cost functions, the current model may provide a more efficient account where motor costs are updated in an online manner and directly depend on the state of the action representations. Hence, motor costs may, at least to some extent, be estimated in parallel to movement generation and updating, for example, based on an efference copy of the current motor command and potential alternative motor commands (Wolpert & Ghahramani, 2004; Scott, 2012).

In that context, another advantage of the current model is that it explicitly takes into account the resulting motor action, and its effect on subsequent decision updates by causing changes in motor costs. In fact, given that in many situations, decision making and action selection are not strictly separate and serial processes (Cisek, 2007; Rushworth et al., 2012; Yoo & Hayden, 2018), it seems essential to incorporate action representations into models of decision making. Yet, previous models of CoM have focused on modelling the point in time when a decision is generated (or reversed) based on when a decision variable crosses a given threshold, without considering the resulting action itself. Hence, these models have not captured how motor output informs the decision process. Although the movement trajectories generated by the current model are very simplistic, the model can easily be extended in order to obtain more biomechanically realistic movements. For example, instead of assuming constant movement velocity after threshold crossing, movement speed could be determined gradually as a function of the current firing rate of the winning action node, and hence, the current state of evidence in favour of a chosen action (Cisek, 2007; Pastor-Bernier & Cisek, 2011; Selen et al., 2012; Thura & Cisek, 2014; Yoo & Hayden, 2018). Additionally, instead of limiting action execution to four categorical movement directions, movement kinematics could be defined as the weighted average of movement directions where weights depend on the current state of each action node (Christopoulos et al., 2015). In line with this, previous studies have provided evidence for spatial averaging of movement alternatives in decision making under conflict (Song & Nakayama, 2009; Travers, Rolison, & Feeney, 2016) or uncertainty (Hudson, Maloney, & Landy, 2007; Chapman et al., 2010). These effects could be captured by implementing more detailed motor control policies in the current model that incorporate gradual differences in movement speed and direction, and hence, capture fine-grained details of realistic movement trajectories and their interaction with the decision process itself. This would allow for a more direct comparison of movements (and changes in movements) produced by the current model and the actual kinematics measured in behavioural paradigms. More detailed insights into the relation between decision processes and motor output are highly important to allow for more accurate inferences about the underlying decision-making process based on observed movement trajectories. For example, this may be useful to obtain better estimates of the point in time at which a decision reversal occurred during an observed movement.

3.4.2 Hierarchical noise control

Finally, the current chapter explored the role of the degree of neural noise, and in particular, the assumed role of voluntary intentions in reducing noise in movement selection (Khalighinejad et al., 2018). Higher noise generally rendered the network more labile, causing faster and more erroneous responses, and more CoM overall – in particular Changes of Movement, given the additional noise in external perceptual inputs that made perceptual decision reversals particularly likely. Top-down noise reduction through voluntary intentions reversed these effects. That is, with higher degrees of hierarchical control, response initiation slowed down and caused fewer erroneous perceptual decisions about the noisy dot-motion stimuli. Consequently, the need to change an ongoing movement later on based on new perceptual evidence was reduced with strong intentions. This suggests that voluntary control in the model reflected an increase in deliberation time that reduced the need to subsequently adjust movements during ongoing action execution.

Hierarchical control also resulted in a lower frequency of Changes of Movement that did not reflect error corrections. Hence, beyond mere error-related processing, noise reduction caused an increased stability in movement selection overall, in line with a recent study showing that voluntary intentions are associated with reduced variability in readiness potentials (Khalighinejad et al., 2018). Importantly, in the current model, these effects further varied with the strength of intentions. Specifically, the effects of top-down noise control were stronger when intentional strength was high. Furthermore, the effects were stronger when sensory stimuli were weak. This suggests that hierarchical control through volition is particularly *effective* when intentions are strong, and may be especially *relevant* when sensorimotor noise is high, which may require a higher degree of deliberate motor control, for example, to shield movement selection from noisy sensory distractions (Kilintari et al., 2018).

3.4.3 Limitations & open questions

It remains to be investigated to what extent such hierarchical control through voluntary intentions in fact exists, and whether it is indeed implemented through noise reduction. The idea of hierarchical organisation in the brain, and within frontal regions, is not new. In fact, in line with the current hierarchical architecture, it has been proposed that within the frontal cortex, more anterior regions representing abstract information (e.g., goals) exert top-down control over more posterior regions involved in lower-level sensorimotor control (R. C. O'Reilly, 2010; Badre & Nee, 2017). How exactly such top-down control is implemented is less clear. It has been suggested that higher-order areas exert control by 'gating' input/output in lower-level areas (Badre & Nee, 2017). This may in fact be closely linked to noise reduction mechanisms in that higher signal-to-noise ratio allows for selection of more relevant pieces of information as opposed to noisy distractors. However, it raises another question: How exactly can noise reduction be achieved in the brain? It has been proposed that the dopaminergic system plays an important role in neural noise regulation. For example, the 'dual-state' theory proposes that the balance between D_1 and

D_2 receptor activation affects signal-to-noise ratio of neural activity, and hence, may be crucial for the balance between stability and flexibility of actions (Durstewitz & Seamans, 2008). Specifically, D_1 states are characterised by attractors that tend to remain stable, whereas D_2 dominated states are characterised by a higher degree of flexibility. Furthermore, dopaminergic medication in Parkinson's disease is closely linked to cognitive flexibility, but also impulsivity, suggesting that the dopaminergic system plays a crucial role in determining the trade-off between flexibility vs. stability (Cools et al., 2003; Sinha, Manohar, & Husain, 2013). However, whether and how these processes can be modulated through processes involved in voluntary control remains an open question. The current model makes novel predictions regarding how such noise regulation would affect the frequency of different types of CoM. Hence, CoM may provide a useful measure to directly test the role of noise (and its regulation through higher-order intentions) for behavioural outcomes, and further investigate the neural mechanisms underlying these putative processes.

The main limitation of the current model may be that it has many free parameters due to the relatively high number of nodes and their connections. Although an attempt was made to limit model parameters based on reasonable conceptual assumptions, more parsimonious models may be able to generate similar outcomes. In that context, formal model fitting would be required in order to allow for direct quantitative comparison with other types of models or different network architectures. However, the aim of this chapter was of a more conceptual nature, and for this purpose, the current model seemed to capture participants' behaviour sufficiently well, and more importantly, could reproduce the predicted pattern of changes in outcomes as a function of changes in model parameters.

3.4.4 Implications

In line with our current approach, previous studies have demonstrated how simulations with attractor network models can provide important new insights into the putative mechanisms underlying behavioural flexibility and its disturbances. For example, it has been shown that increases in excitatory activity can render networks unable to terminate a given attractor state and transition on to another state, causing repetitive patterns of activity that persist over time (Rolls, 2012). This may explain intrusive thoughts and repetitive behaviour in OCD, which has been linked to high levels of glutamatergic neurotransmission (Maia & McClelland, 2012; Rolls, 2012). A similar effect can be caused by increases in NMDA (N-methyl-d-aspartate) receptor conductances, which are characterised by slow base time constants, and hence, slower decay of excitatory activity over time (Rolls, 2012). Additionally, inhibitory competition also contributes to stabilisation of firing rates. For example, reduced GABAergic neurotransmission can render attractor states less stable because, under low inhibitory activity, noise-induced changes in firing rates can evolve into an attractor state (or a change in attractor state) too quickly (Loh, Rolls, & Deco, 2007). This may explain impulsive behaviour or distractibility in ADHD (Lo, Boucher, Paré, Schall, & Wang, 2009). Hence, systematic simulations enable a mechanistic understanding of how observed patterns of behaviour may be generated in the brain, and how changes in intrinsic network properties may account for intra- and inter-individual differences in the flexibility vs. stability of action selection.

3.4.5 Conclusion

The proposed model offers a novel conceptual framework for the dynamic and flexible control of voluntary actions through a network of neural populations that continuously evaluate and integrate information. Intrinsic dynamics of the attractor network can account for CoM during voluntary action, which may either reflect changes in higher-order endogenous intentions or changes in lower-level movements. The model suggests that different types of CoM may have a common underlying mechanism that continuously updates, and integrates, endogenous and exogenous information within the same neural circuit. Which type of CoM occurs depends on the relative strength of evidence in favour of a given action alternative based on the combined activity of different neural modules. Furthermore, hierarchical control through voluntary intentions allows for top-down regulation of the balance between flexibility and stability of action selection. The model may be a biologically plausible account of the neurocognitive mechanisms underlying dynamic control of voluntary action and its disturbances in a wide range of psychiatric conditions.

Chapter 4.

Decoding Changes of Mind in voluntary action – Dynamics of choice representations in a fronto-parietal network

4.1 Introduction

In **Chapters 2** and **3**, the cognitive and computational mechanisms of CoM in voluntary action were investigated. We showed that endogenous intentions are continuously integrated with external information from the environment. Changes in the environment – or in how the environment is perceived – can trigger a CoM, which may involve a change in the ongoing movement and/or a change in the endogenous intention. Whether or not an intention is changed depends on effort or temporal costs associated with pursuing the original intention. The aim of the current fMRI study was to investigate the neural mechanisms underlying these dynamic and integrative processes. Specifically, this chapter addresses the question of how brain regions involved in decision making and action selection integrate new exogenous inputs that provide updates about costs and rewards associated with reaching an endogenous goal – and as a consequence, may trigger a change with respect to the initial intention. While the neural basis of Changes of Movement has been studied extensively (e.g., Wise & Mauritz, 1985; Buch et al., 2010; Pastor-Bernier et al., 2012; Saberi-Moghadam et al., 2016), the mechanisms underlying changes in higher-order endogenous intentions remain largely unclear.

Internally- vs. externally-guided actions have previously been attributed to distinct medial vs. lateral pathways of action selection, respectively (Passingham, 1987). More specifically, voluntary intentions may be generated in media frontal cortex (MFC) and precuneus (Fried et al., 1991; Soon et al., 2008; Bode et al., 2011; Fried et al., 2011; Krieghoff et al., 2011; Bode et al., 2013; Soon et al., 2013; Zapparoli et al., 2018). MFC forms an ‘intentional hub’ that integrates various components of voluntary decisions about *what* to do, *when* to do it, and *whether* to do it at all, whereas the role of partietal cortex appears to be more specific to voluntary *what* decisions (Zapparoli et al., 2018). Precuneus may contribute to these decisions by resolving conflict when choice options appear to be equal, hence preventing behavioural stalemate (Bode et al., 2013). Lateral fronto-parietal areas might be important to represent counterfactual choice options after an initial voluntary decision has been made, for example in dorsolateral prefrontal cortex (dlPFC; Rens et al., 2018). Angular gyrus (AG) has been implicated in shaping the conscious experience of voluntary actions by monitoring the implementation of intentions into motor actions and generating a predictive model of the upcoming movement (Sirigu et al., 2004; Chambon et al., 2012). AG might also contribute to monitoring discrepancies between intended and actual action outcomes upon action completion (Farrer et al., 2008) and therefore is involved at various stages of voluntary action.

However, previous studies investigating the role of fronto-parietal areas in volition have focused exclusively either on processes *prior* to action initiation to investigate how and when conscious voluntary intentions emerge (e.g., Soon et al., 2008; Chambon et al., 2012), or on processes that evaluate actions *after* they have already been completed (e.g., Farrer et al., 2008). Most previous studies have neglected processes that shape voluntary actions *as they evolve*. Consequently, little is known about how changes in external contextual information may lead to dynamic updating of evolving voluntary actions – in particular with regard to changes in higher-order endogenous intentions. This is surprising given that other aspects of action updates, such as mere motoric reprogramming of reaching movements, have been studied in great detail (e.g., Wise & Mauritz, 1985; Buch et al., 2010; Pastor-Bernier et al., 2012; Saberi-Moghadam et al., 2016). Additionally, updating processes have been central to understanding the neuro-cognitive mechanisms underlying other forms of decision making. For example, for perceptual decisions, it has been shown that visual areas provide continuous updates of perceptual information (Tong, Nakayama, Vaughan, & Kanwisher, 1998; Polonsky, Blake, Braun, & Heeger, 2000), and additionally, posterior MFC gradually tracks sensory evidence after an initial decision has been made to signal the potential need for action updates (Fleming et al., 2018). For value-based decisions, several areas in prefrontal cortex, including MFC (Boorman et al., 2013; Kolling, Wittmann, et al., 2016; Shenhav et al., 2016) and frontopolar cortex (Boorman et al., 2009), have been shown to continuously track the values of competing choice options and indicate the need to switch to an alternative option.

The current chapter addresses the yet unresolved questions of whether and how neural representations of *voluntary* decisions, which are at the core of our experience of being free agents, change as new contextual information becomes available and needs to be integrated. Multivariate pattern analysis (MVPA) for fMRI data provided an optimised tool for this because, based on activity patterns in various decision-related brain areas, we could directly decode a) the transition from initial endogenous decisions to later decision updates in a new external context, and b) the specific contextual information that was integrated to form the final decisions. By using cross-classification analyses, we further show in which brain regions neural representations of decisions remained stable despite changes in external context, or instead, changed when integrating new contextual evidence. Finally, functional connectivity analyses revealed how updated information represented in distinct brain areas may be integrated to guide action updates. In our task, participants first made endogenous decisions about arbitrary action goals (i.e., moving towards a face or a house stimulus), but then received new external information that changed the costs and rewards associated with achieving the endogenous goal while the decision unfolded – sometimes prompting a Change of Mind. Our results show that fronto-parietal areas not only generate endogenous intentions prior to action, but additionally, update and revise voluntary intentions continuously throughout an ongoing action by integrating new decision- and action-relevant information.

4.2 Methods

4.2.1 Participants

The study was approved by the Melbourne University Research Ethics Committee, and all participants provided written informed consent prior to the study. Participants were right-handed, healthy, with no history of psychiatric or neurological illness, and no contraindication for MRI. Initially, 37 participants were recruited for a behavioural training session (26 female, age: *M* = 23.3 yr, *SD* = 4.8). Based on performance criteria (see below), 30 participants were re-invited for the fMRI session. Of those, one participant withdrew after training, one participant was excluded due to excessive movement, and three participants were excluded because they did not meet the performance criteria in the fMRI session (see below). Hence, 25 participants (16 female, age: *M* = 23.4 yr, *SD* = 5.2) were included in the final fMRI data set. Participants received $10 for the behavioural session and $45 for the fMRI session, plus a small performance-based reward they could win in each session (max $5).

4.2.2 Apparatus and stimuli

The experiment was programmed in Matlab R2014a and the Psychophysics Toolbox (Brainard, 1997). Greyscale images of faces and houses (170 x 170 pixel) of equal luminance and spatial frequency were presented on a black background. Participants indicated their choices on a HHSC 2x2 button box, using their left and right index and middle fingers, which corresponded to four possible target positions (top/bottom left/right).

4.2.3 Double-step choice task

Participants performed a computer-based decision-making task (**Figure 4.1**), in which they could win points. For each 50 points they won, they received an additional 10 cents at the end of the study. At the beginning of each trial, two images of a face and a house were presented centrally either left/right or above/below a fixation cross for 1–2 sec and participants had to make an endogenous decision between the two images (*initial decision period*). After a jittered delay of 3–9 sec, the images were presented in two of four possible target locations. Target locations were assigned randomly (counter-balanced within blocks) with the restriction that the two images always appeared in neighbouring locations (e.g., house in top-left and face in top-right location). Participants then had to press a response key that corresponded to the location of their initially chosen option, causing a manikin to move towards the chosen image at a constant and slow velocity of 60 pixel/sec (2.2 cm/sec). Only a single key press was required to initiate the movement of the manikin. Once the manikin reached the image, participants won 10 points.

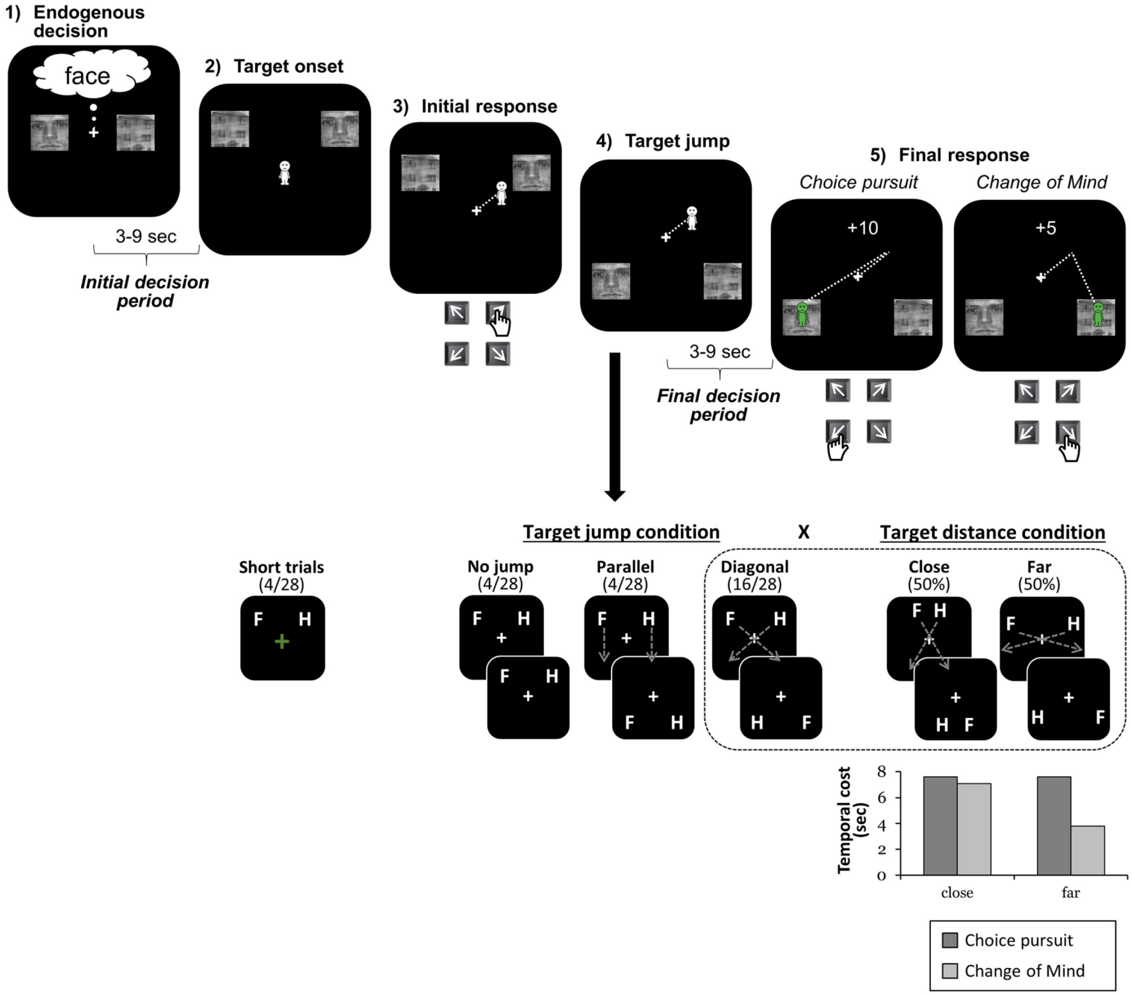

Figure 4.1. Double-step choice task. Participants made an endogenous face/house decision (*initial decision period*) and then had to navigate a manikin to a target location by pressing the key corresponding to the location of the chosen image. On some trials, the images jumped to new locations after action onset and participants then had to decide whether to pursue their initial choice or change their mind and switch to the alternative option (*final decision period*). In the main condition of interest, images jumped to the diagonally opposite location (diagonal trials), and hence, participants could save time by switching to the alternative choice option, instead of pursuing their initial choice. Differences in temporal costs were particularly pronounced in the far-distance condition, whereas costs were similar in the close-distance condition (bottom). Short trials and trials without/parallel target jumps served as control conditions to prevent stereotypical responding.

In the majority of trials, both images jumped to a new location once the manikin had travelled half the distance (~2.5 sec) towards the initially chosen image. Participants then had to press a second response key to redirect the manikin to one of the new target locations. Crucially, target relocation did not simply require motor re-programming of actions, but additionally, required a second choice with regard to the image identity, and hence, a re-evaluation of the initial endogenous intention. Specifically, participants could freely choose to either stick with their initial choice (e.g., face for initial face choice) yielding 10 points, or switch to the alternative option (e.g., house for initial face choice) for 5 points. Participants were told that they had exactly 1h for the experiment in which they should win as many points as possible, and that switching to the other option might sometimes allow them to save time and get to the next trial more quickly (and hence, complete more trials in the allocated time). By contrast, staying with the initially chosen option would win them more points on a given trial. Hence, final decisions depended on a trade-off between rewards and temporal costs. To allow for analysing brain activity related to participants' final decisions, the manikin stopped moving when the images changed their location, and participants had to make their final decisions within a jittered delay period of 3–9 sec (*final decision period*). After the delay, the manikin turned green, which served as a go signal for participants to indicate their final decision.

