The role of planning in motor learning

Hannah Rachel Sheahan

Department of Engineering
University of Cambridge

This dissertation is submitted for the degree of
Doctor of Philosophy

St John’s College September 2018

Declaration

I hereby declare that this dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration except as declared in the Preface and specified in the text. It is not substantially the same as any that I have submitted, or, is being concurrently submitted for a degree or diploma or other qualification at the University of Cambridge or any other University or similar institution except as declared in the Preface and specified in the text. I further state that no substantial part of my dissertation has already been submitted, or, is being concurrently submitted for any such degree, diploma or other qualification at the University of Cambridge or any other University or similar institution except as declared in the Preface and specified in the text. This dissertation contains fewer than 65,000 words including appendices, bibliography, footnotes, tables and equations and has fewer than 150 figures. Partial accounts of this thesis have been published in the following collaborative papers.

Sheahan, H. R., Franklin, D. W., & Wolpert, D. M. (2016). Motor planning, not execution, separates motor memories. *Neuron*, 92, 773–779.

Sheahan, H. R., Ingram, N. J., Zalalyte, M. G., & Wolpert, D. M. (2018). Imagery of movements immediately following performance allows learning of motor skills that interfere. *Scientific Reports*, 8:14330

Hannah Rachel Sheahan
September 2018

Acknowledgements

I would like to acknowledge that this was only possible thanks to an enormous amount of luck and opportunity, and recognise the fact that many others who were more capable than I of writing this thesis were never given the chance. Thank you primarily to my supervisor Daniel Wolpert – the person who did give me the chance, and who subsequently taught me how to be a scientist. Thanks also to James Ingram and Daniel McNamee who listened patiently to my often incoherent and rarely baked ideas, and to the Rutherford Foundation for sending me around the world to Cambridge for the best years of my life so far. More personally, thanks to my brilliant housemates at 1 Richmond Terrace for making the UK feel like home, and to Felix for making me want to stay. Finally this is for my parents who have supported and encouraged all my choices in life, even when those choices took me away from them.

Throughout this thesis I use the personal pronoun ‘we’ to reflect the contributions of everyone mentioned above.

The role of planning in motor learning

Hannah Rachel Sheahan

Humans can learn a remarkable diversity of motor skills. While these skills are sometimes long lasting, they may also be subject to interference. For example, people can learn to reach in the presence of a dynamic (force-field) perturbation generated by a robotic interface. However, when two force fields that act in opposing directions are presented alternately, there is substantial interference, preventing learning of either. Here we examine the role of motor planning in motor memory formation and interference. We challenge a predominant view of motor learning, which suggests that multiple perturbations can only be learned when each is associated (closely in time) with a different physical (or perceived) state of the body. Instead, we show that two opposing perturbations which interfere when experienced over the same movement, can be learned if each is associated with a different neural state (i.e. motor plan). That is, distinct motor memories can be formed by planning each movement through the perturbation as part of a different, wider motor sequence, even if not executed. Exploring the implications of this result, we subsequently show that like planning, motor imagery of different future movements can change the neural state to affect the separation of motor memories. These results lead us to propose that situations which generate different neural responses in motor-related regions will naturally act as different contexts for learning. Interestingly however, we show that the same principle does not appear to underlie motor memory decay. Finally, having established the importance of planning in motor adaptation, we attempt to predict how motor plans should be divided and recombined when task sets become more complex. We simulate normative control policies under the hypothesis that motor chunking may arise from the need to efficiently represent motor commands, and test the implications for concurrent field learning. Together, these results highlight that the actions that humans plan are critical to the representation of motor skills that are learned. This suggests a key role for motor planning in the broad control repertoire humans develop.