In the main condition of interest (16/28 trials per run), the images jumped to the diagonally-opposite locations (*diagonal trials*), causing the initially chosen option to be further away from the current position of the manikin than the alternative option. Hence, participants could save time by switching to the other image (CoM) instead of pursuing their initial choice. In order to induce CoM on some but not all trials with diagonal jumps, we additionally manipulated the distance between the images in order to vary cost-reward trade-offs. The distance of the targets to each other was either close (50% of trials) or far (50%). Importantly, the images were always equally far away from the centre of the screen, but the difference in distance between them caused differences in the *relative* temporal cost associated with each image after target jump. In the far-target condition, the temporal cost of the originally chosen image was roughly twice as large (~7.6 sec) as for the alternative image (~3.6 sec). Hence, participants should be more likely to change their mind. In the close-target condition, the difference in temporal cost was negligible (~7.6 sec for choice pursuit vs. ~7.2 sec for CoM), and hence, participants should be more likely to stick with their initial choice given the higher reward for intention pursuit. The precise distances were adjusted slightly according to each individual's cost-reward trade-off during practice (see below). Finally, in two control conditions, the images jumped in a parallel manner (4/28 trials) or did not jump at all (4/28 trials). These trials served to prevent participants from using stereotypical choice strategies and anticipating if and how the location of the choice options would change. Following a parallel jump, the initial choice option was always closer, regardless of target distance. Consequently, participants should always pursue their initial choice in this condition.

Since we aimed to measure brain activity related to the (abstract) initial choice before target locations were revealed, it was essential that participants indeed chose between the face and house at trial start (frame 1, **Figure 4.1**), rather than waiting for target onset (frame 2, **Figure 4.1**). In the instructions, we stressed that participants should always make a choice between the face and the house as soon as the two images were presented on the screen, and participants were reminded of this instruction between runs. We further used randomly inserted *short trials* (4/28 per run) to ensure compliance with this task instruction. In short trials, the fixation cross turned green and participants then had to respond to the location of their chosen image as fast and accurately as possible to win 50 points. The choice options were only presented very briefly (200 ms) and appeared in diagonally-opposite locations, making it more difficult for participants to select a correct response. Participants were instructed that, in order to be fast and accurate, it would help them to make a choice at the very beginning of every trial and then focus their attention on the choice they made. The point in time at which the fixation cross turned green randomly varied between 0.5–9 sec to ensure that participants focused on their decision throughout the entire initial choice period. The reaction time cut-off for short trials was adjusted based on each individual's RT during training, such that each participant responded fast enough in ~3/4 of all short trials. In all other trial conditions, participants did not have to respond quickly, but were asked to be as accurate as possible.

4.2.4 Behavioural training session

Before the fMRI session, all participants were invited for a behavioural training session in order to 1) familiarise participants with the task and 2) pre-select participants who followed task instructions and showed roughly balanced numbers of CoM and no-CoM trials in the diagonal-jump condition. The training session consisted of a short practice block followed by 3 blocks of 28 trials each. In the first 2 blocks, participants had to verbally indicate their choice at trial start, which helped participants to get used to making their choice at the very start of each trial and enabled us to provide feedback when participants pressed a wrong key (which resulted in a loss of 10 points). In the last block, participants were instructed to "say the choice in their head" (as they would in the fMRI session). For participants who showed a strong preference for either CoM or no-CoM choices, image distances were adjusted after each practice block in order to exaggerate differences in costs, and hence, motivate participants to stay or switch more often, respectively. However, for all participants who were selected for the fMRI session, highly similar image distances resulted (for a given participant, far targets were either 280 or 290 pixels apart, whereas close targets were 120 or 93 pixels apart, respectively), meaning that temporal costs were comparable across participants (choice pursuit: 7.6 sec for all participants in all distance conditions; CoM: either 3.8/7.1 sec or 3.5/7.3 sec in the far/close condition, respectively). Participants were invited for the fMRI session if they reached the following performance criteria by block 3: 1) 6–10 CoM trials per run (37.5%–62.5%) in the diagonal-jump condition, 2) roughly balanced trial numbers for initial face/house choices across all trial conditions (37.5%–62.5% for each choice category), 3) less than 10% errors across all trial conditions, and 4) less than 10% early responses during the final decision period (before the manikin turned green).

4.2.5 fMRI session

In the fMRI session (2–7 days after training), participants were given 1h to complete as many trials as possible. Due to technical issues, one participant only completed 4 runs within that time. All other participants were able to complete all 5 runs of 28 trials each. Because participants were not required to indicate their choices verbally, no error feedback could be provided. Instead, participants were asked to correct themselves when they made an error (which, however, only happened on 0.6% of trials), ensuring that the manikin always moved towards the image they actually wanted to choose. At the end of the fMRI session, participants were asked 1) on what percentage of trials they made a choice at trial start (rather than delaying it to target onset) and 2) what strategy they used to decide whether or not to switch to the alternative option when the images changed their location. All participants reported that they made initial choices in at least 90% of trials (M = 97.5%, SD = 3.5%) and that they used information about target distance to make CoM decisions.

4.2.6 fMRI data acquisition

Functional MRI volumes of the whole brain were acquired using a Siemens Skyra 3T scanner. A 20-channel head coil was used and volumes were acquired using gradient-echo EPI (38 axial slices, repetition time TR = 2200 ms, voxel size: 3x3x3 mm without gap; echo time TE = 30 ms; flip angle 90 degrees). At the end of the fMRI session, high-resolution (1x1x1 mm) structural T1 scans were obtained for spatial normalisation.

4.2.7 Data analysis

The first four volumes of each run were discarded by default to avoid magnetic saturation effects. All remaining EPIs were pre-processed using standard routines as implemented in SPM 12 (http://www.fil.ion.ucl.ac.uk/spm/), including slice-timing correction and correcting for head motion by realigning to the first image of the first run. No spatial normalisation or smoothing were conducted at this stage to preserve the original information structure in each individual's data. General linear models (GLMs) were then estimated for each individual participant using SPM 12, and motion correction parameters were included as regressors-of-no-interest. For each GLM, one beta map with parameter estimates for each voxel was created for each condition (e.g., face vs. house choice) for each of the 5 runs.

The following a priori defined regions of interest (ROIs) were included in the analyses: 1) Inferior occipital gyrus (IOG) and 2) fusiform gyrus (FG), because choice behaviour typically correlates with information processing in visual cortex and visual fixations on choice options (Krajbich, Armel, & Rangel, 2010). 3) The precuneus (PCUN; Soon et al., 2008; Bode et al., 2013), 4) angular gyrus (AG; Farrer et al., 2008), 5) medial frontal cortex (MFC; Soon et al., 2008; Bode et al., 2013; Soon et al., 2013; Zapparoli et al., 2018), and 6) dorsolateral prefrontal cortex (dlPFC; Rens et al., 2018), given their consistent demonstrated involvement in most types of decision making, including voluntary decisions. ROI masks were compiled using the Automated Anatomical Labelling atlas library (AAL; Tzourio-Mazoyer et al., 2002) in MarsBaR (Brett, Anton, Valabregue, & Poline, 2002). Note that MFC and dlPFC correspond to the superior medial frontal and mid frontal AAL regions, respectively (all other ROI names are the same as in the AAL atlas). Bilateral ROIs were generated by combining unilateral ROIs into a single mask. The run-averaged beta estimates were extracted for all voxels within each ROI and served as inputs for separate MVPA analyses.

The Decoding Toolbox (Hebart, Görgen, & Haynes, 2015) was used for MVPA. A linear support vector machine (SVM) with cost parameter $C = 1$ was trained to classify patterns of brain activity from all ROIs according to the categories of interest (e.g., face vs. house choices). A five-fold cross-validation procedure was used in which each of the runs served as test run once with the remaining four runs serving as training samples. Decoding accuracy was then averaged across all runs for each subject. Finally, mean decoding accuracies were compared to results obtained through permutation tests, and above chance decoding (one-tailed *t*-tests) is reported after Bonferroni-correction for the number of ROIs in each analysis.

The main analyses focused on brain activity measured during the initial or final decision period. Event-related activity locked to stimulus onset (frame 1, **Figure 4.1**) and target jump (frame 4, **Figure 4.1**) was analysed, respectively. For decoding analyses on initial decisions, all trial conditions were included, given that the initial decision period was identical across conditions. For analyses of final choices, only diagonal trials were included, given that this was the only condition that required reward-cost trade-offs to guide final decisions. Trials with erroneous responses during final choice (i.e., responses that did not match either of the two final image locations) were excluded ($M = 0.5\%$, $SD = 1.0$). Additionally, trials with responses that occurred too early, i.e., during the delay period were excluded ($M = 4.1\%$, $SD = 6.2\%$) in order to avoid capturing any motor-related activity during this time interval.

4.2.8 Connectivity analysis

Functional connectivity between fronto-parietal ROIs was investigated in a psycho-physiological interaction (PPI) analysis (Friston et al., 1997) using the gPPI Toolbox for SPM (McLaren, Ries, Xu, & Johnson, 2012). Functional images were pre-processed in the same way as for the MVPA analysis, but additionally, spatial normalisation and smoothing were performed. To investigate whether connectivity between dlPFC and PCUN/AG/MFC during the final decision period was different for CoM vs. no-CoM trials, the dlPFC was defined as a seed region. First, a standard first-level analysis was performed to extract the time course of BOLD (blood-oxygen-level dependent) signal from dlPFC for trials with vs. without CoM. The interaction between dlPFC x CoM was then included as a regressor in a second GLM, together with the main effect of dlPFC activity as well as the main effect of CoM and motion correction parameters as regressors-of-no-interest. A second-level analysis was then performed and parameter estimates were extracted for PCUN, AG and MFC using MarsBaR. Both the contrasts CoM > no-CoM and no-CoM > CoM were analysed.

4.3 Results

4.3.1 Behavioural

All participants made highly balanced face/house choices during the initial decision period (face: *M* = 54.0%, *SD* = 4.2%, *Min* = 41.7%, *Max* = 61.4%). Furthermore, during the final decision period, participants had roughly balanced numbers of CoM and no-CoM trials in the diagonal-jump condition (*M* = 50.3%, *SD* = 4.6%, *Min* = 38.8%, *Max* = 62.5%). As expected, CoM was very frequent in the far-target condition (*M* = 95.9%, *SD* = 7.0%) where CoM allowed participants to save time. By contrast, in the *close-target* condition CoM was relatively rare (*M* = 4.7%, *SD* = 7.2%) given that differences in costs were negligible. Furthermore, in parallel trials, only two participants erroneously switched to the alternative option in 1–2 trials, respectively, while none of the other participants showed any CoM in parallel trials. This suggests that overall, participants paid attention to the identity of the chosen images and remembered them correctly throughout the course of a trial.

4.3.2 Decoding decisions

fMRI analyses focussed on investigating the specific information about the decision process that could be decoded from patterns of brain activity in decision-related regions using MVPA (**Figure 4.2A**). *Initial* decisions could be decoded significantly above chance from all ROIs (**Figure 4.2B**, top row; IOG: $M = 72.6\%$, $SD = 17.2$, $t(24) = 6.61$, $p < .001$, $d = 1.32$; FG: $M = 73.5\%$, $SD = 20.1$, $t(24) = 5.85$, $p < .001$, $d = 1.17$; PCUN: $M = 63.7\%$, $SD = 18.9$, $t(24) = 3.64$, $p < .001$, $d = 0.73$; AG: $M = 62.5\%$, $SD = 17.1$, $t(24) = 3.66$, $p < .001$, $d = 0.73$; MFC: $M = 65.0\%$, $SD = 14.6$, $t(24) = 5.15$, $p < .001$, $d = 1.03$; dlPFC: $M = 59.2\%$, $SD = 15.0$, $t(24) = 3.07$, $p = .003$, $d = 0.61$).

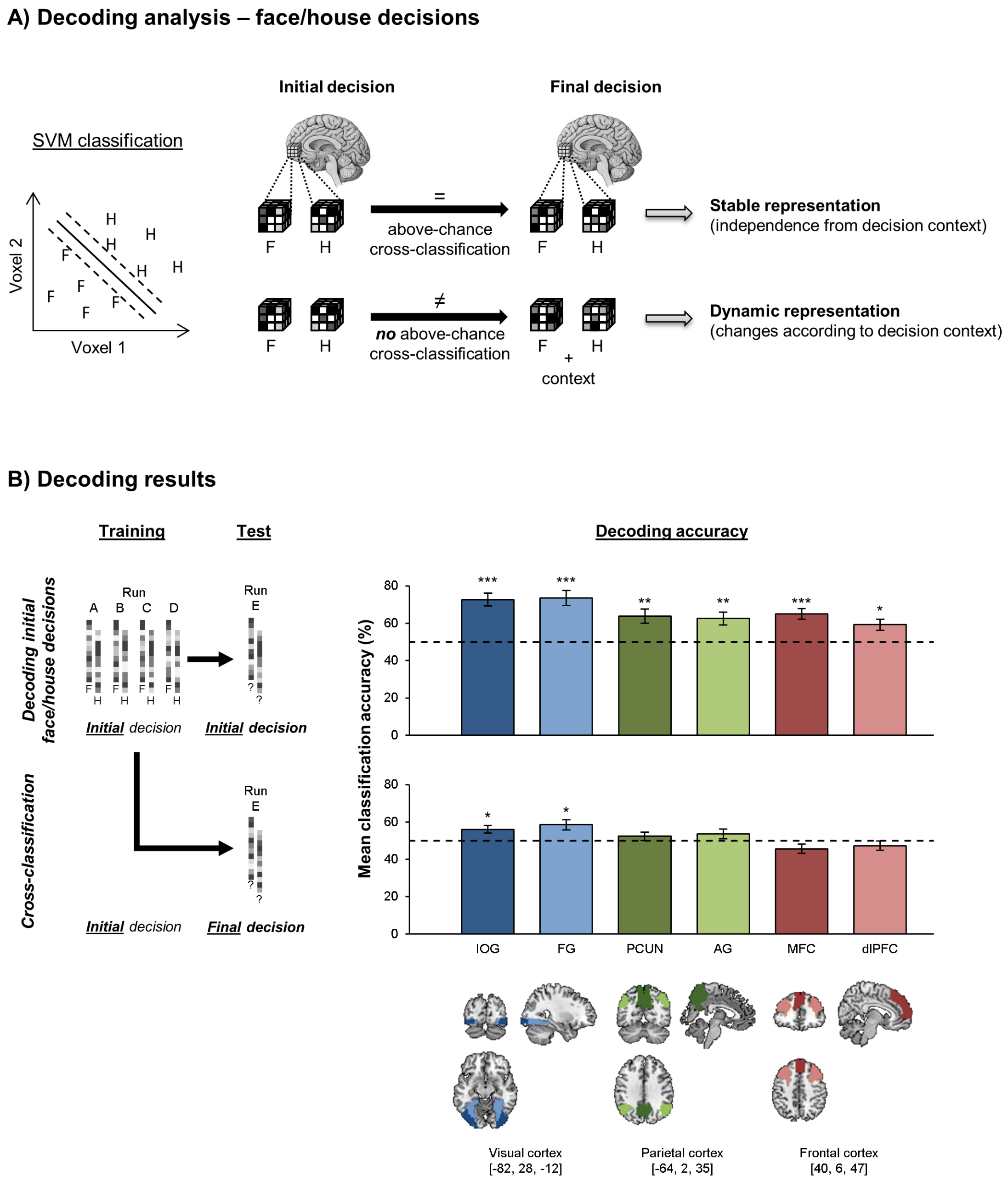

Figure 4.2. Decoding face/house decisions. A) Decoding approach for initial and final face/house (F/H) decisions using SVM classification. Cross-classification across both decision stages allows for investigation of the stability of choice representations. Areas that represent choice options regardless of changes in decision context should support cross-classification, whereas areas that integrate novel information during the course of decision making would not support cross-classification. B) Decoding results: Mean decoding accuracies for initial face/house choices (top row) and cross-classification from initial to final face/house choices (bottom row). Chance level (dashed line) is 50%. Permutation tests were used for statistical testing. Data are represented as mean ± 1SE. *$p < .05/6$, **$p < .01/6$, ***$p < .001/6$ ($N = 25$).

We then tested for each ROI to what extent neural activity patterns for the initial decisions remained stable during the transition to the *final* decision period despite the fact that choice options were now displayed in different locations, and participants were already executing the action corresponding to their initial choice. Areas that represent choice features independently of changes in the external decision context would use similar representations for face/house decisions across both decision stages (**Figure 4.2A**). By contrast, areas that adjust choice representations to the current decision context would dynamically change neural patterns, e.g., in order to integrate decision information from both phases, rather than simply reflecting face/house decisions per se. Cross-classification decoding analyses (Bode et al., 2013) were used for which a decoder was trained on neural patterns of *initial* face/house choices, but was tested on *final* face/house choices (**Figure 4.2B**, bottom row). Hence, training samples for this analysis were identical to the ones used for decoding of initial decisions reported above. Importantly, for final decisions, face/house choices were included regardless of whether a CoM occurred to shed light on how choices were generally represented when contextual information changed, independent of whether or not this required a CoM. Note that cross-classification accuracies were expected to be lower than for within-phase decoding, given that training and test patterns were recorded at different time periods. More importantly, if decoding accuracies for cross-classification are above chance, neural patterns for each choice option are, at least to some extent, similar across the two decision stages – indicating stability of neural choice representations. By contrast, substantial differences in neural patterns – e.g., because different information was represented during initial vs. final decisions – would cause cross-classification to be at chance.

In IOG and FG, cross-classification was above chance, indicating stable representations of choice options across the different decision stages (**Figure 4.2B**, bottom row; IOG: $M = 56.0\%$, $SD = 10.0$, $t(24) = 2.95$, $p = .004$, $d = 0.59$; FG: $M = 58.5\%$, $SD = 13.5$, $t(24) = 3.26$, $p = .002$, $d = 0.65$). By contrast, cross-classification was not significantly above chance in any of the fronto-parietal ROIs (PCUN: *M* = 52.3%, *SD* = 11.4, *t*(24) = 1.13, *p* = .135, *d* = 0.23; AG: *M* = 53.6%, *SD* = 13.2, *t*(24) = 1.21, *p* = .120, *d* = 0.24; MFC: *M* = 45.6%, *SD* = 12.3, *t*(24) = -1.85, *p* = .038, *d* = -0.37; dlPFC: *M* = 47.3%, *SD* = 12.5, *t*(24) = 1.14, *p* = .132, *d* = -0.23). Hence, in all fronto-parietal ROIs, neural choice representations changed from the initial to the final decision phase. This suggests that during final decisions, neural patterns in these regions did not encode pure face/house decisions any longer, but might potentially predict the external information that had to be integrated. In line with this, decoding face/house choices from the final decision stage alone was not significant in fronto-parietal regions (all $p > .100$; data not shown)[4]. Next, we investigated whether these areas indeed incorporated representation about external decision context during final choices.

4.3.3 Fronto-parietal areas integrate new information

One plausible reason for changes in fronto-parietal neural patterns is that new action- and decision-relevant information was available for making final decisions, whereas initial decisions were abstract and endogenous. More specifically, during final decisions, the external context provided information about 1) *target locations*, which was required to successfully transform the final decision into an appropriate motor action, and 2) *target distance*, which guided re-evaluation of the initial choice based on cost-reward trade-offs. In order to investigate to what extent neural patterns in fronto-parietal areas incorporated these new pieces of external information, we performed separate decoding analyses for the location of the chosen image (left/right) and the distance between the target locations (close/far; **Figure 4.3**).

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[4] Note that face/house choices could not be decoded from visual areas during the final decision period either (both $p > .100$), despite successful cross-classification of face/house decisions across stages in these areas. This suggests that lower trial numbers for conditions with final decisions (trials = 16) caused the classifier trained on final face/house choices to perform worse compared to the (cross-)classifier trained on initial decisions that included all trial conditions (trials = 28). Hence, it is likely that some information about face/house decisions was still present during the final decision period, but was too weak/noisy to be detected by the decoder that was trained on final decisions.