Table of contents

List of figures

List of tables

Nomenclature

Acronyms / Abbreviations

ANOVA	Analysis of variance
AUROC	Area under the receiver-operater characteristic curve
BMI	Brain-machine interface
CNS	Central nervous system
CCW	Counter clockwise
CW	Clockwise
EMG	Electromyography
GLM	Generalised linear model
MDL	Minimum description length
MI	Motor imagery
MPE	Maximum perpendicular error
OFC	Optimal feedback control
tDCS	Transcranial direct current stimulation
TMS	Transcranial magnetic stimulation

Chapter 1

Introduction

If your defining feats of motor performance are less comparable to Simone Biles on the balance beam than the act of reaching for another glass of wine, take solace. From a computational standpoint, all forms of voluntary movement are quite remarkable. All interactions we have with our environment are mediated by the motor system, a functional control loop which estimates, predicts, plans and executes actions in the diverse and uncertain world in which we live. What makes this especially difficult, is that humans live in environments that change, have bodies that grow and fatigue, and execute tasks which vary and develop with life and social conventions, meaning that the control signals required for generating movement cannot be entirely pre-specified or ‘hard-wired’. Experiencing novel environmental dynamics for the first time, such as those encountered when learning to swim, clamber across rough terrain or navigate a pair of high heels, show motor learning as the true saviour of survival in a changing world. For behaviour to be flexible, the motor system must adapt.

This thesis focuses on the role of motor planning in understanding how the brain adapts movement in such changing dynamic environments. By theoretically and experimentally decomposing motor behaviour, we explore how humans develop a diverse motor repertoire, learning multiple separate skills without disrupting others, and how planning is fundamental in this learning process. We have structured the following introductory literature review based on the premise that motor control should at first be understood at an abstract, computational level which focuses on behaviour and function, and that computational models that also perform such functions can provide useful tools for complementing traditional hypothesis testing (Krakauer et al., 2017; Kriegeskorte and Douglas, 2018; Newell, 1973). We subsequently attempt to make connections between basic goal-directed reaching behaviours observed in healthy humans, and those in non-human primates for which neural data provides a neurobiologically-grounded basis for the implementation of these computations. Occasionally, italicized text is used to introduce concepts that we see as being particularly important to the contents of the chapter.

In all parts of this thesis we focus on goal-directed reaching, as it captures many features that make motor control a hard computational problem. That is, the supposedly simple task of reaching from A to B requires bringing a nonlinear, nonstationary, redundant system from an uncertain state to a selected goal quickly and efficiently, using delayed, signal-dependent, noisy error feedback that can be accredited to many different sources (for a review of these computational challenges see Franklin and Wolpert (2011)). We therefore primarily review the motor control and learning literature that focuses on goal-directed arm movements carried out in constrained, laboratory-based tasks. We further review how systematically perturbing such reaching behaviour using immersive virtual reality interfaces can begin to isolate some of the elements that underlie the adaptation and de-adaptation of controlled reaching, and how motor tasks may be divided or chunked in familiar and unfamiliar environments.

1.1 The neural control of movement

Movement is the only way we have of interacting with the world. To understand voluntary behaviour at its most fundamental, we must therefore understand how the motor system uses sensory signals to generate movement. While the majority of this thesis concerns how control policies are learned, we begin by considering the end goal, which is coordinated motor control, and how this might be achieved computationally and biologically by the human motor system.

1.1.1 Internal models

Computationally, the control of movement can be considered as simply the problem of finding a particular input which will result in some desired output of the system to be controlled. In humans, this corresponds to selecting a set of *motor commands* that results in some desired sensory feedback. How might this be achieved? Let's consider the case of bringing a cup of coffee to one's mouth to drink. Our desired end-state is feeling the delicious caffeinated beverage on our tongue, but to get there, we need first to know where our arm and the coffee cup are located, i.e. the system's current state. If we are already grasping the cup, the control task is to generate some motor commands that instruct the necessary muscles in the arm to contract, bringing the cup towards the mouth. Before deciding on a particular solution for selecting these commands, we must address a fundamental problem: how will we know if and when we have reached our goal? *Delays* in sensory feedback are on the order of 30-100 ms[1], meaning that if we continue pouring until the taste of coffee is detected, we will have poured out too much and covered ourselves with hot coffee. If we instead make only conservative, incremental muscle contractions and wait for sensory feedback to arrive after each step, then a single sip will take far too long to execute than is practical. Purely reactive *feedback control* is therefore inadequate for fluid movement.