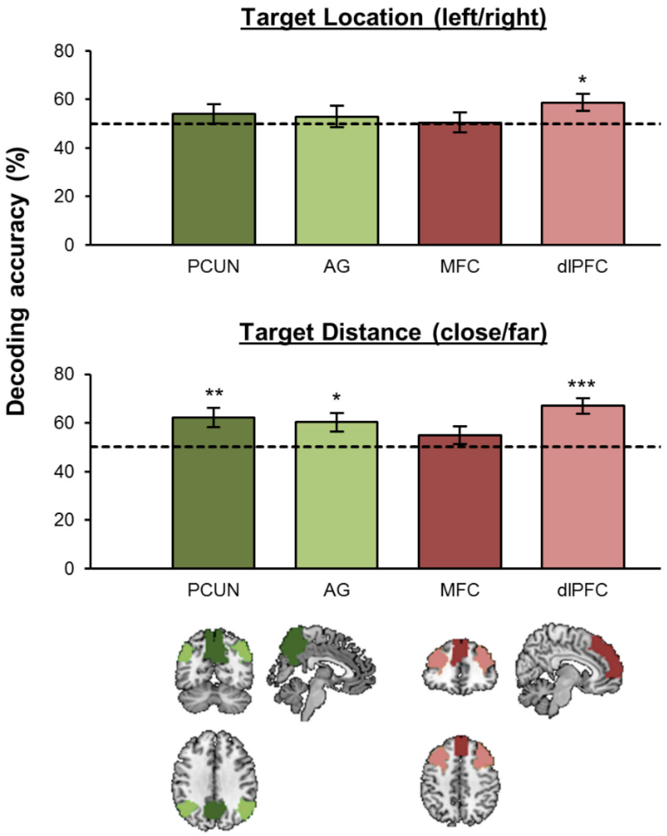


Figure 4.3. Decoding decision context during final decisions in fronto-parietal ROIs. Mean decoding accuracies (± 1SE) for location of the chosen target (top row) and target distance condition (bottom row). Chance level (dashed line) is 50%. *p < .05/4, **p < .01/4, ***p < .001/4 (N = 25).

The only fronto-parietal ROI found to be predictive of location of the chosen image was dlPFC ($t(24) = 2.45$, $p = .011$, $d = 0.49$; all other ROIs: $p > .170$). This suggests that dlPFC had access to information that was required to successfully transform final decisions into motor actions. Target distance could be decoded from PCUN, AG and dlPFC (PCUN: $t(24) = 3.13$, $p = .002$, $d = 0.63$; AG: $t(24) = 2.72$, $p = .006$, $d = 0.54$; dlPFC: $t(24) = 5.68$, $p < .001$, $d = 1.14$), but not from MFC ($t(24) = 1.30$, $p = .104$, $d = 0.26$). Note that target location and distance could also be decoded from both ROIs in visual cortex (all $p < .001$). However, IOG and FG presumably represented these pieces of information in terms of their low-level visual features. Given that cross-classification of face/house choices was above chance in visual areas, representations of target location and distance did not seem to substantially change, or interfere with, representations about the choice options themselves. By contrast, in fronto-parietal areas, integration of information about target distance and location towards a decision may explain changes in neural patterns during the final decision phase.

As the distance between the images was constant within a given trial, information about target distance condition was already available as soon as the images first appeared in their respective locations (*target onset*; frame 2 **Figure 4.1**), immediately after the initial decision period. AG did not encode target distance at this early point (*M* = 50.8%, *SD* = 18.9, *t*(24) = 0.21, *p* = .417, *d* = 0.04), but instead, only integrated target distance information when it became relevant for the decision-making process – i.e., during the final decision period when participants decided to stay/switch. By contrast, PCUN and dlPFC already encoded distance as soon as the targets appeared (PCUN: *M* = 58.9%, *SD* = 17.6, *t*(24) = 2.53, *p* = .009, *d* = 0.51, dlPFC: *M* = 58.7%, *SD* = 17.7, *t*(24) = 2.46, *p* = .011, *d* = 0.49). This suggests some functional separation within the fronto-parietal network in tracking information that is currently *relevant* for the decision process (AG) vs. information that is currently *available*, but may only become relevant later on (PCUN and dlPFC) – possibly in anticipation of a potential future decision reversal.

4.3.4 Decoding CoM

The new decision context provided during final decisions was systematically tailored to trigger CoMs in trials in which the distance to the originally chosen object was substantially higher. Decisions for CoM (no-CoM/CoM; irrespective of face/house) could be decoded significantly above chance from all six ROIs (**Figure 4.4**; IOG: *t*(24) = 3.31, *p* = .001, *d* = 0.66; FG: *t*(24) = 3.35, *p* = .001, *d* = 0.67; PCUN: *t*(24) = 3.97, *p* < .001, *d* = 0.79; AG: *t*(24) = 3.22, *p*

= .002, *d* = 0.64; MFC: *t*(24) = 3.22, *p* = .002, *d* = 0.64; dlPFC: *t*(24) = 4.61, *p* < .001, *d* = 0.92). In both visual areas, neural patterns associated with face/house choices could be cross-classified from initial to final decisions, suggesting an ongoing tracking of the visual stimulus properties – and hence, a dynamic reversal of patterns in CoM trials. Given that distance was the criterion for most CoM decisions, and target distance could indeed be decoded from PCUN, AG, and dlPFC during the same time period, it is highly likely that these areas integrated initial decision information with target distance information to prepare CoM decisions. Interestingly, MFC was the only ROI that did not allow for decoding of target distance, even though decoding of CoM decisions was significantly above chance in this area. While one has to be careful not to over-interpret null-results, this finding suggests that processing of target distance and CoM were not perfectly correlated at the neural level and should be regarded as separate processes. Hence, we next investigated whether the neural representations of CoM in MFC could be explained by some CoM decisions not being based on target distance, but instead, being prepared endogenously.

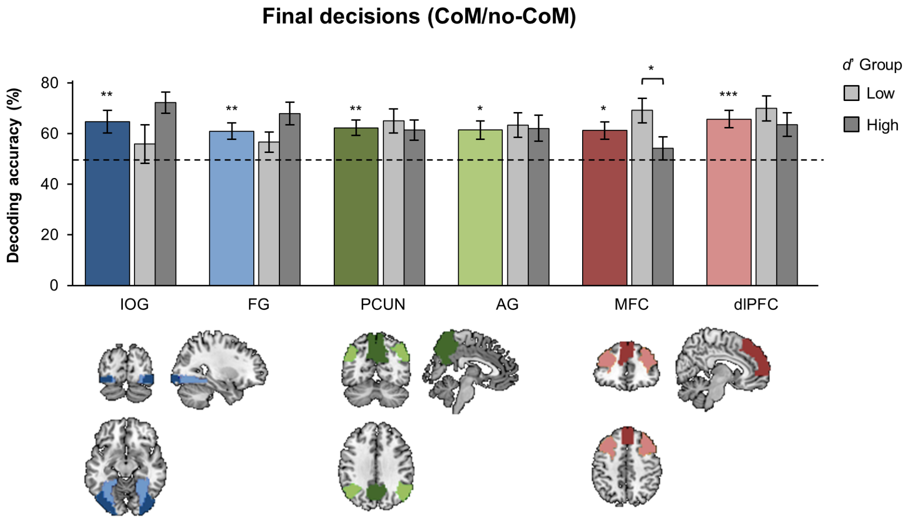


Figure 4.4. Decoding CoM decisions during final decision period. Mean decoding accuracies (± 1SE) for CoM/no-CoM decisions. Chance level (dashed line) is 50%. **p* < .05/6, ***p* < .01/6, ****p* < .001/6 (*N* = 25).

4.3.5 Endogenous CoM decisions

Although overall, CoM decisions were largely based on external information about distance, some participants occasionally decided to change their mind (or refrain from doing so) independently of target distance. For example, during debriefing, some participants reported that they sometimes "particularly liked one of the two images", thought that "the little man should go into the house", or just "randomly wanted to mix it up from time to time". These decisions were not related to the external task cues, but instead, were generated internally. Hence, decoding CoM from MFC, which did not explicitly represent target distance, might have been driven by those participants who based their CoM decisions less strongly on target distance, and instead more strongly on endogenous factors. To quantify the extent to which each participant's CoM decisions were based on target distance, a sensitivity parameter *d*' was calculated according to signal detection theory (D. M. Green & Swets, 1966):

$$d' = z(\text{hit rate}) - z(\text{false alarm rate}),$$

where hits correspond to CoM in the far-target condition, whereas false alarms correspond to CoM in the close-target condition. For participants with hit / false alarm rates of 100% / 0%, values were adjusted by -/+ 1% to allow for computation of *d*' (Stanislaw & Todorov, 1999). Within the context of the current task, *d*' does not strictly reflect perceptual sensitivity, but rather should be interpreted as an indicator of a participant's decision-making strategy – i.e., how strongly decisions were informed by external information about target distance. Higher *d*' reflects higher sensitivity of CoM decisions to target distance, while lower *d*' reflects higher influence of endogenous factors on CoM.

A median split analysis was conducted, splitting the sample into a high-*d*' group (*d*': *Mdn* = 4.65, *IQR* = [4.38, 4.65]) and a low-*d*' group (*d*': *Mdn* = 3.08, *IQR* = [2.79, 3.61]). Note that *d*' was high in both groups, reflecting that overall, image distance was the most important driving factor for CoM (as intended). However, importantly, the difference in *d*' was significant between groups (Mann-Whitney U test for non-normal data: *Z*(22) = 4.27, *p* < .001), indicating that the division into high and low-*d*' groups was meaningful. MFC decoding performance for CoM decisions was only above chance in the low-*d*' group (**Figure 4.4**; *t*(11) = 4.24, *p* = .001, *d* = 1.23), but not in the high-*d*' group (*t*(11) = 0.86, *p* = .408, *d* = 0.25), and the group difference in decoding accuracies was significant (*t*(22) = 2.27, *p* = .034, *d* = 0.93). Furthermore, when we excluded trials in which CoM decisions did not follow target distance, CoM could not be decoded anymore from MFC in the low-*d*' group (*M* = 57.5%, *SD* = 22.2, *t*(11) = 1.17, *p* = .267, *d* = 0.33), suggesting that decoding of CoM from MFC was indeed driven by trials in which endogenous decision criteria, rather than target distance, were the crucial drivers.

In order to explore whether any of the other ROIs showed differences between the high- and low-*d*' group, an ANOVA with the factors ROI (IOG/FG/PCUN/AG/dlPFC) and *d*' group (low/high) was conducted. No significant main effect of ROI or group was found (both *F* < 1), but the interaction of ROI x group was significant (*F*(4,1) = 2.87, *p* = .037, η^2 = .115). This was driven by the visual ROIs, which showed a non-significant (after Bonferroni-correction) trend in the opposite direction (stronger effects for a stronger influence of target distance; IOG: *t*(22), = -1.89, *p* = .072, *d* = 0.77, FG: *t*(22) = -1.88, *p* = .074, *d* = 0.77). In all other ROIs, decoding accuracies for CoM decisions were comparable between the two groups (all *p* > .350). Importantly, both *d*' groups had similar trial numbers for CoM/no-CoM decisions (% CoM in low-*d*' group: *M* = 50.3%, *SD* = 6.7; high-*d*' group: *M* = 50.1%, *SD* = 0.6; *t*(24) = 0.92, *p* = .916, *d* = 0.04), and the groups did also not differ in the precise target-distance values (*t*(22) = .405, *p* = .689, *d* = 0.17), meaning that these factors cannot explain the group differences in decoding accuracies.

4.3.6 Functional connectivity during CoM decisions

After establishing that the fronto-parietal ROIs differed in what decision-related information they represented – and presumably contributed to final decisions – we analysed the functional connectivity between them. This might provide additional insights into how these areas communicated to exchange information to update the unfolding decision process. We focussed on dlPFC, which constituted a critical cortical node because it encoded both target location and distance during the final decision period, and hence, represented all information relevant to implement a CoM. A PPI analysis (Friston et al., 1997) was conducted with dlPFC as a seed region. The aim of this analysis was to measure whether functional connectivity between dlPFC and PCUN/AG/MFC differed for CoM vs. no-CoM trials during the final decision period.

First, we established whether fronto-parietal regions showed any functional connectivity during final decisions by analysing the main effect of dlPFC BOLD signal on PCUN, AG and MFC activity. A significant effect was found in PCUN ($b = 0.61$, $t(24) = 4.51$, $p < .001$) and AG ($b = 0.65$, $t(24) = 5.36$, $p < .001$), and a trend was observed in MFC ($b = 0.24$, $t(24) = 1.44$, $p = .082$). This indicates that time courses of activity in these areas were correlated, suggesting that these areas were functionally connected. More importantly, the PPI effect was analysed to check whether the strength of connectivity varied as a function of CoM (**Figure 4.5**). A significant effect (corrected $\alpha = .05/3$) was found for dlPFC-MFC connectivity, revealing increased connectivity for CoM compared to no-CoM trials ($b = 0.50$, $t(24) = 2.80$, $p = .005$). In fact, dlPFC and MFC only showed functional connectivity in CoM trials ($b = 0.49$, $t(24) = 2.64$, $p = .007$), but not in no-CoM trials ($b = -0.01$, $t(24) = -0.08$, $p = .531$). A similar trend for increased connectivity during CoM was found for dlPFC-AG connectivity ($b = 0.33$, $t(24) = 2.15$, $p = .021$), although this effect was only marginally significant after correction for multiple comparisons. No effect of CoM on dlPFC-PCUN connectivity was observed ($b = 0.17$, $t(24) = 0.89$, $p = .292$).

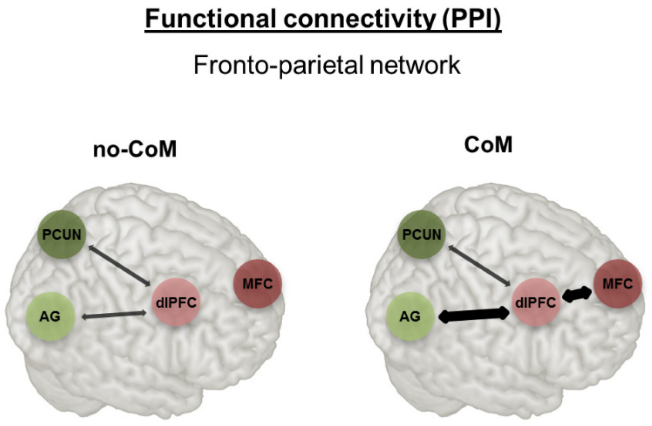


Figure 4.5. Functional connectivity during final decisions. Schematic illustrating functional connectivity between fronto-parietal ROIs during the final decision period. Psycho-physiological interaction analyses revealed that AG and MFC showed increased activity with dlPFC in trials with CoM compared to trials with no-CoM. PCUN-dlPFC connectivity was not different for CoM vs. no-CoM trials.

Given that CoM decoding from MFC depended on how strongly decisions were based on endogenous factors, we also checked whether modulation of dlPFC-MFC connectivity was driven by participants with low *d*'. As expected, increases in dlPFC-MFC connectivity in CoM compared to no-CoM trials were only observed in the low-*d*' group ($b = 0.74$, $t(11) = 2.73$, $p = .010$), but not in the high-*d*' group ($b = 0.28$, $t(11) = 1.07$, $p = .155$). Hence, CoM may be implemented through functional connectivity of dlPFC with both AG and MFC, allowing for integration of externally-cued information encoded in lateral fronto-parietal areas with endogenous information from MFC.

4.3.7 Additional analyses – Sub-regions within large ROIs

Given that some ROIs, especially PCUN, MFC and dlPFC, were relatively large, the main analyses were repeated splitting these ROIs into dorsal and ventral sub-regions. The pattern of results in each sub-region was comparable to the respective original ROI (Appendix B, **Figure B1**). However, in PCUN, effects tended to be stronger in the dorsal region, whereas in MFC, effects were more pronounced in the ventral area. Finally, in dlPFC, decoding of target locations was largely driven by the dorsal sub-region, in line with the assumption that information about target locations was used by areas involved in the implementation of decisions in motor actions.

4.4 Discussion

The current study investigated the neural dynamics that enable agents to integrate new information about choice options as endogenous intentions evolve. First, participants were required to generate an arbitrary endogenous decision for a visually presented face or house stimulus without any choice outcome being associated with rewards at this stage. We derived ROIs from previous studies and confirmed that initial voluntary decisions were encoded in MFC, PCUN, dlPFC and AG (Brass & Haggard, 2008; Soon et al., 2008; Bode et al., 2011; Krieghoff et al., 2011; Bode et al., 2013; Soon et al., 2013; Zapparoli et al., 2018). Additionally, decisions could be decoded from visual cortex, presumably due to visual fixation of, and attention to, visual features of the chosen image (Krajbich et al., 2010; Voigt et al., 2018). More importantly, we then analysed whether and how neural patterns associated with initial endogenous decisions changed during the integration of exogenous factors as on some trials the locations of the choice options changed, and participants had to re-evaluate their original intention based on new information about costs and rewards associated with pursuing or changing the initial decision.

Our results revealed that neural representations of choice options in visual cortex were similar during the initial and final decision period, as indicated by above-chance cross-classification between decision stages. Hence, low-level perceptual features of choice options were represented in a stable manner that was, at least to some extent, independent from additional information that became available, and independent of a change in location. Consequently, although sensory areas provide continuous updates of dynamic external stimuli (Tong et al., 1998; Polonsky et al., 2000), the underlying neural code appears to be relatively static. By contrast, in fronto-parietal cortex, decisions could not be cross-classified between task stages. This cannot simply be explained by initial decoding accuracies being slightly lower in fronto-parietal areas compared to visual areas. First, decoding accuracies cannot be compared across regions because of potentially different underlying coding schemes (Bhandari, Gagne, & Badre, 2018). Second, even relatively low initial decoding accuracies would allow for significant cross-classification if patterns were sufficiently stable across decision stages. Instead, our findings showed that neural codes in fronto-parietal regions changed dynamically between decision phases and represented new decision-relevant information, suggesting that integration of novel exogenous information occurred during endogenous decision making.

4.4.1 Dynamic coding in fronto-parietal cortex

While previous studies have provided evidence for dynamic coding of decisions in fronto-parietal cortex, these studies have largely focused on tasks where actions were fully instructed by external stimuli (Toth & Assad, 2002; Woolgar, Hampshire, Thompson, & Duncan, 2011; Stokes et al., 2013; Schuck et al., 2015), rather than involving endogenous choice. Furthermore, previous studies have focused on post-decision processes that continuously evaluate a single source of evidence – either perceptual (Fleming et al., 2018) or value-based information (Boorman et al., 2009) – whereas our study shows how dynamic coding in fronto-parietal cortex could contribute to integration of several internal and external sources of evidence. This may be particularly relevant for voluntary decisions, which need to integrate internally-generated intentions with contextual information about alternative courses of action and their respective costs and rewards.

Across fronto-parietal areas, we observed differences in *what specific* information was encoded and *when* it became available. Both parietal ROIs, precuneus and AG, integrated information about target distance, which in turn informed cost-reward trade-offs guiding CoM decisions. Interestingly, AG did not encode distance information immediately when it was available, but only during the final decision period when it became relevant for the decision-making process. Hence, changes in the external environment may have triggered a re-computation of current intentions in AG (Sirigu et al., 2004; Chambon et al., 2012), taking into account new information about target distance. By contrast, precuneus started to encode distance information as soon as it was available, regardless of whether it was immediately relevant for the current decision. There are two possible explanations for this finding. First, given its proximity to dorsomedial occipital lobe, precuneus may have represented purely visual information about distance (Pitzalis et al., 2006), which was available as soon as the choice options first appeared in their respective locations. Alternatively, in line with its role in prospective memory (Burgess, Gonen-Yaacovi, & Volle, 2011), precuneus may have started to extract decision-relevant evidence early on in order to anticipate future re-evaluation of the current intention. This is particularly likely given the high frequency of trials with diagonal image relocation, which in principle allowed participants to predict to some extent whether and how actions may need to be changed. This explanation would further be in line with other studies showing early decision encoding in precuneus (e.g., Soon et al., 2008; Soon et al., 2013). Finally, both precuneus and AG specifically represented the distance between images, regardless of their actual locations, suggesting that both areas encoded abstract features reflecting decision-relevant information about externally-cued rewards and costs associated with each choice option. This suggests that precuneus and AG were not simply involved in representing low-level sensorimotor information to transform decisions into movements, but instead, provided information guiding the decision process itself.

The dlPFC was the only area that encoded both target distance and location, and hence, represented decision- as well as action-relevant information. Previous studies have shown that dlPFC represents alternative choice options (Rens et al., 2018), and is involved in value updates of competing choice alternatives (Izuma et al., 2010; Mengarelli, Spoglianti, Avenanti, & Di Pellegrino, 2013). Here we show that these representations can be used to guide switches to an alternative choice option when values change. The dlPFC may have directly integrated value-based updates with action representations in order to guide changes in action selection. In support of this, it has previously been proposed that information about decisions and their implementation into motor actions can be represented in a common neural space (Cisek, 2007; Thura & Cisek, 2014; Yoo & Hayden, 2018). Such concurrent representations might allow dlPFC to compute action updates in a fast and efficient manner. Additionally, similarly to precuneus, dlPFC already encoded distance information at target onset, suggesting a role in integrating currently available information to prepare future decision reversals and their implementation into flexible changes in action (MacDonald, Cohen, Stenger, & Carter, 2000; Koechlin & Summerfield, 2007).

4.4.2 Integration of endogenous and exogenous information

Interestingly, precuneus, AG and dlPFC switched from encoding *internal* decisions to encoding *externally*-cued information during final decisions. This suggests that neural substrates underlying endogenous and exogenous choice may not follow clear neuroanatomical boundaries, nor clear dissociations into medial vs. lateral regions (Passingham, 1987; Fried et al., 2017). Instead, different modes of decision making may be implemented through different functional codes (Yoo & Hayden, 2018), where a given brain area can dynamically change neural representations to encode internal or external information, depending on the evidence that is currently available. Previous studies have reported response costs when people need to switch between internal and external modes of action selection (Obhi & Haggard, 2004). Based on our findings, it seems plausible that costs incurred by these switches may at least partially be caused by the need to change representations *within* a given neural structure, rather than switching *between* different structures.

Nevertheless, in line with the idea that a medial frontal pathway is of particular importance for endogenous action selection (Passingham, 1987; Brass & Haggard, 2008; Soon et al., 2008; Bode et al., 2013; Fried et al., 2017; Zapparoli et al., 2018), we found that MFC was the only area that represented endogenous components of both initial decisions and later decision reversals. More specifically, MFC encoded CoM in participants who more strongly considered endogenous information, but not in those who exclusively relied on external cues, i.e., target distance. This shows that the same choice can result from different sources of information, or different decision strategies, and the underlying processes in turn recruit partially distinct neural circuits. Although this finding was based on a post-hoc group split, it could not be accounted for by other between-subject differences, such as overall frequency of CoM. Furthermore, it is unlikely that engagement of MFC simply reflected detection of erroneous (no-)CoM decisions (Ridderinkhof, Van Den Wildenberg, Segalowitz, & Carter, 2004) since in that case, information about target distance itself should still be present in MFC. Instead, our findings suggest that some participants occasionally 'detached' the decision process from external cues and made endogenous CoM decisions. In that sense, the observed dissociation in the pattern of MFC activity provides a powerful test of the hypothesis that MFC plays a distinct and crucial role in endogenous choice because it isolates the specific aspect of the design where endogenous decisions were exposed to exogenous cues that were in principle highly informative. Overcoming, or actively going against, such exogenous cues may represent a particularly strong aspect of volitional control (Ach, 1935). While it is not clear why and how exactly some participants occasionally used these internal strategies for decision reversals, our study is the first to capture CoM that is not exclusively guided by externally-cued perceptual or value-based information. In this case, just as initial decisions, later decision reversals can be generated endogenously, which appears to rely on continuous involvement of MFC.

Finally, we tested whether endogenous and exogenous components of decisions may be integrated via changes in functional connectivity between regions that encode different sources of information (J. X. O'Reilly, Woolrich, Behrens, Smith, & Johansen-Berg, 2012). We found that when participants changed their mind, dlPFC showed increased connectivity with both AG and MFC, compared to trials without decision reversals. dlPFC-MFC connectivity was only increased in participants who also showed endogenous CoM decisions, suggesting that connectivity between the medial action pathway and dlPFC is required to incorporate internally-guided decision updates. Although PPI analyses do not reveal causality or directionality of connectivity (J. X. O'Reilly et al., 2012), it seems plausible that AG and MFC provided dlPFC with information about external and internal decision updates, respectively, enabling dlPFC to integrate both sources of information in order to guide changes in decision making. Hence, dlPFC may serve as a critical node that allows for convergence of external and internal decision updates and their implementation into flexible action (Ridderinkhof et al., 2004).

This flexibility enables agents to adjust their behaviour to the current context. Impairments in the processes underlying intention updates may result in escalation of commitment (Staw, 1981) or rigidity of behaviour, such as in obsessive compulsive disorder (Gruner & Pittenger, 2017). However, in some situations, intentions need to remain stable despite external changes. In fact, goal attainment often requires continuous pursuit of an initial intention in the face of challenges or costs (Gollwitzer & Oettingen, 2012). Hence, the balance between flexibility and stability of intentions is crucial for adaptive behaviour (Goschke, 2014). In our study, participants maintained their intentions when costs of intention pursuit were only slightly larger than for CoM. Such optimal behaviour may be achieved through the interplay of several fronto-parietal areas that weigh different sources of evidence to generate a 'distributed consensus' (Cisek, 2012; Yoo & Hayden, 2018) about whether or not the original intention should be changed.

4.4.3 Conclusion

Voluntary actions require continuous evaluation, and integration, of dynamically changing external and internal information – creating the opportunity, and sometimes the need, to change one's own intention after an action has already been initiated. Our study provides important insights into the fundamental processes underlying volition by establishing a direct link between an initial intention and the subsequent processes that shape voluntary actions as they evolve. Our results show that the fronto-parietal network uses dynamic neural codes in order to continuously integrate different sources of evidence informing updates in endogenous decision making. These insights into the neurocognitive mechanisms that determine the stability vs. flexibility of voluntary intentions are essential for our understanding of the mechanisms underlying adaptive behaviour in a complex and dynamic world.

Chapter 5.

Reduced intention pursuit in post-stroke fatigue

5.1 Introduction

In **Chapter 2** and **Chapter 4** of this thesis, we showed that people sometimes deviate from their original intention during an ongoing action, in particular when intention pursuit is costly in terms of time or effort. This shows that intentions are reversible, and can be changed flexibly. However, overall, participants were relatively reluctant to change their own intentions, unless costs associated with intention pursuit were substantially higher than costs associated with CoM. This was true even though changing an intention did not cause any (**Chapter 2**) or only very small monetary losses (**Chapter 4**). Hence, voluntary intentions are in essence relatively stable, allowing people to pursue their goals even when an easier action alternative is available. Indeed, a certain degree of stability is highly important for goal attainment in real life, where intentions often need to be pursued over long periods of time despite challenges or distracting factors (Gollwitzer & Oettingen, 2012). However, costs in real life can be much larger than costs induced in laboratory tasks. In particular, motor actions are typically associated with effort costs that have to be overcome in order to reach a goal. For example, hiking up a mountain requires a high degree of perseverance. Even attaining goals in daily life, such as getting out of bed to go to work or staying healthy, require a certain degree of willingness (or motivation) to invest effort, and 'giving up' on these goals too readily can lead to adverse outcomes. Insights into the processes underlying long-term goal pursuit may be particularly relevant with regard to psychiatric and neurological conditions that are associated with motivational deficits, such as apathy, i.e., a reduced willingness to exert effort (Marin, 1990; Bonnelle et al., 2015; Husain & Roiser, 2018). The aim of the current chapter is to investigate the link between effort-based decision making and intention pursuit in patients with post-stroke fatigue. Specifically, we tested whether chronic fatigue is associated with reduced perseverance when intention pursuit requires sustained effort.

Fatigue is a multidimensional concept that encompasses both objective muscle fatigue (i.e., a decrease in muscle force output; Enoka et al., 2011), but also a subjective feeling of being tired or exhausted (Nadarajah & Goh, 2015). It typically occurs when effort is exerted for a long period of time, and subsequently reduces the willingness to expend further effort (Müller & Apps, 2018). Importantly, in healthy people, rest can restore energy levels, and hence, allows for recovery from fatigue (Meyniel, Sergent, Rigoux, Daunizeau, & Pessiglione, 2013). However, fatigue can also be a pathological, chronic condition where patients experience persistent and extreme tiredness, exhaustion, or weakness (Jason, Evans, Brown, & Porter, 2010; Kuppuswamy, 2017). Pathological fatigue is common in disease, such as multiple sclerosis, cancer, Parkinson’s disease or stroke (Swain, 2000; Levine & Greenwald, 2009; Jason et al., 2010). Post-stroke fatigue (PSF) affects between 25 to 85% of stroke patients and is relatively independent of stroke type or location (Ingles, Eskes, & Phillips, 1999; Ponchel, Bombois, Bordet, & Hénon, 2015; Cumming, Packer, Kramer, & English, 2016). Crucially, PSF is considered a distinct symptom that is dissociable from mere motor impairments and other symptoms, such as depression, typically observed after stroke (Ingles et al., 1999; Ponchel et al., 2015). PSF predicts poor quality of life and higher mortality, and is reported to be one of the most disabling symptoms by 40% of stroke patients (Ingles et al., 1999; Naess, Lunde, Brogger, & Waje-Andreassen, 2010; Naess, Lunde, & Brogger, 2012).

It has been proposed that PSF is caused by deficits in sensorimotor mechanisms underlying effort processing (Kuppuswamy, Rothwell, & Ward, 2015). More specifically, PSF patients perceive their own actions to be more effortful than before the stroke (Flinn & Stube, 2010;

Young, Mills, Gibbons, & Thornton, 2013). This may be caused by reduced corticomotor excitability observed in PSF, where stronger motivational inputs from higher centres into motor cortex are required in order to produce a given movement (Kuppuswamy, Clark, Turner, Rothwell, & Ward, 2015). In other words, PSF patients need to invest more *subjective* effort in order to produce the same motor output as healthy people, or as they did prior to stroke. Additionally, physical deconditioning typically observed after stroke may contribute to these mechanisms by reducing muscular strength, and hence, increasing the effort that needs to be invested to produce motor actions (Lewis et al., 2011). It has been proposed that physical deconditioning and increased effort perception form a vicious cycle that causes a general aversion to effortful activities, which may then contribute to the manifestation of fatigue as a chronic symptom (Nadarajah & Goh, 2015).

Aversion to effort in PSF may be particularly pronounced for actions that need to be maintained over long time periods. In fact, some definitions of chronic fatigue refer to a 'difficulty in […] sustaining voluntary activities' (Chaudhuri & Behan, 2004), or the 'inability or difficulty to sustain even routine activities' (Annoni, Staub, Bogousslavsky, & Brioschi, 2008). In line with this, self-report questionnaires of PSF include items such as 'My fatigue prevents sustained physical functioning' (Krupp, LaRocca, Muir-Nash, & Steinberg, 1989). A reduction in prolonged voluntary actions may be directly linked to adverse behavioural outcomes in everyday life. For example, stroke patients with high levels of fatigue show reduced physical and social activities (Ingles et al., 1999; Choi-Kwon, Han, Kwon, & Kim, 2005; Flinn & Stube, 2010; K. K. Miller et al., 2013), reduced probability to return to work 2 years post-stroke (Andersen, Christensen, Kirkevold, & Johnsen, 2012), and low levels of participation in rehabilitation programmes (Michael, 2002; Morley, Jackson, & Mead, 2005; Lerdal & Gay, 2013; Nadarajah & Goh, 2015). The latter finding points to a critical issue: Fatigue can impose an additional challenge on recovery after stroke by reducing patients' willingness to pursue rehabilitation or intervention programmes.

Hence, better insights into motivational deficits in PSF are highly relevant with regard to recovery and quality of life in stroke patients.

However, previous studies on PSF and its link to motivation have largely relied on self-report measures or clinical observations (e.g., Shaughnessy, Resnick, & Macko, 2006; Flinn & Stube, 2010; Caeiro et al., 2013; Elf, Eriksson, Johansson, von Koch, & Ytterberg, 2016). By contrast, laboratory measures of effort-based decision making are surprisingly rare in the PSF literature, whereas they are commonly used in other clinical populations that are associated with motivational deficits, such as apathy in Parkinson's disease (Chong et al., 2015), depression (Treadway et al., 2012) or schizophrenia (Hartmann et al., 2014). Laboratory decision-making tasks can provide more detailed insights into the mechanisms underlying specific impairments in effort-based choice by controlling for confounding factors, such as motor impairments, and avoiding potential biases associated with self-report measures. Previous laboratory studies of effort-based decisions have typically used binary choice tasks that, on each trial, require a single decision based on anticipated rewards and costs (e.g., Prévost et al., 2010; Hartmann et al., 2013; Chong et al., 2015). Here, a slightly different approach is introduced to capture participants' willingness to *maintain* effortful actions in order to reach a goal, rather than measuring the willingness to *initiate* a brief effortful action (c.f., Meyniel et al., 2014). Specifically, in a double-step choice task, PSF patients and healthy control subjects generated voluntary goal intentions and then had to implement their intentions into effortful actions by squeezing a hand-held dynamometer. Intention pursuit required effortful actions to be maintained for several seconds, whereas CoM occasionally allowed participants to take a short-cut to a nearby option that only required a shorter duration of effort exertion. This task may provide a more sensitive measure for potential motivational impairments in patients with chronic fatigue, because it relates directly to the self-reported difficulties that patients face. We hypothesised that PSF is associated with reduced perseverance, causing patients to give up on their own voluntary intentions more readily, and hence, show an increased frequency of CoM compared to healthy controls. This would suggest that chronic fatigue after stroke is not only associated with sensorimotor impairments (Kuppuswamy, Rothwell, et al., 2015), but additionally, motivational deficits linked to changes in effort-based decision making.

Furthermore, the task allowed us to gain more detailed insights into the mechanisms underlying motivational deficits in PSF. Specifically, we tested whether effort-based decisions in PSF patients depended on whether effortful actions had to be executed with the hand that was affected by the stroke (contralateral to stroke side) or the unaffected (ipsilateral) hand – while controlling for differences in motor performance between the two hands. Lateralisation of effort-based decisions would suggest that choices are directly linked to lower-level movement aspects related to contralesional motoric impairments observed in hemiplegic stroke (Cramer, Nelles, Schaechter, Kaplan, & Finklestein, 1997; Mani et al., 2013). By contrast, if no differences between affected and unaffected hands are observed, effort-based decisions likely depend on higher-order mechanisms that are common to actions generated in both hemispheres, rather than being lateralised to contralesional limbs that are affected by motoric impairments. This would be in line with the assumption that PSF itself is generalised (Macko et al., 1997) and with the conceptualisation of motivation as a global, energizing drive (Hull, 1943; Kouneiher et al., 2009).

5.2 Methods

5.2.1 Participants

The study was approved by the London Bromley Ethics Committee (REC reference number: 16/LO/0714). Participants provided written informed consent prior to the study. Fifteen post-stroke fatigue patients (PSF) were recruited through the National Hospital for Neurology and Neurosurgery (NHNN), Queen Square. One patient withdrew from the study after block 1 of the behavioural task, reporting pain in her hand, and the data from that patient were excluded from all analyses. Hence, a final sample of 14 PSF patients was tested (13 right-handed). Age-matched healthy control subjects (CTLs; *n* = 17, all right-handed) were recruited through the ICN subject database.

All PSF patients were screened prior to the study based on the following criteria: They were first-time, hemiplegic (ischaemic or haemorrhagic) stroke patients with fatigue scores higher than 4 on the Fatigue Severity Scale (FSS; Krupp et al., 1989), in line with previous studies using the same cut-off for high levels of chronic fatigue (Kuppuswamy, Clark, et al., 2015). Strokes occurred at least 3 months prior to the study (*M* = 42.0 months, *SD* = 31.5, range = 7 months – 10.2 years). Furthermore, patients had no other neurological disease, had depression scores ≤ 11 (moderate depression) on the Hospital Anxiety and Depression Scale (HADS; Zigmond & Snaith, 1983) and were not taking anti-depressants. Additionally, grip strength and manual dexterity of the hand affected by the stroke had to be at least 60% of the unaffected hand in order to ensure that patients had relatively high motor abilities and would be able to perform the task. Manual dexterity was assessed using the 9-hole peg test (Kellor, Frost, Silberberg, Iversen, & Cummings, 1971). Within the PSF group, 6 patients had left-hemispheric and 8 patients had right-hemispheric stroke. **Table 5.1** provides an overview of sample characteristics for CTLs and PSF patients.

Table 5.1. Demographic information and screening questionnaires [*M* (*SD*)].

	n	**Female**	**Age**	**FSS**	**HADS depression**	**HADS anxiety**
CTL	17	11	60.5 (8.0)	2.2 (1.2)	4.4 (2.9)	4.7 (3.1)
PSF	14	6	60.8 (11.3)	5.4*** (1.2)	6.1 (3.1)	6.7^{+} (3.1)

Asterisks indicate significantly higher scores in PSF patients than CTLs. $^{+}p < .1$, ***$p < .001$

5.2.2 Apparatus and stimuli

The task was programmed in Matlab R2014a and the Psychophysics Toolbox (Brainard, 1997). Choice options were presented as rectangular targets (3.5° x 4.9°) of different colours, and were located 10.6° from the centre of the screen. Participants used two Biometrics hand grip dynamometers, one in their left and one in their right hand, to indicate choices by squeezing the dynamometer corresponding to the location of the chosen target colour.

5.2.3 Effort-based intention pursuit

Participants performed a double-step choice task in which they could win points (**Figure 5.1**). On each trial, participants first made a free choice between two colour options (random pair of blue/green/red/yellow). Colour options were presented above/below the centre of the screen and participants said their chosen colour out loud. The two colours were then presented in target locations on the left and right side of the screen – either at the top or bottom (counterbalanced). Participants' task was to navigate a manikin on the screen to the chosen colour by *continuously* squeezing a dynamometer with their left or right hand, depending on the location of their chosen colour. For example, if the colour choice was blue and blue appeared on the right side, participants had to squeeze with their right hand (regardless of whether the colours appeared at the top or bottom of the screen). If participants used the wrong hand, a warning message appeared and the trial was repeated. A minimum force of 60% of an individual's left/right maximum voluntary contraction (MVC) was required in order to move the manikin towards the chosen colour. Importantly, participants had to maintain the required squeeze force to move the manikin at a slow and constant velocity of 2.1°/sec towards the chosen colour. Once the manikin reached the target location (~5 sec), participants won 10 points. If the applied force dropped below 60% MVC, the manikin stopped until the required force was reached again. Participants were asked to try and avoid this by maintaining the required level of force once the manikin had started moving.