An attractive hypothesis is that the brain overcomes such delays by using a *forward model*, which mimics the body's sensorimotor mapping in the forward or causal direction, to predict the consequences of motor commands (Miall et al., 1993). Forward models use information about the current state of the system and an efference copy of the commands to estimate the outcome of an action before sensory feedback is available. Therefore, the internally estimated outcome of an action can be used to determine the subsequent commands. Computationally, forward models are also important for filtering sensory information, by enabling sensory anticipation and sensory cancellation (Blakemore et al., 1998; Wolpert et al., 1995). They can also be used to provide a teaching signal for learning, by comparing the predicted and actual sensory outcomes of a movement. This can then be mapped into the required changes in motor commands for the subsequent attempt at the same or a similar task (Jordan and Rumelhart, 1992). Theoretically, forward models may also underlie our ability to mentally simulate or imagine action outcomes, and may therefore be useful for sampling different possible actions, learning through mental practice or by observing others, by comparing observed movements to possible simulated controllers (Wolpert and Flanagan, 2001). In addition to the theoretical justification for their importance, psychophysical evidence for the existence of forward models comes from a variety of sources. For example, in force-field adaptation studies, participants adapt trial-by-trial to altered movement dynamics by predicting the perturbation on the subsequent trial (Kawato, 1999; Shadmehr and Mussa-Ivaldi, 1994). Furthermore, participants in grip-force experiments have been observed to modulate the strength of their grip in parallel with fluctuations in load force and do this with no delay, strongly suggesting the use of predictive models in control (Flanagan et al., 2003; Flanagan and Wing, 1997; Johansson and Westling, 1984).

---

[1] Note that these depend on sensory modality, for examples of these delay times, see Franklin and Wolpert (2011); Miall et al. (1993)

Equipped with a forward model, planning becomes a feasible option for the central nervous system (CNS). A source of debate is how motor commands are selected for executing such feed-forward control. To successfully generate skilled and efficient movements, the motor system must find a way to coordinate a complex body with over 600 muscles, and many more degrees of freedom than needed to perform any particular task. For example, when reaching from one point to another, there are an infinite number of hand paths that can accomplish this task, and an infinite number of ways to coordinate the muscles that lead to a single one of these end-point trajectories. This is the problem of *redundancy*. Despite this flexibility in the way different motor problems can be solved, humans are highly stereotyped in the way they execute many movements. For example, hand trajectories remain smooth and relatively straight from a start to goal location, reliably and repeatedly accomplishing task goals (Flash and Hogan, 1985; Morasso, 1981). Moreover, when environmental dynamics change and movements are perturbed, trial-by-trial adaptation results in hand paths that are gradually brought back towards their baseline, straight trajectories (Shadmehr and Mussa-Ivaldi, 1994). As a result, considerable research has focused on how the brain plans a desired trajectory from the initial state of the body to the final behavioural goal (Bizzi et al., 1984; Flash and Hogan, 1985; Harris and Wolpert, 1998; Thoroughman and Shadmehr, 2000; Uno et al., 1989).

Two main styles of feed-forward control schemes have been debated. The first suggests that the control signal is planned prior to movement using an internal *inverse model* of the motor system, which inverts the mapping from motor command to sensory consequence in order to select a control input that results in the desired change in state (Kawato, 1999; Wolpert and Kawato, 1998). An alternative theory proposes that muscle visco-elasticity and peripheral reflex loops in the motor system are key to motor planning. That is, the visco-elastic properties of muscles pull perturbed parts of the body back towards their equilibrium positions, and so comprise a type of peripheral feedback control which may be exploited by the brain to plan movements. Specifically, the *equilibrium-point hypothesis* argued that, by adjusting muscle co-contraction and reflex gains, the brain could rely on muscle visco-elasticity for local control and simply plan a series of stable equilibrium positions. Thus, in theory the number of degrees of freedom that need to be controlled is reduced, creating movement without triggering resistance from posture-stabilizing mechanisms, and questioning the need for internal models at all (Bizzi et al., 1984; Feldman, 1966; Feldman and Levin, 1995; Flash, 1987; Gribble et al., 1998). Critically, the forces that act on links in the arm grow with the square of the velocity, such that under the equilibrium-point hypothesis, viscoelastic muscle forces would have to increase significantly as movements sped up (Kawato, 1999). Empirically, however, well-practiced movements are often made with lower stiffness than this hypothesis is thought to require, shifting support towards the existence of inverse models (Gomi and Kawato, 1996; Morasso and Schieppati, 1999).

The equilibrium-point hypothesis explains only how a reference trajectory can be used to guide movement, but neglects to account for how such a trajectory might be computed in tasks which are more complex than point-to-point reaches (Todorov, 2004). The idea that forward and inverse models were many and paired has subsequently come to dominate views on control, providing a theory for how multiple context-dependent controllers might exist for use by the CNS (Wolpert and Kawato, 1998).

While this debate was long-lasting, a critical limitation of both inverse models and equilibrium-point control is that they both plan movements through an open-loop optimisation process. That is, they plan a sequence of motor commands prior to execution, and this planning process ignores online sensory feedback. Any deviations from this trajectory due to noise or external perturbations are corrected online with a servomechanism-like feedback controller, which simply tries to cancels the online discrepancy between the desired and actual states to revert the system back to the original planned path. Therefore, feedback is not taken into account in the optimisation phase.

1.1.2 Optimal feedback control

Open-loop planning models can predict average movement trajectories well, under a variety of different formulations (Bizzi et al., 1984; Flash and Hogan, 1985; Harris and Wolpert, 1998; Thoroughman and Shadmehr, 2000; Uno et al., 1989). However, such planning models fail to account for trial by trial variability in trajectories and observations that this variability tends to demonstrate organisation, constrained to task-irrelevant dimensions that do not affect goal achievement (Scholz and Schöner, 1999). Moreover, mid-movement perturbations result in slow (Diedrichsen, 2007) and fast (Nashed et al., 2012, 2014; Pruszynski and Scott, 2012) feedback corrections that are goal-directed, rather than compensating for online errors by directing movements back to an originally intended trajectory.

An alternative hypothesis, based on the theory of *stochastic optimal feedback control* (OFC) resists this strict separation between planning and execution, and instead suggests that in the presence of uncertainty, the optimal control policy is to resolve both trajectory and mechanical redundancy moment-by-moment with intelligent use of delayed sensory feedback

(Todorov and Jordan, 2002). Under this framework, planning[2] can instead be considered the specification of a closed-loop optimal feedback control law L_t (Figure 1.1). This is computed by taking the estimated initial state and desired goals of the system, and evaluating the best course of action, or control signal u_t as a function of each estimated state of the limb $\hat{x}_t$ at each point in time t according to some pre-determined *cost function*, or performance criteria. The optimisation process is thus a closed-loop feedback cycle. In this framework and in those that follow, the description of a control policy as 'optimal' is therefore a formal usage of the term as it pertains to numerical optimisation, and so simply communicates that a particular policy yields a set of state-dependent motor commands which minimize a given cost-function.

In cases such as biological motor control, where uncertainty is inherent in the initial state of the motor system (Faisal et al., 2008), there is noise in the consequences of motor commands (Jones et al., 2002; Schmidt et al., 1979) or dynamics model of the world (Izawa et al., 2008) and movements take longer than the shortest sensorimotor delay to execute (i.e. sensory feedback is available and informative of progress), the optimal policy is a feedback controller of this style that corrects only those errors that adversely affect the behavioural goal. Intuitively, in the case of such uncertainty, responding to perceived errors that do not directly affect task performance does not impact the value of the cost function, and may themselves introduce errors that are detrimental to task success. Therefore, the theoretically optimal approach is to act only when it is strictly useful. That is, to *minimally intervene* as had been observed in human movements by Scholz and Schöner (1999) and others.