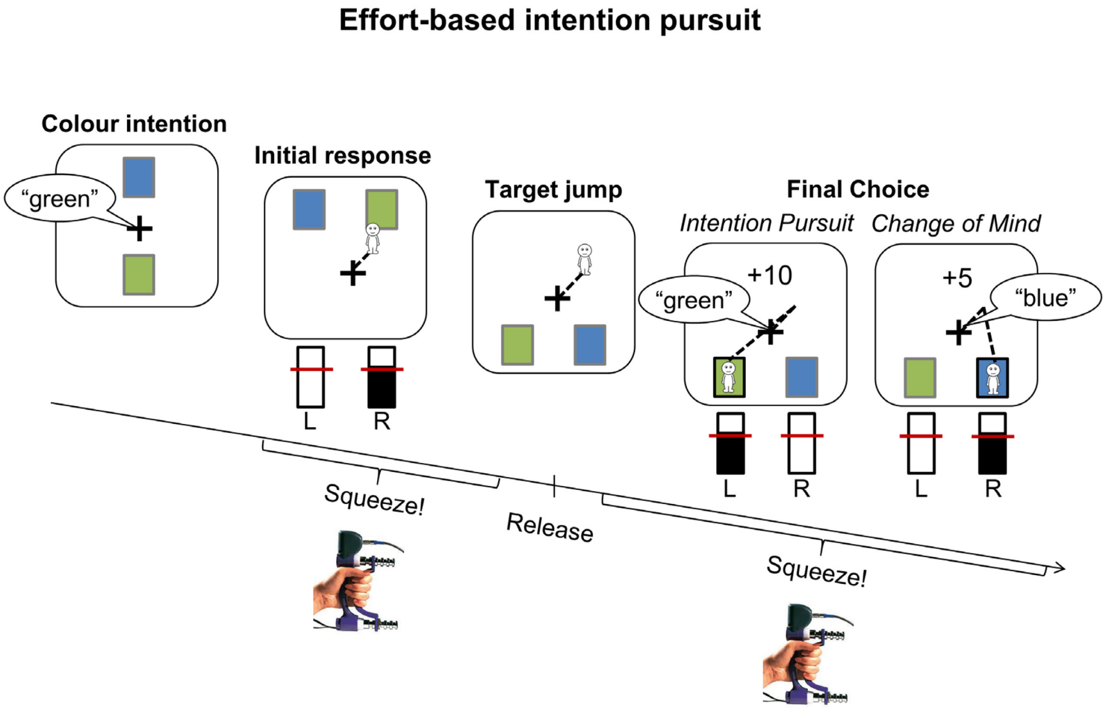
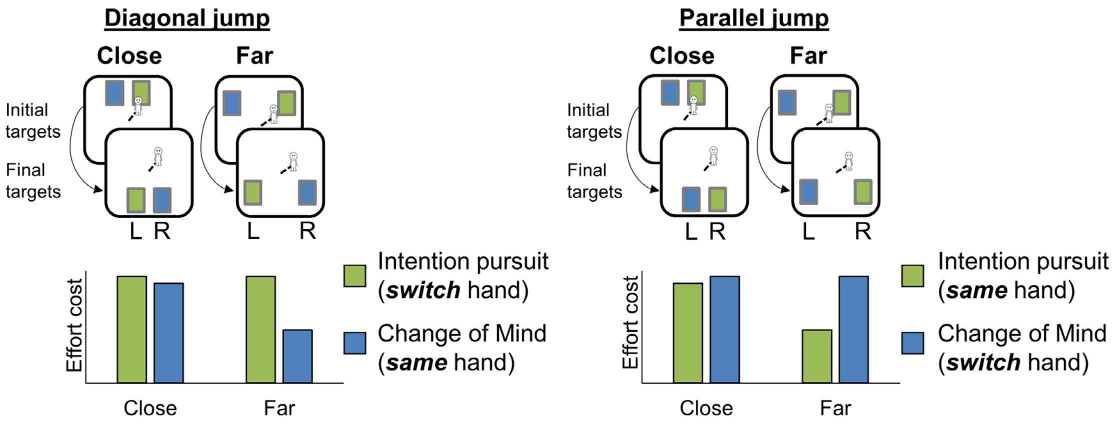


Figure 5.1. Effort-based intention pursuit task. Participants made a voluntary decision between two colours (e.g., green). They then had to navigate a manikin to the location of the chosen colour by continuously squeezing a dynamometer with the left or right hand, depending on to the location of the chosen colour (e.g., green = right). On some trials, the colours jumped to a new location once the manikin had travelled half the distance towards the initial choice. Participants then had to decide whether to pursue their initial intention (green; 10 points) or change their mind and switch to the alternative colour (blue; 5 points). They then had to indicate their final decision by continuously squeezing with the hand corresponding to the location of their final colour choice until the manikin reached the target.

In 2/3 of trials, the manikin stopped after having travelled half the distance (2.5 sec) towards the initial choice and participants were asked to stop squeezing. Both colour targets then jumped to the other side of the screen – i.e., from the two top locations to the two bottom locations or v.v. This required participants to make a second decision where they could choose to either pursue their initial colour choice for 10 points, or instead, switch to the alternative colour (CoM) for 5 points. Once participants had made their final decision, they were asked to start squeezing again – now with the hand corresponding to the location of their *final* colour choice (either same or different hand as initial choice; see below). Again, participants had to maintain the squeeze until the manikin reached the target.

Final decisions were expected to depend on an effort-reward trade-off. Although the amount of force was kept constant throughout the task, effort requirements of intention pursuit vs. CoM differed according to how long the effort had to be maintained for, and hence, depended on the locations of the final targets. Similar to the paradigm used in **Chapter 4**, this was manipulated by varying 1) whether targets jumped in a parallel/diagonal manner and 2) whether the targets were close/far from each other (**Figure 5.2A**). In diagonal-jump trials (1/3), the alternative colour choice was closer than the initially chosen colour, and hence, switching to the alternative colour allowed participants to save effort. By contrast, in parallel-jump trials (1/3), the initially chosen colour was closer than the alternative colour. Differences in distance, and hence effort, were particularly pronounced in the far-target condition (50% of trials), whereas effort requirements were similar in the close-target condition (50%). Participants were explicitly instructed that the time of the task was not limited, and hence, that longer distances were only costly in terms of their associated effort, but not in terms of mere temporal costs.

A) Trial conditions – Differences in effort



B) Predicted effects on CoM

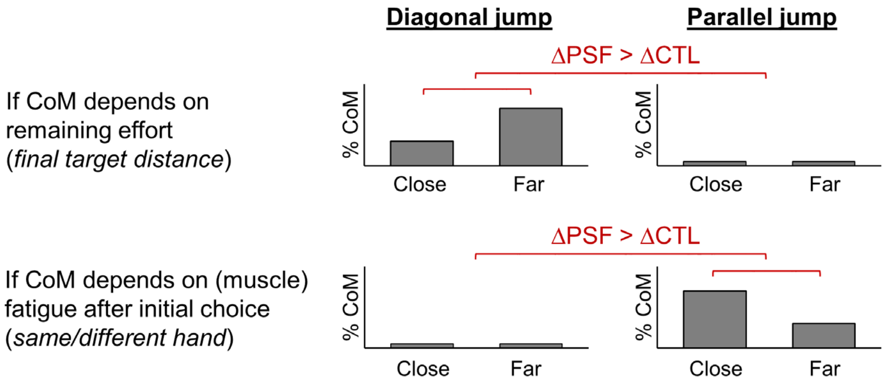


Figure 5.2. Trial conditions and predicted effects of effort on % CoM. A) Effort-reward trade-offs varied according to target-jump condition (diagonal/parallel) and target distance (close/far). In diagonal trials, the initial choice was further away from the current location than the alternative colour, hence, intention pursuit required longer sustained effort than CoM. By contrast, in parallel trials, the initial colour choice was closer than the alternative colour, and hence, intention pursuit was less costly. Differences in effort costs were particularly pronounced in the far-target condition. B) If CoM decisions are sensitive to final target distance (i.e., how long the effort associated with the final choice had to be maintained for), CoM should be more frequent in diagonal > parallel trials, in particular when targets are far compared to when they are close. By contrast, if final decisions merely depend on muscle fatigue of the hand that implemented the initial choice, participants would be more likely to switch in parallel > diagonal trials, given that this allowed for a switch to the alternative response hand, rather than continuing to squeeze with the same hand (in particular when targets were close, see Figure 5.2A). The predicted effects were hypothesised to be stronger in PSF patients compared to CTLs.

If participants took into account differences in target distance when making their final decisions, CoM should be more frequent in diagonal compared to parallel trials (**Figure 5.2B**). Moreover, in diagonal trials, participants should be particularly likely to switch to the alternative colour when the targets were far compared to when they were close. This is because in the far-target condition, pursuing the original intention was twice as effortful (squeezing for 7.6 sec) as switching to the alternative colour (3.8 sec), whereas in the close-target condition, costs were similar for intention pursuit (7.6 sec) and CoM (7.1 sec). Crucially, intention pursuit was always associated with the same degree of effort, but the cost associated with CoM differed, and hence, the *relative* cost of intention pursuit in diagonal trials was lower in the close- than far-target condition. We hypothesised that PSF patients would be particularly sensitive to differences in effort, and hence, would be more likely than CTLs to change their intention in diagonal trials, especially when targets were far.

A crucial difference to the paradigm reported in the previous chapter is that in the current task, costs may not purely depend on target distance, but also on 1) which hand had to be used to implement a given choice (e.g., ipsi- vs. contralateral to the stroke side) and 2) whether or not final responses required responding with the same vs. different hand relative to the initial choice. Specifically, in diagonal trials, intention pursuit always required a switch between the left and right hand, whereas CoM required participants to continue squeezing with the same hand (**Figure 5.2A**). It is possible that effort costs did not only depend on distance to the final target locations, but also on whether or not a given decision required continuous squeezing with the same hand, which may have fatigued during the initial choice. For example, having used the right hand to implement the initial decision might render continuous squeezing with the right hand more effortful/difficult than switching to the left hand. This may increase overall preference for intention pursuit in diagonal trials (regardless of target distance). Hence, diagonal trials alone did not allow us to dissociate whether higher overall frequencies of intention pursuit indicated higher willingness to persevere, or instead, simply a preference to switch hands based on muscle fatigue after the initial choice. However, parallel-jump trials enabled us to differentiate between these alternative explanations (**Figure 5.2B**). That is, in parallel trials, response mappings were reversed: Intention pursuit required squeezing with the same hand, whereas CoM was associated with switching hands. Hence, if effort-based decisions merely depended on whether or not participants had to continue squeezing with the same hand, participants would show a tendency for CoM in parallel trials despite the fact that the initial colour choice was closer. Additionally, CoM in parallel trials would be more frequent in the *close-target* condition, where intention pursuit required longer continuous squeezing with the same hand (7.1 sec) than in the far-target condition (3.8 sec). Hence, the two alternative explanations made opposite predictions regarding the overall frequency of CoM in diagonal vs. parallel trials and regarding the effect of target distance on CoM in each condition. This allowed us to test to what extent decisions between intention pursuit and CoM depended on target distance associated with final choices vs. on mere (muscle) fatigue of the hand that was used to implement the initial choice.

Participants completed 4 blocks of 12 trials each, resulting in a total number of 48 trials. If squeeze force dropped below 60% in more than 25% of the time within a given block, the required force level was decreased by 10% in the following block to control for muscle fatigue that may occur during the task and could introduce potential confounds, such as frustration due to failure to maintain the required force level.

5.2.4 MVC calibration

Prior to the task, participants' MVC was determined separately for each hand. Participants were asked to squeeze as hard as possible and hold the squeeze for 6 sec. This was repeated 3 times for each hand. In each trial, the median force applied during the time period from 2–4 sec was extracted, and MCV was defined as the average of that value across the 3 trials. Participants were then presented with a single trial that required them to squeeze at 120% of the MVC of each hand. If participants were able to reach that level of force, the calibration procedure was repeated and participants were reminded to squeeze at their maximum force during calibration.

5.2.5 Protocol

PSF patients were recruited as a sub-sample of an ongoing large-scale study on PSF, and hence, completed additional tasks that are not reported here. The study consisted of three separate sessions conducted within a time period of 5–6 weeks. All sessions involved a range of clinical questionnaires, behavioural tasks and measurement of corticomotor excitability using TMS. The task reported here was completed in session 3. Note that most PSF patients ($n = 11/14$) additionally received transcranial direct current stimulation (tDCS) over motor cortex during session 1 (i.e., 5–6 weeks prior to the data reported here). Because this intervention was not specifically targeted at the current research question, and because the task reported here was only conducted on a sub-set of the larger patient sample, we were not able to control which patients received tDCS in session 1. Hence, given the unbalanced sample of patients with tDCS vs. sham stimulation, we were not able to test whether tDCS may have affected performance in the current task. Potential confounds that the tDCS intervention may have introduced will be addressed in the discussion.

5.2.6 Analyses

Statistical analyses were performed using IBM SPSS Statistics for Windows, version 21 (Corp, Released 2012). For most dependent variables, the assumption of normality was violated (as tested with Kolmogorov–Smirnov tests for normality). Hence, given the relatively small sample size in each group, non-parametric tests were used for all analyses and medians (*Mdn*) and interquartile ranges (*IQR*) are reported. Mann–Whitney U tests were applied for between-subject analyses and Wilcoxon signed-rank tests were used for within-subject analyses. Two-tailed *p*-values obtained by exact tests are reported ($\alpha = .05$).

5.3 Results

5.3.1 Frequency of effort-induced CoM

Figure 5.3 illustrates the frequency of CoM, separately for each group (CTL/PSF), target-jump condition (diagonal/parallel) and target-distance condition (close/far). Both CTLs and PSF patients showed higher % CoM in diagonal- (CTL: *Mdn* = 6.3%, *IQR* = 0–34.4%; PSF: *Mdn* = 56.3%, *IQR* = 6.3–87.5%) compared to parallel-jump trials (in both groups: *Mdn* = 0%, *IQR* = 0–0%) and the difference was significant in both groups (CTL: $Z = 2.67$, $p = .004$, $r = 0.48$; PSF: $Z = 2.85$, $p = .002$, $r = 0.51$). Furthermore, within diagonal trials, both groups showed significantly higher frequencies of CoM in the far-target condition (CTL: *Mdn* = 12.5%, *IQR* = 0–43.8%; PSF: *Mdn* = 93.8%, *IQR* = 12.5–100%) compared to the close-target condition (CTL: *Mdn* = 0%, *IQR* = 0–12.5%, $Z = 2.20$, $p = .039$, $r = 0.40$; PSF: *Mdn* = 12.5%, *IQR* = 0–75%, $Z = 2.94$, $p < .001$, $r = 0.53$). This suggests that both groups largely based CoM decisions on how long final actions had to be maintained for (depending on final target distance), rather than simply on whether or not intention pursuit required continuing to squeeze with the same hand (see Methods, **Figure 5.2B**). In fact, only 3 participants (1 CTL and 2 PSF) showed CoM in a low number of parallel trials, where CoM allowed for switching hands. These CoM only occurred in the close-target condition in line with the assumption that motor fatigue of the hand associated with the initial choice would be more likely to induce CoM in close than far parallel trials. However, given that this occurred extremely rarely, within-trial effects of motor fatigue did not seem to have a substantial effect on task performance, neither in CTLs nor PSF patients.

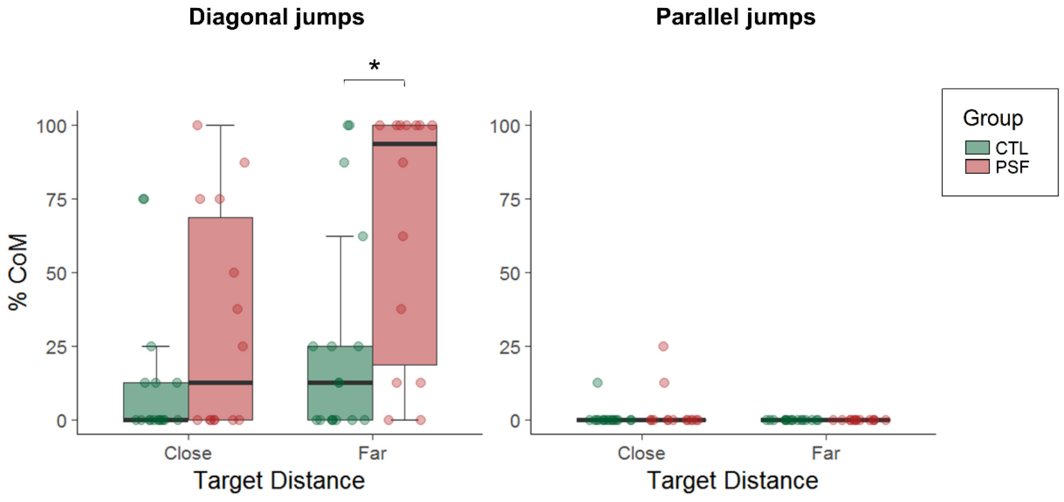


Figure 5.3. Frequency of CoM in effort-based intention pursuit task. Boxplots illustrate the median % CoM for CTLs (green) and PSF patients (red) in diagonal and parallel trials, separately for each target-distance condition. Boxes represent IQRs and whiskers represent 1.5*IQR. Dots correspond to individual data points.

More interestingly, group comparisons revealed that in diagonal trials, PSF patients showed significantly higher frequencies of CoM than CTLs (collapsed across target-distance conditions: $Z = 2.33$, $p = .021$, $r = 0.42$). This effect was driven by the far-target condition ($Z = 2.46$, $p = .017$, $r = 0.44$), whereas the group difference was not significant in the close-target condition ($Z = 1.33$, $p = .246$, $r = 0.24$). Hence, as hypothesized, PSF patients were more sensitive than CTLs to the effort associated with pursuing their initial intentions, rendering patients more likely to change their mind in diagonal trials, in particular when targets were far.

Interestingly, the group difference seemed to be more strongly driven by patients with left-hemispheric stroke ($n = 6$) who all switched to the alternative colour in 100% of far diagonal trials. By contrast, patients with right-hemispheric stroke ($n = 8$) showed significantly lower frequencies of CoM (far diagonal trials: *Mdn* = 81.3%, *IQR* = 3.1–81.3%; $Z = 2.90$, $p = .005$, $r = 0.78$), which was only descriptively higher than CoM in CTLs (Z = 0.91, p = .383, r = 0.24). The observed difference between left- and right-hemispheric stroke patients in the current sample needs to be interpreted carefully due to the small number of patients in each sub-group. However, given the relatively large and consistent difference, it is plausible that stroke side might at least account for some of the variance in the frequency of effort-induced CoM.

5.3.2 No effect of motor performance

Next, we checked whether higher frequencies of CoM in PSF patients may have been caused by potential motor impairments in PSF. Patients and CTLs had comparable MVCs (collapsed across both hands, CTL: *Mdn* = 21.9 kg, *IQR* = 18.2–30.0 kg; PSF: *Mdn* = 24.1 kg, *IQR* = 20.0–32.1 kg; Z = -0.52, p = .625, r = 0.09). Additionally, effort requirements were adjusted to each individual. Accordingly, motor performance should be highly comparable across participants. In order to test this, 2 separate measures of motor performance were analysed (**Figure 5.4**). First, we measured the amount of force applied during the time period of each trial where participants squeezed with at least 1/3 of their MVC in order to capture the time points at which participants tried to squeeze at all. The percentage of time within this period in which participants reached the required level of 60% of the MVC was then computed, serving as an indicator of how successful participants were in reaching the required force level while they applied any force at all (% success, **Figure 5.4**, left). Note that this measure does not capture time periods where participants did not squeeze at all (e.g., to take a brief rest during an ongoing trial). Hence, a second measure was used where the time from action initiation to target hit was computed for trials without target jump in order to check whether participants differed in rest periods they may have taken during the task (movement time, **Figure 5.4**, right). Note that the manikin speed was constant, and hence, slower movement times reflect longer rest durations in which the manikin did not move.

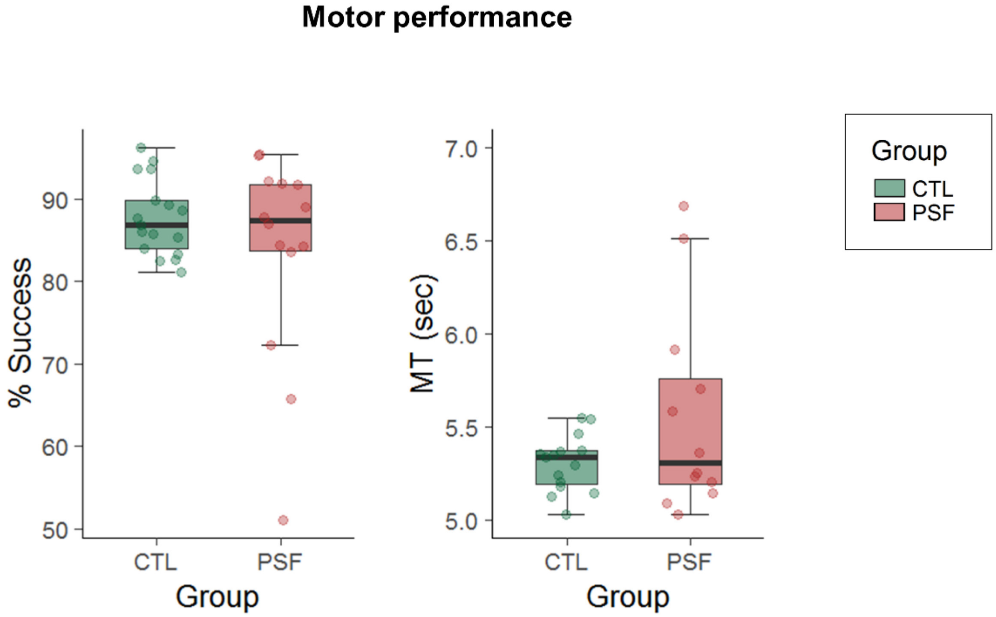


Figure 5.4. Motor performance. Boxplots illustrate median motor performance in CTLs (green) and PSF patients (red) as indicated by the % of time in which participants were squeezing successfully above the required effort level (left) and movement times (right). Boxes represent IQRs and whiskers represent 1.5*IQR. Dots correspond to individual data points.

Although some PSF patients showed slightly reduced motor performance, no significant group difference was observed for % success (CTL: *Mdn* = 86.8%, *IQR* = 83.6–91.8%, PSF: *Mdn* = 87.4%, *IQR* = 80.8–92.0%, *Z* = -0.16, *p* = .891, *r* = 0.03), nor movement times (CTL: *Mdn* = 5.30 sec, *IQR* = 5.14–5.37 sec, PSF: *Mdn* = 5.24 sec, *IQR* = 5.07–5.76 sec, *Z* = 0.56, *p* = .597, *r* = 0.10). Additionally, within patients, no significant difference was observed between left- and right-hemispheric stroke patients on either measure of motor performance (both *p* > .100, with a descriptive trend for worse performance in right-hemispheric patients). Hence, overall, motor requirements were well adjusted to each individual's motor ability, thus ruling out that potential motor impairments in patients can account for the observed group difference in intention pursuit. In line with this, no across-subject correlation was found between % success and % CoM in diagonal trials ($r_S(29) = -.03$, $p = .885$), nor between moment times and % CoM ($r_S(29) = -.14$, $p = .449$). This result suggests that CoM decisions did not depend directly on motor impairments, but instead, were related to some factor relatively independent of motor performance ability.

Although overall motor performance was highly comparable between groups, a slight decrease in motor performance was observed across the task in PSF patients, as indicated by a significant decrease in % success in the second half of the task (*Mdn* = 85.8%, *IQR* = 75.9–91.5 %) compared to the first half (*Mdn* = 88.6%, *IQR* = 83.0–92.6%, $Z = 2.23$, $p = .025$, $r = 0.40$), and a descriptive trend for an increase in movement times in the second (*Mdn* = 5.37 sec, *IQR* = 5.16–6.04 sec) compared to the first half (*Mdn* = 5.13 sec, *IQR* = 4.98–5.50 sec, $Z = 1.73$, $p = .091$, $r = 0.31$). By contrast, performance was highly stable in CTLs (both $p > .300$). Hence, it is possible that patients were more likely to change their mind in the second half of the task, due to decreases in motor performance, which may have driven the overall group difference. However, in PSF patients, % CoM was highly comparable in the first half (*Mdn* = 62.5%, *IQR* = 12.5–87.5%) and the second half of the task (*Mdn* = 50%, *IQR* = 0–90.6%, $Z = -0.54$, $p = .707$, $r = 0.10$), in both far and close diagonal trials (both $p > .700$). Hence, PSF patients used the same decision strategies throughout the task, despite slight decreases in motor performance, suggesting that patients' decision strategies for CoM were independent from mere motor performance.

5.3.3 No lateralisation of effects within patients

Finally, within patients, the hand contralateral to the stroke side was significantly weaker (MVC: *Mdn* = 20.4 kg, *IQR* = 15.3–32.9 kg) than the ipsilateral hand (MVC: *Mdn* = 29.1 kg, *IQR* = 22.2–36.8 kg, $Z = 2.48$, $p = .011$, $r = 0.45$). However, given that MVCs were adjusted to each hand separately, no difference in motor performance was observed between the affected and unaffected hand, neither for % success (affected hand: *Mdn* = 87.6%, *IQR* = 77.6–92.5%; unaffected hand: *Mdn* = 87.7%, *IQR* = 78.9–93.0%; *Z* = 0.47, *p* = .670, *r* = 0.08), nor for movement times (affected hand: *Mdn* = 5.28 sec, *IQR* = 5.05–5.95 sec; unaffected hand: *Mdn* = 5.16 sec, *IQR* = 5.00–5.57 sec; *Z* = 1.29, *p* = .217, *r* = 0.23). Despite no differences in motor performance, it is possible that patients' CoM decisions depended on whether or not intention pursuit required responding with the hand affected by the stroke or with the unaffected hand. That is, even though motor ability of each hand was controlled for, subjective fatigue might be lateralised, and hence, may disproportionally affect effortful actions with the affected hand. However, in patients, no significant difference in % CoM in diagonal trials was found between contralesional (*Mdn* = 56.3%, *IQR* = 12.5–87.5%) and ipsilesional hand (*Mdn* = 50.0%, *IQR* = 0.0–87.5%; *Z* = 1.00, *p* = .531, *r* = 0.18), which was true for both target-distance conditions (both *p* > .350). Hence, patients' CoM decisions did not seem to be affected by whether intention pursuit required responding with the affected or unaffected hand. Although caution is required in interpreting null results, particularly from small samples, effect sizes of differences in CoM were much smaller than effect sizes observed for differences in grip strength between contra- and ipsilesional hand. Hence, even if there was a small lateralisation of effort-based decisions, this appears to be negligible compared to pure motoric effects. Hence, it is unlikely that motivational deficits are lateralised to the same extent as motoric impairments, but instead, they seem to affect actions generated in both hemispheres.

5.4 Discussion

Fatigue is a debilitating symptom that affects a substantial number of stroke survivors (Ingles et al., 1999; Nadarajah & Goh, 2015). Previous studies have mainly focused on sensorimotor aspects of fatigue, such as physical deconditioning (Lewis et al., 2011), limb heaviness (Kuppuswamy, Clark, Rothwell, & Ward, 2016) and changes in corticomotor excitability (Kuppuswamy, Clark, et al., 2015). Others have relied on self-report measures to capture motivational deficits associated with PSF, such as self-reported apathy (Caeiro et al., 2013) or reports of reduced physical, social and professional activities (Ingles et al., 1999; Choi-Kwon et al., 2005; Flinn & Stube, 2010; K. K. Miller et al., 2013). Here, a laboratory decision-making task was used in order to test whether PSF is associated with reduced motivation to invest continuous effort to reach a goal, while controlling for any potential motor deficits.

We found that PSF patients showed reduced perseverance in the face of effort compared to healthy, age-matched control subjects. Specifically, when pursuing an initial goal required sustained physical effort, patients were more likely to switch to an alternative choice option that was easier to attain. Patients were particularly likely to give up on their initial goal when the relative difference in effort between the two choice options was large (far targets), whereas they did not differ from healthy controls when choice options were associated with similar degrees of effort (close targets). Note that in both conditions, the absolute effort associated with intention pursuit was equal. This is important for two reasons: 1) it suggests that, compared to CTLs, patients were more sensitive to *differences* in effort between action alternatives, rather than simply showing a general tendency to give up on intentions when absolute effort was high, and 2) it shows that patients were in principle able to overcome effort costs associated with intention pursuit, but were only willing to do so when no low-effort action alternative was available. Hence, a reduction in sustained physical activity typically associated with PSF (Krupp et al., 1989; Chaudhuri & Behan, 2004; Annoni et al., 2008) may not purely reflect a reduced *ability*, but rather, a reduced *willingness* to maintain voluntary actions over time, suggesting a strong link between chronic fatigue and motivational deficits.

In line with this, we further showed that the observed effects were not due to differences in motor abilities between subjects, and could also not be accounted for by the slight reduction in motor performance across the task that was observed in PSF patients. Additionally, given that movement times were comparable across groups, differences in intention pursuit cannot be explained by potential effects of motor performance on temporal discounting of rewards due to longer delays associated with slower movement times (Shadmehr et al., 2010). Instead, reduced perseverance in patients was presumably driven by higher experienced effort associated with intention pursuit, which consequently influenced effort-reward trade-offs (Müller & Apps, 2018). It has been suggested that reduced corticomotor excitability in PSF causes patients to perceive their actions to be more effortful (Kuppuswamy, Clark, et al., 2015). That is, in PSF a stronger input drive from higher 'volitional' centres into the motor cortex is required to produce a given level of motor output. This may increase the *subjective* effort associated with a given action. This would explain why patients were less willing to expend effort to pursue their initial intentions, even though objective force requirements were matched to each individual's motor abilities.

5.4.1 Global motivational deficits in PSF

Furthermore, within patients, we did not observe any lateralisation of the effect, and hence, no difference in intention pursuit between the contra- and ipsilateral hand with respect to the stroke side. This is in line with the assumption that chronic fatigue is generalised, rather than specifically affecting actions executed with the limb affected by the stroke (Macko et al., 1997). As a consequence, motivational deficits associated with fatigue do not appear to be driven by processes that are directly associated with contralesional motoric impairments that are a primary consequence of the stroke itself (Cramer et al., 1997; Mani et al., 2013). Instead, the results seem to be driven by changes in effort perception that is generated in higher-order centres and is common to actions generated in both hemispheres. Previous studies in rats have provided evidence for lateralisation of effort-based decisions, showing that unilateral MFC lesions result in a reduced willingness to expend effort with the contralesional limb (Croxson, Walton, Boorman, Rushworth, & Bannerman, 2014). However, in PSF, changes in effort-based decision making appear to be generalised, presumably due to the fact that fatigue itself is not directly linked to a specific lesion side or laterality (Macko et al., 1997; Ingles et al., 1999; Cumming et al., 2016). Instead, fatigue may result from secondary neurodegeneration, possibly caused by inflammatory processes after stroke (Ponchel et al., 2015; De Doncker, Dantzer, Ormstad, & Kuppuswamy, 2017), that may affect higher pre-motor stages that are engaged in global motivation of behaviour irrespectively of which hemisphere is involved in executing the action (Hull, 1943; Kouneiher et al., 2009). Specifically, a network of areas including dorsal anterior cingulate cortex, dlPFC and insula has been proposed to be involved in the subjective evaluation of effort, and in particular, the decision whether or not to maintain an effortful action based on integration of internal states and effort-reward trade-offs (Holroyd & Yeung, 2012; Kolling, Wittmann, et al., 2016; Müller & Apps, 2018). These areas may take into account the strength of inputs into motor cortex that are required to drive a given action.

The fact that decisions were not lateralised further suggests that increased switching frequency in PSF patients was not caused by an avoidance to use the hand affected by the stroke due to other potential factors, such as pain (Widar, Samuelsson, Karlsson-Tivenius, & Ahlstrom, 2002). Additionally, neither control subjects nor PSF patients used decision strategies that indicated a preference to alternate hands in order to avoid using the same hand for initial and final choice. Hence, our results do not reflect mere peripheral muscle fatigue that may have occurred during an ongoing trial (i.e., fatigue of the hand that was used to implement the initial choice). Instead, in both PSF patients and healthy controls, intention pursuit depended on the remaining effort associated with the final decision, which varied as a function of target distance. Hence, reduced intention pursuit in patients seemed to be caused by a strategy that aimed at minimizing the *total* effort (distributed across both hands) of a given trial, rather than simply avoiding to continue squeezing with the same hand. This further suggests that the task successfully avoided capturing mere ‘state’ fatigue that may have been induced by the task itself (Müller & Apps, 2018). Instead, our pattern of results suggests that the task measured differences in chronic fatigue (or ‘trait’ fatigue) and its effect on the motivation to invest effort to pursue one’s intentions.

5.4.2 Alternative explanations & open questions

Although it is possible that factors other than chronic fatigue may have contributed to between-group differences, we can rule out that depression can account for differences in motivation (Treadway et al., 2012), given that PSF patients and CTLs did not differ in depression scores. Moreover, although, patients showed slightly higher anxiety compared to CTLs, anxiety does not appear to be directly linked to effort-based decision making (Treadway et al., 2012; M. F. Green, Horan, Barch, & Gold, 2015), and hence, is unlikely to have caused the observed group difference. Interestingly, high frequencies of CoM further imply that PSF patients did not have any deficits in executive control functions that may have affected their ability to switch goals (Mecklinger, Yves von Cramon, Springer, & Matthes-von Cramon, 1999; Shallice, Stuss, Picton, Alexander, & Gillingham, 2008; Gläscher et al., 2012). Similarly, our results cannot be explained by potential difficulties in motor response switching in PSF patients, given that in close-target trials, intention pursuit (and hence, switching of response hands) was comparable between PSF patients and healthy controls. Instead, group differences were specific to the far-target condition, and hence, appeared to be driven by differences in effort-based decisions. Nevertheless, further studies need to test how specific and direct the link between chronic fatigue and effort-based intention pursuit is by controlling for a larger range of additional factors and potential comorbidities in stroke patients.

Moreover, the difference between left- and right-hemispheric stroke we observed in the current sample should be further investigated in future studies with larger samples. We found that left-hemispheric patients showed a stronger reduction in perseverance than patients with right-hemispheric stroke. Indeed, it has previously been proposed that the left hemisphere is more strongly associated with goal-directed behaviour, showing a dominance over the right hemisphere in controlling voluntary movements of *both* sides of the body (Haaland, 2006; Serrien, Ivry, & Swinnen, 2006) and a more prominent role in goal-directed as opposed to stimulus-driven attention (Corbetta & Shulman, 2002). Hence, it is plausible that the left hemisphere might be particularly relevant in voluntary action control and endogenous goal pursuit.

5.4.3 Component processes of effort-based decisions

As opposed to previous effort-based decision-making tasks that have been used to study motivational deficits in Parkinson's disease (Chong et al., 2015), depression (Treadway et al., 2012), or schizophrenia (Hartmann et al., 2014), the degree of effort in the current study was manipulated by varying the duration effortful actions had to be maintained for, rather than varying the amount of force per se. While we assumed that the current task would be particularly sensitive to potential motivational deficits in PSF, it is possible that typical binary-choice tasks would show similar effects in PSF patients. Direct comparisons between these tasks might allow us to further disentangle the specific motivational impairments in PSF. For example, simple binary-choice tasks capture the willingness to initiate an action based on anticipated costs and rewards. By contrast, in the current task, patients always had to initiate an effortful action, but could subsequently decide how long to maintain an action for in order to pursue the initial choice. Furthermore, given that the amount of force was always constant, decisions did not only rely on estimation of future efforts based on visual cues, but also depended on the experienced effort that had already been expended. Hence, the different types of decision-making tasks might be able to capture distinct aspects of effort-based decision making: 1) Willingness to *initiate* an action based on *anticipated* effort and 2) willingness to *maintain* an effortful action based on *experienced* effort during ongoing action execution (Meyniel et al., 2014). Presumably anticipating effort requires an internal model of the relation between a movement and the likely effort it will require. This model is presumably based on the actual experience of effort. Our study is novel in studying the experience of effort directly, rather than decisions based on a previously-learned model of effort.

5.4.4 Implications

Deeper insights into these putative component processes underlying effort-based decisions are highly relevant for our understanding of the specific motivational impairments across different patient populations, with potential implications for interventions. In particular, deficits in perseverance may be highly relevant with regard to intention pursuit in patients' everyday life. For example, giving up on intentions too readily when effort is high may be an underlying cause of reduced likelihood to return to work (Andersen et al., 2012) or pursue rehabilitation programmes (Michael, 2002; Morley et al., 2005; Lerdal & Gay, 2013; Nadarajah & Goh, 2015) in stroke patients with high levels of fatigue. Hence, our results may have important implications for quality of life and recovery after stroke. That is, in stroke patients that experience high degrees of chronic fatigue, rehabilitation programmes may need to specifically target motivational deficits in addition to pure motor impairments. In fact, increasing motivation could increase physical activity, which may in turn be able to reduce fatigue (Zedlitz, Rietveld, Geurts, & Fasotti, 2012), possibly by breaking the vicious cycle between physical deconditioning and effort aversion.

This raises the question of how exactly motivation can be increased. The current laboratory measure provides a starting point to test the effect of potential interventions on the willingness to expend effort in PSF patients. For example, it has been proposed that cognitive-behavioural interventions that promote physical activity can reduce fatigue (Zedlitz et al., 2012; Aguiar et al., 2017; Wu et al., 2017), and hence, may be able to increase intention pursuit. Additionally, if reduced corticomotor excitability causes an increase in subjective effort in fatigue (Kuppuswamy, Clark, et al., 2015), then increasing excitability, e.g., through tDCS interventions, may be able to increase motivation to expend effort. Given the low and imbalanced number of patients with vs. without tDCS stimulation in the current sample, we were not able to test this directly. However, considering that most patients received tDCS stimulation, and yet, the patient group still showed lower intention pursuit compared to CTLs, it is unlikely that tDCS has a strong and long-lasting effect. Furthermore, previous studies investigating the effect of tDCS on PSF suggest that effects vary strongly across patient sub-populations (Elsner, Kugler, Pohl, & Mehrholz, 2013; Marquez, van Vliet, McElduff, Lagopoulos, & Parsons, 2015; Kubis, 2016). Hence, future large-scale studies need to test more systematically if, and under which conditions, tDCS may be an effective intervention for PSF.

5.4.5 Conclusion

Post-stroke fatigue is a multi-dimensional syndrome that can have wide-ranging consequences for patients' quality of life and recovery after stroke. Our results provide new insights into motivational aspects of fatigue, pointing to a deficit in PSF patients to sustain voluntary actions in order to reach a goal. These findings suggest a critical role for effort-based decision making in intention pursuit and pave the way for future research into the specific impairments of the underlying component processes in chronic fatigue, with the potential to develop novel interventions.

Chapter 6.

General discussion

6.1 Summary of findings

Previous studies on Changes of Mind have largely focused on perceptual decision making (e.g., Resulaj et al., 2009; Albantakis & Deco, 2011; Burk et al., 2014; Kiani, Corthell, & Shadlen, 2014; Moher & Song, 2014; van den Berg et al., 2016). By contrast, the current thesis investigated reversals of *voluntary* action decisions. While voluntary actions have often been studied in separation of their external context, the studies presented here explicitly accounted for the role of external cues in guiding action selection, for example, by providing sensorimotor information relevant for movement selection, or value-based information about rewards and costs associated with executing a given action alternative. Specifically, we proposed that voluntary actions are characterised by highly dynamic and integrative processes that continuously integrate endogenous intentions with sensory and value-based information, even after an action has already been initiated. As a result, changes in the external environment can trigger Changes of Mind during voluntary actions.

We assumed that two different types of CoM can occur in voluntary action. First, people may change their mind about *what* endogenous intention to pursue (Change of Intention) and/or they may change *how* to implement the intention into motor action (Change of Movement). This is in line with hierarchical accounts of action encoding (e.g., Mele, 1992; Cooper & Shallice, 2000; Pacherie, 2008; Cisek, 2012). In **Chapter 2**, a modified version of the random-dot motion task was introduced in which participants had to integrate perceptual decisions about dot-motion direction with an endogenous intention about target colour. Analysis of continuous movement trajectories indicated if and when participants changed their minds about the dot-motion direction, which could either result in a Change of Movement, or additionally, a Change of Intention that involved switching to a nearby target of different colour. Changes of Movement + Intention were less frequent when colour intentions were strong and when the motor cost of pursuing the intention was relatively low. The effects of motor costs were particularly strong when intentions were transformed into motor plans at late stages of action preparation. These results suggest that aspects related to *how* intentions are implemented directly inform re-evaluation of intentions themselves.

Chapter 3 introduced an attractor network model consisting of multiple neural nodes that represented higher-order voluntary intentions, perceptual information from the environment as well as actions and their associated costs. Information was integrated through interconnections between neural populations. Firing rates were updated continuously, and hence, the model occasionally transitioned from one attractor state to a different state, indicating either a Change of Movement and/or a Change of Intention. Similarly to our behavioural results, we found that the frequency of each type of CoM depended on the strength of intentions and their trade-offs with motor costs. Hence, the model provides a biologically plausible neuro-computational mechanism through which dynamically changing information from different endogenous and exogenous sources is integrated by a network of neural populations that guide action selection in a continuous manner.

In **Chapter 4**, fMRI was used to investigate the neural dynamics underlying the integration of new information, which can trigger changes in voluntary intentions after action initiation. Multivariate pattern analysis showed that, in fronto-parietal areas, neural patterns changed dynamically as decisions evolved. Precuneus, angular gyrus and dorsolateral prefrontal cortex represented new contextual information about rewards/costs to guide the implementation of CoM into action. Furthermore, activation patterns in medial frontal cortex predicted decision reversals in participants whose CoM decisions were not exclusively guided by external evidence, suggesting a role for this area in continuously providing endogenous cues to inform both initial intentions and later intention reversals. Finally, CoM was associated with an increase in functional connectivity between the lateral and medial action selection pathways (Passingham, 1987), allowing for integration of endogenous and exogenous components of action selection. These results suggest that dynamic representation – and integration – of information in a fronto-parietal network allows agents to flexibly adjust their actions as they evolve in changing environments.

Finally, in **Chapter 5**, we investigated the role of effort-based decisions in intention pursuit. Reaching a goal often requires perseverance in the face of effort. Patients with post-stroke fatigue showed a reduced willingness to invest continuous effort to pursue their original goal intention compared to healthy controls, suggesting that chronic fatigue is associated with motivational deficits that cause a reduction in sustained voluntary actions. Importantly, these findings were not caused by mere motor impairments in stroke patients, nor by a preference to use the unimpaired hand. Instead, our results suggest that, in post-stroke fatigue, subjective effort-reward trade-offs are shifted, causing patients to give up on their own intentions more readily when goal pursuit requires sustained effort.