Since it's introduction as a theory for biological movement coordination in 2002, optimal feedback control has maintained it's position as the dominant model of voluntary motor behaviour, accounting for multiple previously unaccounted for movement phenomena, such as the sophisticated task-dependency of motor corrections (Diedrichsen, 2007; Nashed et al., 2012, 2014; Pruszynski and Scott, 2012), intelligent shaping of motor variability (Scholz and Schöner, 1999), muscle synergies or lower dimensionality 'building blocks' for control (D'Avella et al., 2003; Ivanenko, 2003), and over-compensation in response to velocity-dependent curl field perturbations[3] (Thoroughman and Shadmehr, 2000; Todorov, 2002). While not the first to consider optimality principles in the control of human movement (Flash and Hogan, 1985; Harris and Wolpert, 1998; Uno et al., 1989), Todorov and Jordan

---

[2] Note that in Chapter 5 we consider motor planning as the formulation of a closed-loop optimal feedback control policy as formulated by Todorov and Jordan (2002), and use this terminology without implying a temporal distinction between planning and execution.

[3] We utilise such perturbations extensively in this thesis, and discuss their implementation more thoroughly in Section 1.3

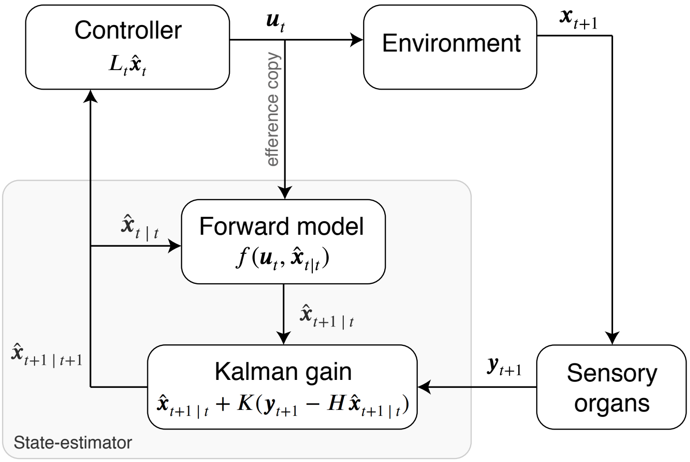

Fig. 1.1 **A block diagram illustrating optimal feedback control theory.** The state-estimator (Kalman filter) requires an efference copy of the motor commands u_t in order to predict the future state of the body $\hat{x}_{t+1\,|\,t}$ with a forward model. This estimate is subsequently updated when noisy sensory information y_{t+1} regarding the actual motor state x_{t+1} arrives. K is the Kalman gain, which determines the size of the state-estimate update when sensory information is received, and H is a matrix that maps the estimated state of the body into an expected sensory input.

(2002) showed how these seemingly disparate phenomena emerge naturally under a single, normative framework.

However, while the idea that sensory feedback is used intelligently in motor planning has made significant mileage as a theory of behaviour, motor planning is far from a solved problem. Evidence for the neural correlates of OFC is currently lacking, and experimental manipulations that alter the system's sensory noise as a function of state (Yeo et al., 2016) or noise in the model of the environmental dynamics (Izawa et al., 2008) observe behaviours that are better fit by model variants on the original OFC formulation. Additionally, the exact form of the motor cost function used by the brain remains unclear. Several cost functions have been proposed, typically consisting of a linear composition of a performance metric, defined around a set of hard, externally-instructed constraints (i.e. task goals, such as movement time, end-point velocity, or intermediate points along a trajectory), and a regulariser to avoid 'over-controlling' the system, such as minimising the integrated squared jerk (Flash and Hogan, 1985; Hogan, 1984; Todorov, 1998), the derivative of joint torque (Uno et al., 1989), end-point variance (Harris and Wolpert, 1998) or energy consumption (Todorov and Jordan, 2002; W. L. Nelson, 1983). However there is little consensus regarding which of these metrics most closely reflects human behaviour and why. Moreover, exactly how task constraints such as movement time or subgoals are selected with planning[4] remains an open question, if indeed they are selected at all (Liu, 2008). Finally, all attempts to establish a single cost function for biological motor control do so by performing a search for the set of parameters that will best control an individual movement, and so ignore the potential of contextual or sequencing effects. With limited exception (Izawa et al., 2008), these models also assume the environmental dynamics to be stationary and known with complete accuracy. For these reasons, all such models which claim to be 'optimal' within the restricted domain declared by the form of their cost function, are likely to perform poorly under non-zero environmental volatility (Behrens et al., 2007), or under noisy estimates of the environment's dynamics (Izawa et al., 2008). In Chapter 5 we consider a new variant of this cost function, which extends the classic OFC formulation from optimising the commands needed for a single movement, to instead consider encoding efficiency over a set of several movements made within a given task set.

---

[4] For a more comprehensive review of this point on subgoaling or 'chunking', see Section 1.2.3

1.1.3 Generating movement with neurons

While optimal feedback control now dominates the computational view of voluntary motor behaviour, how movement is controlled neurally remains a major point of contention. Broadly speaking, the cerebellum is thought to be critical for predicting the consequences of movements, that is encoding forward models (Herzfeld et al., 2015; Kawato et al., 2003; Miall et al., 1993; Nowak et al., 2007; Wolpert et al., 1998). The cerebellum is also considered to be important for supervised learning (Doya, 2000; Galea et al., 2011; Herzfeld et al., 2018, 2014b; Smith and Shadmehr, 2005), adapting responses following the experience of a sensory error transmitted in the climbing fibers to Purkinje cells. Activity in motor cortex however, is less well agreed upon. Despite decades of research on the primate motor cortex, there is little consensus regarding what activity in premotor (PMd) and primary motor cortex (M1) reflects (Kalaska, 2009; Omrani et al., 2017; Shenoy et al., 2013).

Much of the debate centres on the cortical control of arm movements in rhesus macaques, and this debate still mirrors questions that arose over thirty years ago when motor cortex neurons were observed to respond to both movement force (Cheney and Fetz, 1980; Evarts, 1968), and movement direction (Georgopoulos et al., 1982, 1986; Tanji and Evarts, 1976). In particular, much of the discussion has focused on the question of whether motor cortex encodes low-level joint torques or muscle activity, or higher-level movement parameters such as velocity, each of which have different temporal patterns or signatures (see Kalaska (2009); Omrani et al. (2017); Scott (2008); Shenoy et al. (2013) for reviews). M1 activity has been observed to correlate with parameters from both hypotheses. These correlates also change across behaviours, and individual neuron responses often appear complex and variable (Churchland and Shenoy, 2007; Scott, 2008). More recently, a different hypothesis has grown in popularity which attempts to reconcile these results by focusing, not on how movement correlates are described in the brain, but on how the motor system produces it.

The *dynamical systems perspective* instead treats motor cortex as a pattern generator, shifting the focus in explanatory approach from determining what is statically ‘represented’, to how dynamical internal processes generate the motor outputs that are sent to the spinal cord and muscles (Churchland et al., 2012; Shenoy et al., 2013). Within this framework, the mix of motor correlates observed in M1 may reflect both the output motor commands, and the underlying time-varying pattern of control signals that drive them, which may broadly correlate with high-level movement parameters such as velocity (Michaels et al., 2016). In this sense, the dynamical systems view extends the idea that motor cortex produces a muscle-like output, but centres the effort on understanding the nature and impact of evolving neural dynamics. Recently, neural population activity has been observed to demonstrate primarily ramping behaviour during motor preparation, and oscillatory dynamics during execution (Churchland et al., 2012). Thus motor preparation, or planning is thought to 'seed' a dynamical motor cortex system with an initial state, while execution produces rotations of the neural state away from this origin, resulting in low-dimensional rotations at the population level and quasi-oscillations in single neuron responses (Churchland and Cunningham, 2014; Churchland et al., 2012). While such preparatory activity was originally observed under an imposed prepare-and-hold delay period, similar responses, although rapid, have since been observed for self-chosen (Lara et al., 2018) or pressured reaction times (Ames et al., 2014), suggesting that such a preparatory state may be an obligatory part of movement production.