6.2 Theoretical implications

The studies reported in this thesis capture important characteristics of volition: Voluntary actions evolve continuously over time, they compete with alternative courses of action that are linked to other possible outcomes, and decisions between these alternatives depend on integration of multiple sources of endogenous and exogenous information. The ability to change actions allows agents to flexibly adjust their behaviour to the current environmental context, which is crucial for adaptive behaviour in a complex and dynamic world. However, importantly, this flexibility needs to be counterbalanced by a certain degree of stability of one’s own intentions, which is necessary for successful long-term goal attainment. Hence, voluntary actions require a *balanced* integration of endogenous intentions with dynamically-changing exogenous information. Investigating when, why and how people change their minds is a fruitful approach to capture the degree of flexibility of voluntary actions, and more broadly, gain novel insights into the fundamental neurocognitive mechanisms that generate behaviour. Hence, the findings reported in this thesis have several important theoretical implications – both with regard to our understanding of the mechanisms underlying CoM, but importantly, also the general processes that shape voluntary intentions and their implementation into action.

6.2.1 Implications for theories of CoM

First, our results provide new insights into the mechanisms underlying CoM. The current studies offer a broader conceptual view on decision reversals by investigating CoM in the context of voluntary action, rather than studying mere perceptual decisions. By considering how a multitude of sources of information is integrated, we identified dissociable types of CoM – and hence, different aspects of action that may be changed during ongoing action execution. The distinction between changes in sensorimotor processes vs. changes in endogenous intentions seems crucial, given that these types of CoM may have different underlying causes, and may result in different consequences. Specifically, CoM driven by perceptual reversals may be re-interpreted as a correction of an initially erroneous response based on new sensory evidence (Resulaj et al., 2009; Yeung & Summerfield, 2012; Fleming et al., 2018). By contrast, voluntary intentions often do not have an objectively correct or erroneous choice option. In fact, within the context of the current tasks, initial intentions were largely arbitrary and could not be based on some external criterion or instruction. Hence, changes in intentions did not simply reflect corrections of an initial 'error', but instead, more broadly reflected adjustments of decisions to a new (action) context that provided new information about rewards and costs associated with pursuing the initial intention. Thus, Changes of Intention depended more strongly on internal and subjective factors, including the strength of voluntary intentions and motivational aspects. As a result, alterations in these internal factors, such as increased subjective experience of effort in chronic fatigue (Kuppuswamy, Clark, et al., 2015), are directly linked to decisions about whether or not to pursue one's initial intentions to attain a goal.

Hence, our studies provide novel insights into the processes that dynamically integrate multiple sources of internal and external information in order to guide actions as they evolve. Past studies on CoM have neglected such integrative processes, and instead, have focused on decisions that are purely driven by perceptual evidence. As a consequence, previous computational models of CoM – both accumulator models (Resulaj et al., 2009) and attractor network models (Albantakis & Deco, 2011) – have only taken into account a single source of (perceptual) information, while disregarding how more complex decisions that involve multiple sources of dynamically changing information are generated and updated. The attractor network model proposed in the current thesis extends previous models by accounting for multiple action alternatives, and competition between them, which is guided by several pieces of hierarchically-organised endogenous and exogenous information. Hence, the current model captures different types of CoM that may occur during ongoing action selection. More broadly, our model suggests that a continuous interplay of multiple neural populations is crucial for flexible and dynamic actions (Cisek, 2012; Christopoulos et al., 2015; Yoo & Hayden, 2018). Similarly, our fMRI results suggest that integration of information in a network of fronto-parietal areas allows humans to change voluntary actions as they evolve. These findings provide new insights into fundamental principles of information processing in the brain by showing that fronto-parietal cortex uses dynamic neural codes in order to represent multiple sources of information that become available during ongoing action execution. Thus, studying CoM in voluntary action cannot only provide a better understanding of CoM, but also, of the general neurocognitive mechanisms underlying voluntary actions.

6.2.2 Implications for theories of voluntary action

First of all, by studying Changes of Intention, we gained novel insights into intentions themselves. Within the fields of psychology and neuroscience, there is a tendency to conceptualise voluntary intentions either in terms of ‘strong determining tendencies’ (Ach, 1935), or instead, as weak and labile motor intentions that can readily be changed (Fleming et al., 2009; Salvaris & Haggard, 2014; Kaufman et al., 2015). The results reported in this thesis suggest that intentions vary gradually in strength, are evaluated continuously, and can be reversed even when an action has already been initiated. Hence, volition is not a uniform and static phenomenon, but instead, is in its essence dynamic and malleable. By studying how, when and why intentions change, we can gain new knowledge about how ‘determining’ intentions are, and under which conditions they are maintained vs. abandoned.

Our results further suggest that intentions guide ongoing action execution in an online manner, rather than being mere retrospective confabulations (Wegner, 2002). That is, when intentions change, actions need to be changed, and this in turn can affect the outcome of an action. However, conversely, the need to change an ongoing movement can also induce changes in the intention itself. Hence, there are strong reciprocal links between lower-level movements and abstract goal intentions that determine action selection in a dynamic and interactive manner (Cisek, 2012). Thus, our studies fill in a key gap in cognitive theories of voluntary action. Specifically, most theories of voluntary action are hierarchical in some sense, for example, by distinguishing higher-order goal intentions from details of movement implementation and execution (Mele, 1992; Pacherie, 2008; Kouneiher et al., 2009). However, most existing models of voluntary action do not have a clear conceptualisation, nor means of measuring, what a goal intention is or how strong it is. Instead, theories about voluntary action largely rely on intuitions about ends and means. One crucial aspect that has been neglected in particular is the fact that goals have a recurrent feedback pathway that allows goals to be changed when they are not worth it, or when an equally-appealing action alternative is available. Whether or not people switch to an alternative course of action may be highly informative of how valuable, or strong, the initial goal intention was, by providing a measure of how willing people are to invest costs/effort into attaining the goal in the long term. Hence, a tractable way to study the dynamic links and dependencies between goals and movements allows one to 'price' goals in terms of how well they are sustained in the face of increased costs of execution. The studies presented in this thesis have introduced a novel, systematic laboratory approach to studying goal intentions and their relations to the actions that fulfil them. This provides a major advance in providing a clear notion of what 'goals' mean.

Finally, our findings point to an important contribution of *how* decisions in voluntary action, in addition to *what*, *when* and *whether* aspects of action (Brass & Haggard, 2008). While the importance of *how* aspects in action selection has been recognized for a long time (Goodale & Milner, 1992; Kawato, 1999; R. C. O'Reilly, 2010), these types of decisions typically receive little attention in the context of voluntary action. This is presumably due to the fact that *how* decisions may largely rely on external, sensory context, or sensorimotor constraints, rather than endogenous factors. Indeed, in the current studies, decisions about *how* to implement intentions were mainly guided by sensorimotor aspects. However, crucially, we showed that changes in *how* to implement an intention can induce changes in *what* intention to select. Hence, *how* decisions play an essential role in shaping endogenous actions, even though these types of decisions themselves may be largely guided by exogenous information. In addition to affecting objective action selection, *how* aspects may also play a crucial role in the subjective experience over actions. For example, in **Chapter 2**, reduced Sense of Agency was reported for actions that were associated with longer movement times, even when this did not affect the outcome of an action. Hence, *how* a given goal has been achieved (e.g., how 'fluent' or easy the executed movement was) may in some situations be of greater importance to an agent than *what* goal has been achieved. Thus, the subjective experience over our own actions depends on a wide range of factors other than the outcome that the action caused. These results further suggest that Sense of Agency does not merely depend on prospective cues associated with selection of an initial action and retrospective inference about outcomes after action completion (Chambon et al., 2014), but additionally, takes into account information related to the continuous execution of actions. Finally, the mere ability to reverse actions, and potentially choose an alternative course of action, may strongly contribute to our general sense that we are 'free' and responsible agents. That is, not only do we have a notion of "I could have done otherwise" (Kulakova et al., 2017), but in fact, we sometimes "do otherwise", and this may be important to our overall sense of being in control over our own actions and their outcomes.

6.3 Practical implications

In addition to theoretical implications, studying CoM may have important practical implications. In particular, the fact that CoM can affect action outcomes – either in a positive or negative way – is highly relevant with regard to personal and social consequences. This is especially true for Changes of Intention, which induce a mismatch between the initially-intended vs. actual outcome. Whether or not switching to an alternative course of action is desirable largely varies with context, and is often difficult to determine for the individual, given that potential action alternatives are hypothetical, or counterfactual. Representations of these counterfactuals presumably play an important role in feelings of regret over actions that have not actually been chosen (Kirkebøen, Vasaasen, & Teigen, 2013; Frith & Haggard, 2018).

Furthermore, although there may not be a general optimum, or a 'desirable' frequency of CoM, extremely high or low flexibility is clearly maladaptive and may be linked to psychopathology. For example, rigidity of behaviour in OCD (Maia & McClelland, 2012; Remijnse et al., 2013; Gruner & Pittenger, 2017) vs. impulsivity (Churchill & Jessop, 2011), e.g., in ADHD (Gawrilow et al., 2011; Hauser et al., 2016), or Parkinson's disease (Cools et al., 2003; Sinha et al., 2013), may represent opposite extremes on the spectrum of behavioural flexibility. In fact, disturbances in the balance between goal-shielding vs. goal-switching may be the underlying mechanism of a large range of psychiatric and neurological conditions, and hence, understanding the processes underlying this balance is crucial to well-being and mental health (Goschke, 2014). Additionally, motivational aspects, such as the willingness to persevere when facing costs or challenges, are directly linked to CoM regarding one's own goals. Hence, deeper insights into motivational deficits observed in fatigue (**Chapter 5** of this thesis), depression (Treadway et al., 2012), schizophrenia (Hartmann et al., 2014; M. F. Green et al., 2015), or Parkinson's disease (Chong et al., 2015) can be gained by investigating CoM. In addition to improving our understanding of the mechanisms underlying these disorders, developing novel tasks that measure behavioural flexibility and its relation to motivation could be useful to improve diagnostic tools, and may also inform future means of intervention.

Beyond psychopathology, insights into the mechanisms underlying the flexibility vs. stability of our decisions are highly relevant for everyday-life behaviour in healthy populations. How can we ensure that people pursue a healthy lifestyle and follow through with their own personal goals? Why is it that so many people give up on their New Year's resolutions? Or what does it take to change voters' minds in political elections? Studying the continuous and dynamic decision-making processes that shape our actions provides an important starting point to find answers to these questions, and to identify the mechanisms that underlie inter-individual differences in decision outcomes. For example, people with extreme political views are less susceptible to external influences when making decisions (Brandt, Evans, & Crawford, 2015). Similarly, a recent study showed that people's tendencies to process information in a flexible vs. rigid manner predicted their political and societal beliefs, and was linked to their voting choices in the Brexit referendum (Zmigrod, Rentfrow, & Robbins, 2018). Hence, real-life decisions can be directly linked to the fundamental mechanisms that determine how people evaluate and process information, and how readily they adjust their own decisions based on new evidence.

In addition to individual factors, environmental variables need to be considered. The current thesis points to a critical role of contextual cues in triggering decision updates, e.g., by providing information about the costs and rewards associated with CoM. Hence, environments that promote/prevent CoM can be created by building certain infrastructures or contexts, for example, through 'nudging' (Thaler & Sunstein, 2008). For instance, given that switching to an alternative option is often costly, defining favourable default options, e.g., for organ donations, can be a useful approach for policy makers to guide desirable decision outcomes. An alternative approach would be to make CoM easier when it is desirable – e.g., facilitating transitions to a more environmentally-friendly life-style by providing low-cost eco-friendly choice options and incentivising behavioural change.

6.4 Limitations, open questions & future directions

Studying CoM in any decision domain has been challenging due to the typically low trial numbers associated with overt CoM (e.g., Resulaj et al., 2009; Albantakis & Deco, 2011; van den Berg et al., 2016). **Chapter 2** of this thesis similarly faced this limitation. Yet, the increasing number of studies on CoM in the literature have provided reason for optimism that the findings are reproducible and meaningful. That is, reported frequencies of perceptual CoM in a given RDM task condition have been highly consistent across many studies (e.g., Resulaj et al., 2009; Albantakis & Deco, 2011; van den Berg et al., 2016), including the current experiments. Furthermore, repeated findings of factors that reduce/increase the frequencies of CoM (e.g., motor costs; Burk et al., 2014; Moher & Song, 2014) have enabled deeper insights into the basic mechanisms that shape decisions as they evolve.

Hence, provided that measures are sufficiently reliable, even rare events can be highly informative of neurocognitive processes. Consider other examples of relatively rare events, such as ‘tip-of-the-tongue’ phenomena (Brown & McNeill, 1966; Schwartz & Metcalfe, 2014), false memories (Roediger & McDermott, 1995; Loftus, 2005), or hallucinations (Waters et al., 2012), which have been studied extensively, not least because of the crucial insights into general functioning they can provide. Hence, deviations from normal or frequent behaviours are of particular interest in many domains of psychology as well as psychiatry. Finally, the fact that CoM is relatively rare may in itself be an interesting observation that merits future investigation. That is, why is it that people seem relatively reluctant to change their minds? To date, the answer to this question has largely focused on the role of motor costs associated with correcting an ongoing movement (e.g., Resulaj et al., 2009; Burk et al., 2014; Moher & Song, 2014). However, other phenomena, such as self-consistency biases (Luu & Stocker, 2018), choice-induced preference (Sharot et al., 2010; Voigt et al., 2017), or sunk costs (Arkes & Blumer, 1985) associated with making an initial choice may further contribute to this phenomenon.

6.4.1 Methodological considerations

Although important insights can be gained from rare events, limited trial numbers may nevertheless call for additional rigour in the design of experiments and further need for replication of findings. In that context, systematic attempts to increase the frequency of CoM may be useful for future research. This is particularly important for studies investigating the neural mechanisms of CoM, given the low signal-to-noise ratio of many neural measures, including BOLD signal in fMRI (Parrish, Gitelman, LaBar, & Mesulam, 2000; Murphy, Bodurka, & Bandettini, 2007). In order to increase trial numbers, and hence power, **Chapter 4** of this thesis introduced a novel task that aimed to mimic CoM occurring in the RDM task, without relying on spontaneous perceptual CoM. That is, in analogy to double-step tasks commonly used to study changes in movements (e.g., Goodale et al., 1986; Buch et al., 2010; Saberi-Moghadam et al., 2016), choice targets were relocated to induce action updates. However, importantly, target relocation in the current studies did not simply require motor re-programming of actions, but additionally triggered re-evaluation of an initial higher-order goal intention, which occasionally induced CoM with regard to the intention. This approach provides a new means of studying CoM in a more systematic manner by allowing for stronger experimental control over when and how often CoM occurs.

Yet, target relocation introduced a ‘perturbation’ of the ongoing decision-making process through changes in the external context. While this was crucial for the above-mentioned reasons, it may raise conceptual questions as to whether CoMs in this task are comparable to the more spontaneous CoMs in RDM tasks, which are induced by noisy fluctuations in sensory stimuli. Importantly, across all tasks, changes in external stimuli (or in how they were *perceived*) simply induced a need to change an ongoing movement, but did not instruct participants as to whether they should change their mind about their own voluntary intentions. Hence, Changes of Intention were still to some extent spontaneous and endogenous, even when the need for re-evaluation of the intention was induced exogenously. This is an important difference to previous studies investigating the flexibility of voluntary intentions, in which external cues explicitly instructed participants whether to stay or switch (Obhi & Haggard, 2004; Fleming et al., 2009; Obhi, Matkovich, & Chen, 2009; Obhi, Matkovich, & Gilbert, 2009), hence requiring a transition from endogenous to exogenous action selection. By contrast, the studies presented here introduced changes in external context that had to be *integrated* with endogenous intentions, rather than requiring a *switch* to purely exogenously-driven action selection. Intuitively, Changes of Intention may occur even without any external triggers. In fact, if voluntary intentions are the result of an accumulation process that integrates noisy endogenous signals over time (Schurger et al., 2012; Khalighinejad et al., 2018), Changes of Intention may occur due to stochastic fluctuations in this process even in the absence of external changes. Yet, such spontaneous and purely internally-driven Changes of Intention may be difficult to capture experimentally.

6.4.2 Conceptual considerations – What are CoMs?

In this context, conceptual questions need to be considered. One important question is to what extent switches to an alternative choice option reflected ‘true’ Changes of Intention in the tasks presented here. That is, did participants really change their original intention, or did they simply change to a different action without changing their actual underlying intention? In other words, can actions be separated from intentions? Indeed, in the literature on error processing, it has been argued that errors reflect a mismatch between intended vs. actual action (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1990; Sato & Yasuda, 2005), suggesting that in some cases, intentions can be dissociated from motor actions. Similarly, in the case of CoM, one may argue that a person who fails to quit smoking still intends to do so, and hence, that there is a mismatch between intention and action, rather than a *change* with respect to the actual intention. In fact, in the computational model, Changes of Intention did not require a complete reversal of decisions within the nodes encoding endogenous intentions, but instead, reflected changes between action alternatives that were associated with different intentions.

This opens a larger discussion about what CoM is, and if we need to move away from simply measuring CoM through changes in an overt action, and instead, define CoM based on covert changes that can be measured on a neural level, e.g., through changes in brain activity that is systematically linked to decision variables (Kiani, Cueva, et al., 2014; Kaufman et al., 2015; Fleming et al., 2018). While this may be appropriate for certain research questions, this thesis specifically focused on CoM that involved changes in action, for the following reasons: 1) Humans and non-human animals rarely make decisions that do not involve an action (either immediately or delayed). In fact, the neurocognitive systems underlying action selection and decision making are so highly interconnected (Cisek, 2012) that studying them in separation may only provide very limited insights into the mechanisms underlying cognitive processes. 2) Actions allow us to control events in the environment, and hence, are essential to our conscious experience of ourselves as agents. 3) Changes in actions can affect outcomes, and hence, may have important implications for the consequences of an individual's behaviour.

A final aspect that needs to be addressed is the potential link between CoM and other forms of behavioural flexibility, such as exploration vs. exploitation in dynamic and uncertain environments (Cohen et al., 2007; Humphries et al., 2012; Rushworth et al., 2012), or updating of information during learning (e.g., probabilistic reversal learning; Fellows & Farah, 2003; Izquierdo et al., 2017). These phenomena are typically measured via changes in sequential actions, or behavioural changes that occur across several trials/blocks, and hence, are driven by relatively slow updates. Additionally, in the case of learning, changes are based on feedback, whereas CoM can occur before any feedback is provided, and in fact, before an action is completed. Thus, CoM occurs on a much faster timescale that is immediately relevant for online action selection during ongoing execution. Nevertheless, it seems plausible that different kinds of behavioural flexibility vs. stability are, at least to some extent, caused by similar underlying neuro-computational mechanism. For example, our results from the fMRI study revealed a fronto-parietal network of brain areas that continuously updated information about action alternatives and their associated values. Previous studies on value updating, foraging decisions and reversal learning have identified similar brain areas (Cohen et al., 2007; Boorman et al., 2009; Tsuchida et al., 2010; Camille et al., 2011; Rushworth et al., 2012; Economides et al., 2014; Kolling et al., 2014; Shenhav et al., 2016). Hence, brain mechanisms involved in the generation and updating of decisions may operate at various timescales to generate different facets of behavioural flexibility. We propose that investigating CoM allows for a novel perspective on these processes by capturing extremely rapid decision updates, which occur even in the absence of feedback (e.g., due to internal dynamics) and have an immediate effect on ongoing movements. These characteristics of CoM allow for unique insights into the highly continuous and dynamic nature of decision-making processes and their reciprocal relations with the mechanisms that generate motor actions.

6.5 Final conclusion

Humans and non-human animals act in a world full of choices where information is often uncertain, complex and can change dynamically. Hence, flexible action selection mechanisms are required to allow for continuous adjustment of behaviour to the current context. At the same time, actions need to be sufficiently stable to enable goal attainment despite challenges or costs. Changes of Mind provide a window into the fundamental processes underlying the flexibility vs. stability of decisions. This thesis presents a novel perspective on Changes of Mind within the context of voluntary actions and introduces innovative laboratory paradigms that capture the dynamic nature of the neurocognitive mechanisms that shape actions as they evolve. We provide a more detailed insight into what voluntary intentions (or goals) are, how they can be tracked experimentally, and how stable they are, by describing the conditions under which they are retained or abandoned. We propose that volition is the result of continuous processes that flexibly integrate endogenous intentions with external contextual information and motivational factors related to the movements that are required to achieve those goals. Accordingly, voluntary actions rely on a network of brain areas that dynamically integrate a variety of sources of information to guide choices between alternative competing goals, and also between alternative competing actions that aim at achieving those goals. These insights are highly relevant for our understanding of the fundamental principles underlying voluntary control of behaviour and its impairments in a large range of psychiatric and neurological disorders.

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Appendix A. Supplementary material for Chapter 3

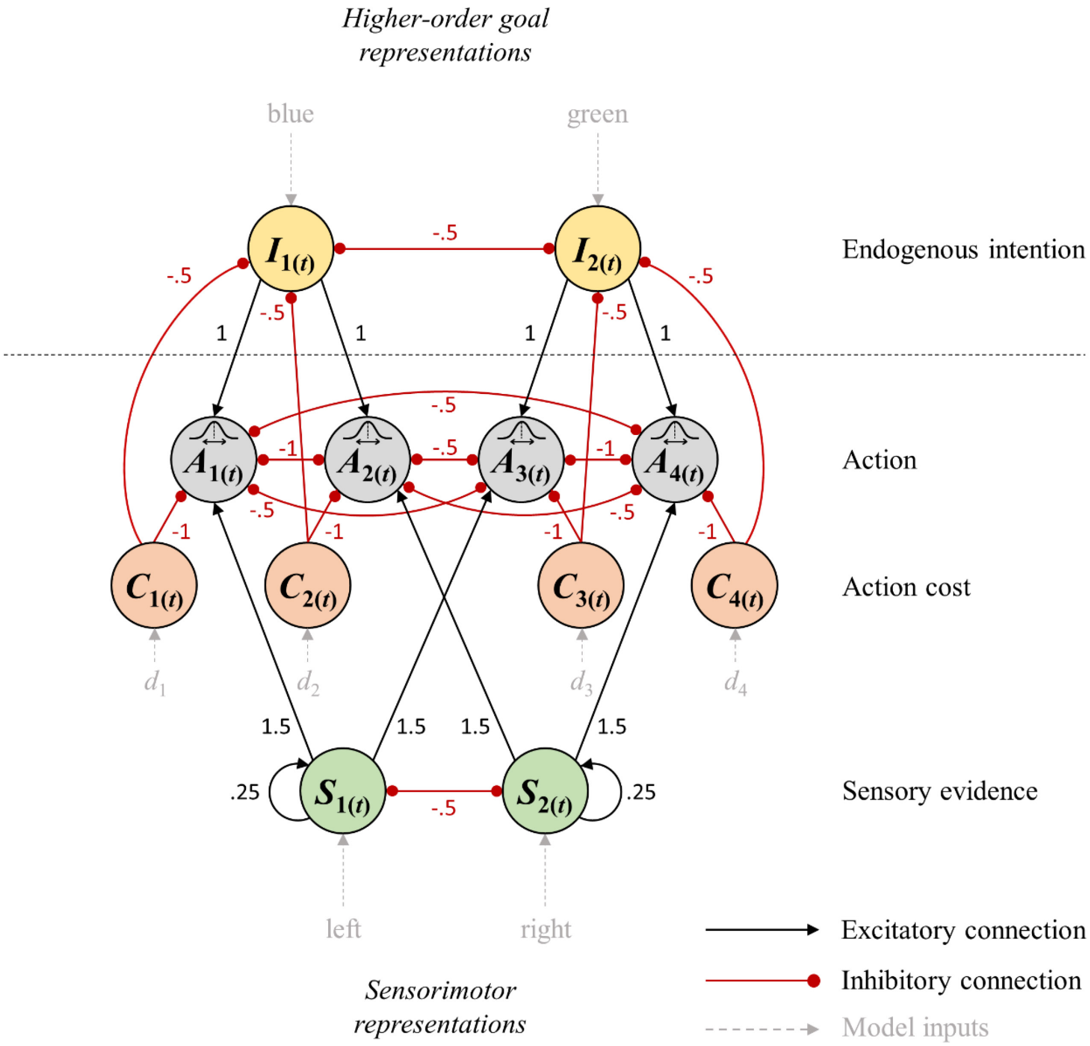

Figure A1. Attractor network model with connectivity weights. Strength of neural connections between nodes are indicated by the weights associated with each connection. Stronger weights correspond to stronger influence of a given node on the firing rate of its target node.

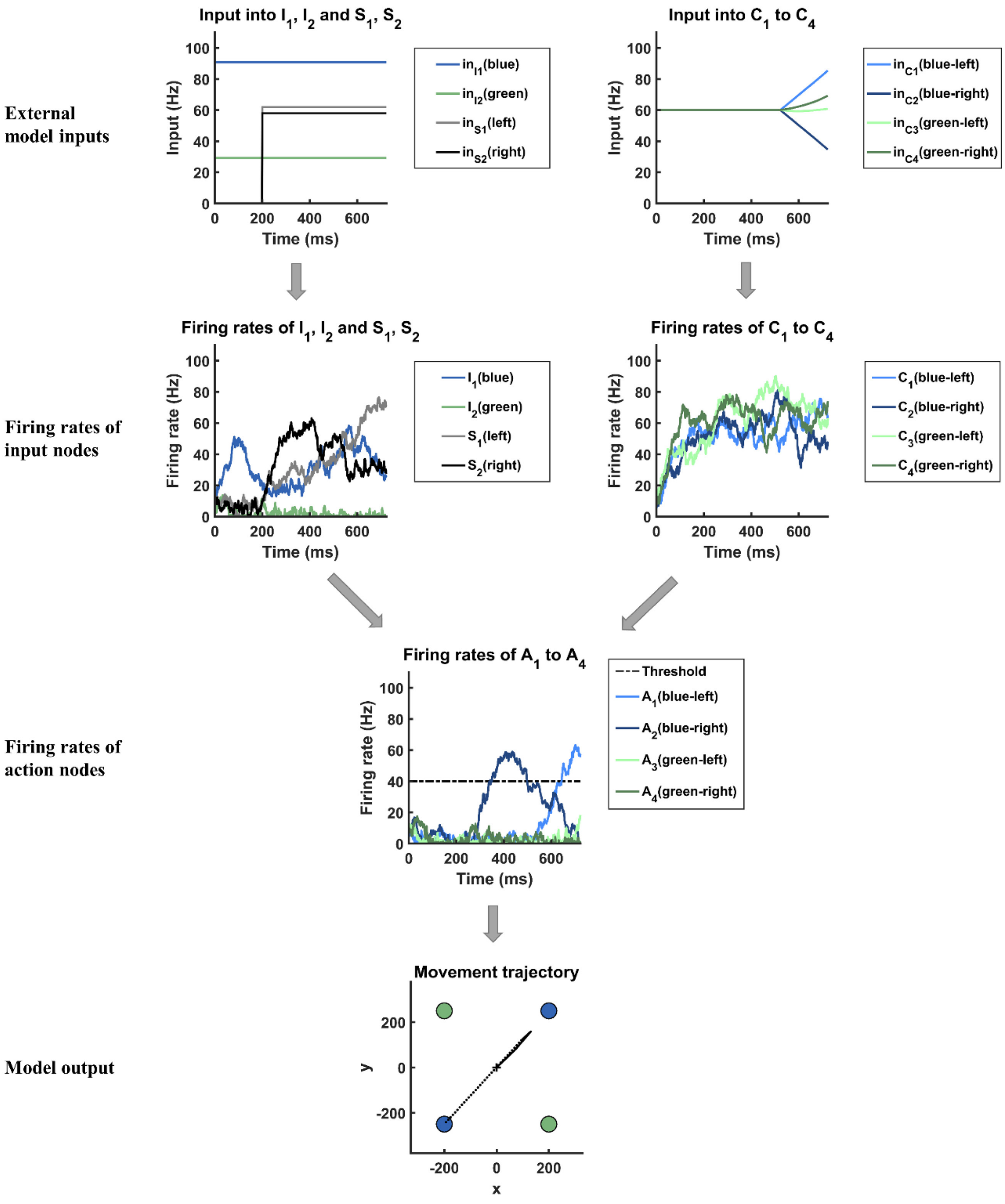

Figure A2. Example trial with Change of Movement (with all firing rates). Firing rates of S_1 and S_2 illustrate the occurrence of a perceptual CoM that is driving the switch from right to left blue target, without a change in the colour intention.

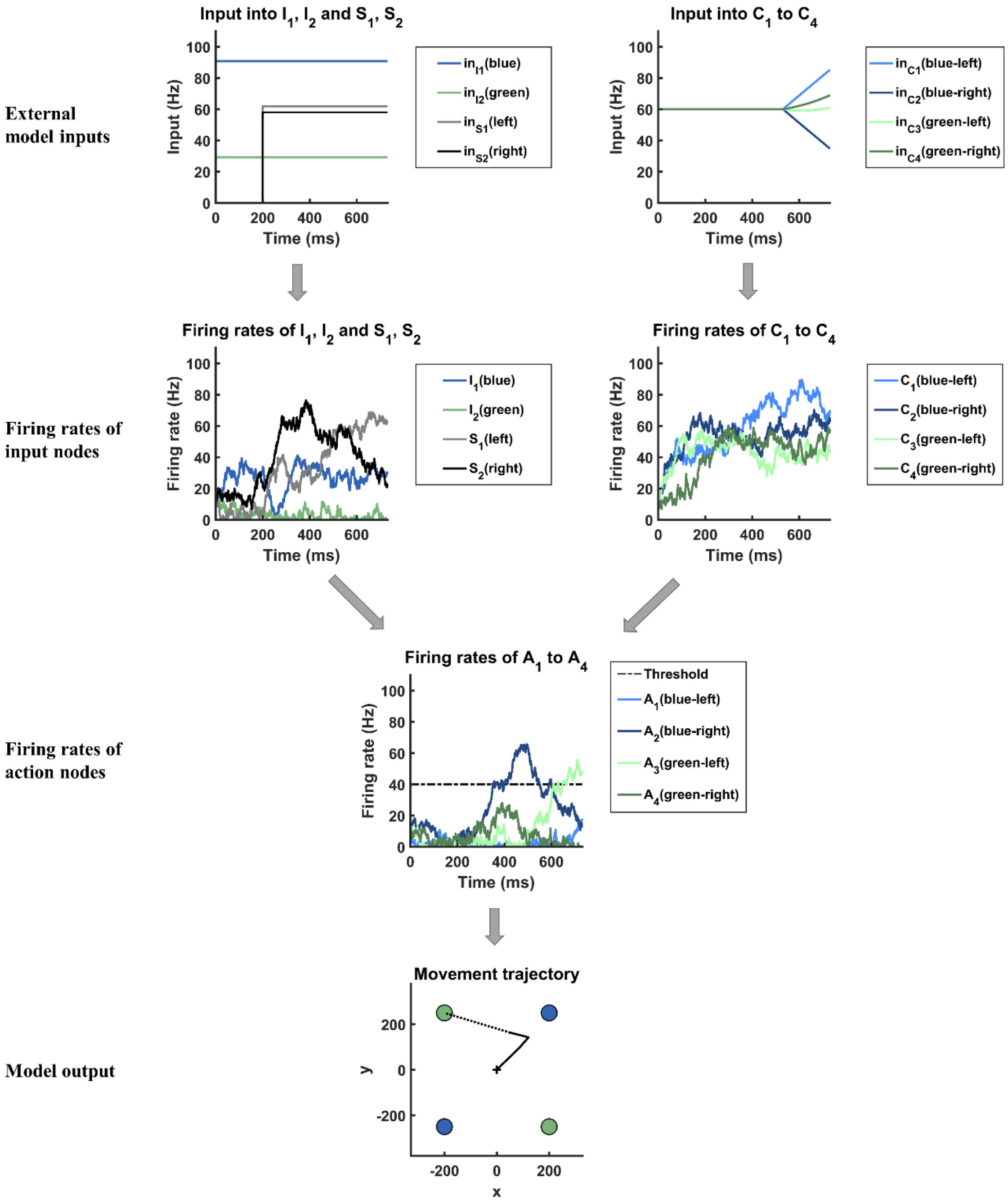

Figure A3. Example trial with Change of Movement + Intention (with all firing rates). Firing rates of S1 and S2 illustrate the occurrence of a perceptual CoM that is driving the switch from right to left target, which additionally involves a switch from blue to green, given that the cost associated with the green-left target is lower than the cost associated with blue-left (see firing rates of C_1 to C_4).

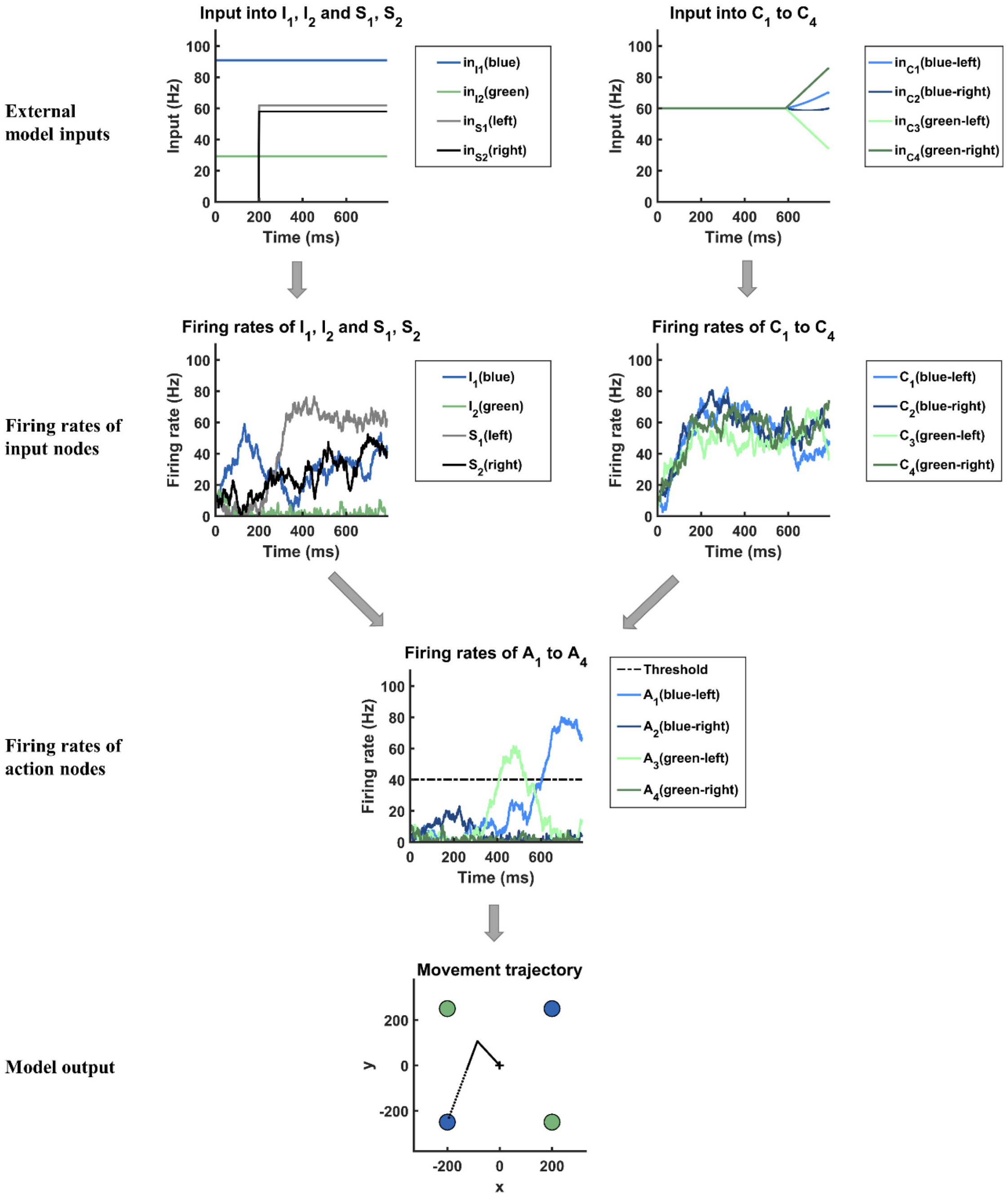

Figure A4. Example trial with Change of Intention (with all firing rates). Due to noise in firing rates, the model erroneously selects the left-green target, although I1 (blue) is stronger. The colour error is later on corrected in favour of the true colour intention. Note that the model correctly switches to the left-blue, rather than the right-blue target, given that the dot-motion correction is left.

Appendix B. Supplementary material for Chapter 4

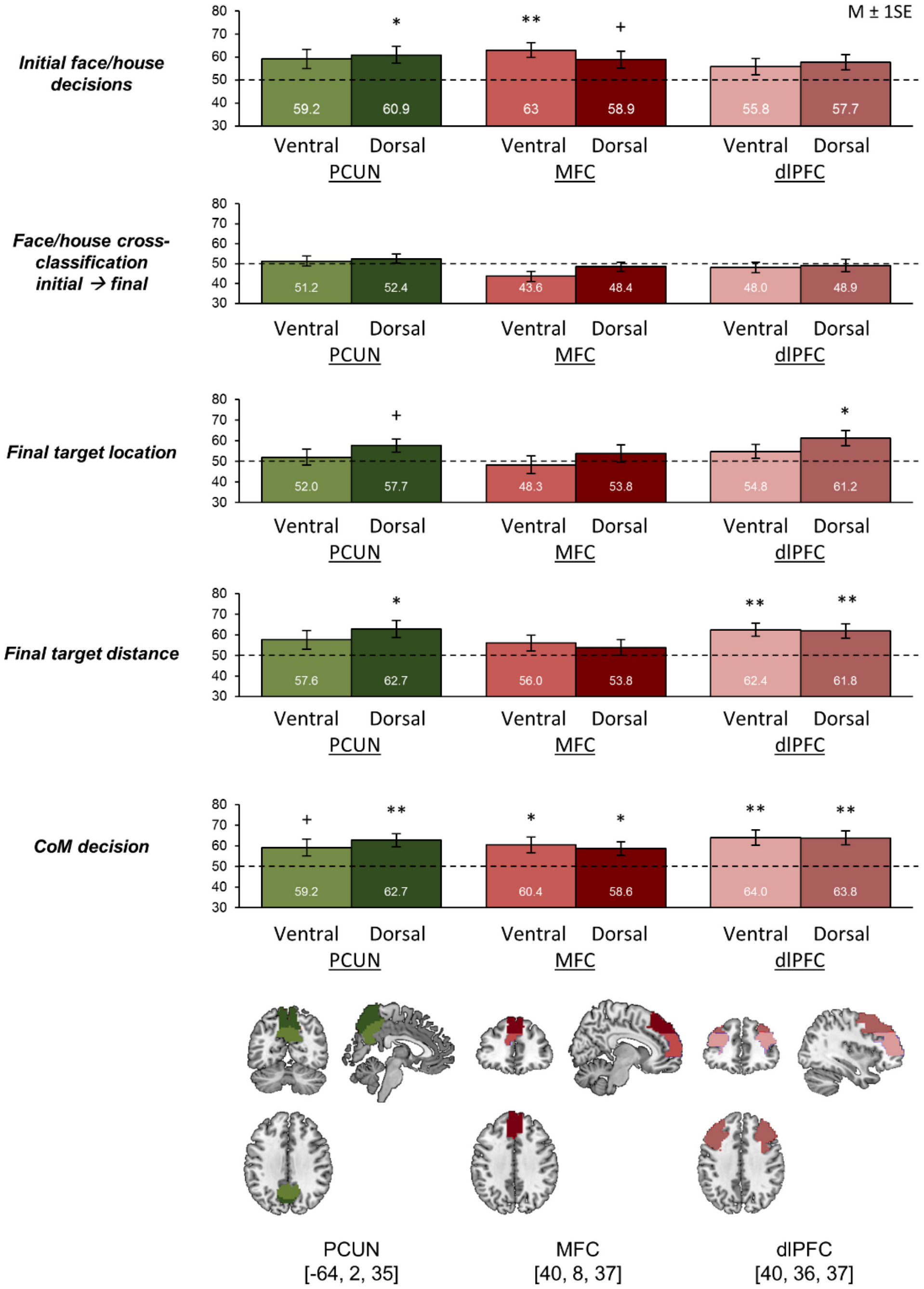

Figure B1. Decoding results for sub-ROIs. Large ROIs (PCUN, MFC, dlPFC) were split into ventral and dorsal sub-regions. The pattern of results in each sub-region largely corresponds to the pattern observed in the overall ROI, although in PCUN, decoding accuracies were overall slightly higher in the dorsal than the ventral region, and in MFC, decoding accuracies were slightly higher in the ventral region. Finally, in dlPFC, final target location was more strongly represented in the dorsal region, presumably due to the fact that dorsal regions are more closely located to motor areas that presumably used information about target location to transform decisions into actions.