If muscle activity is a readout of neural activity, how are PMd and M1 so active during motor planning or preparation (Riehle and Requin, 1989; Tanji and Evarts, 1976; Weinrich and Wise, 1982), without triggering actions prematurely? Observations that this preparatory activity is not simply a weaker or sub-threshold version of movement activity in the same neurons (Churchland et al., 2010; Crammond and Kalaska, 2000), have led to the interesting hypothesis that neural activity in PMd and M1 may be structured into output-potent and output-null dimensions, which do and do not result in movement respectively (Kaufman et al., 2014). Specifically, during motor preparation (Kaufman et al., 2014), or early in response to online visuomotor perturbations (Stavisky et al., 2017), motor cortical activity may cancel out at the population level read out by targeted muscles, creating a dimension of output-null activity. Indeed this was what was observed empirically in the monkey during a prepare-and-hold phase, while activity during execution traversed both output-null and output-potent dimensions. This suggests that, although correlated with the phase and amplitude of the subsequent neural trajectory during execution, motor preparatory activity may be largely orthogonal to movement related activity, enabling M1 and PMd to initialise the neural states needed to produce the correct movement.

Finally while most electrophysiological work on motor cortex responses have been performed in monkeys, oscillatory dynamics of the type reported by Churchland et al. (2012) have also been observed in humans with Amyotrophic Lateral Sclerosis (Pandarinath et al., 2015), and neural network models of motor cortex (Hennequin et al., 2014; Sussillo et al., 2015), providing support for further exploration of a more dynamical, over representational, view of movement generation in the brain.

1.2 Learning to move

Motor control can be hard-wired or learned through experience. While innate, or hard-wired control may speed up skill acquisition or result in immediate, acceptable performance on a restricted assortment of tasks, flexible behaviour places a premium on motor learning. This learning occurs on many timescales, over long periods as the dynamics of our bodies change from infancy to adulthood, and more rapidly such as when adapting the angle of a tennis strike on a particularly windy day. It should be noted that adaptation entails adjustments across the body, and so is not solely cortical in nature (for example, muscles hypertropy with training). However, here we focus on shorter timescale adaptation that can be attributed to the central nervous system.

Motor learning involves adaptation of both forward and inverse models. That is, as both models depend on the dynamics of the motor system, humans must learn to both predict the consequences of our movements and to control them. Forward models can be learned relatively easily through supervised learning, by comparing the expected and actual movement outcomes directly (Jordan and Rumelhart, 1992). In contrast, training a controller is more difficult, as the error in motor command is not readily available and there are many potential changes in motor command that could produce the same change in movement outcome. To be able to use the movement outcome as a teaching signal for learning a controller, the nervous system needs to estimate the gradient of the error with respect to the motor command. If the correct motor command was known such that an error signal in command space could be computed, this would render the inverse model pointless (Wolpert et al., 1998). The theoretical result that forward models are, in general, easier to learn, has also been observed in motor learning behaviour. When moving an object through a dynamic perturbation, participants have been shown to quickly learn to predict the consequences of their own actions, measured by their grip-force on the object. However it took significantly longer for the same participants to learn to generate the appropriate actions for precisely controlling the trajectory (Flanagan et al., 2003).

1.2.1 The need for multiple motor memories

Humans perform an enormous number of tasks in a multiple of environments that influence the dynamics of the body. To control movement effectively, the motor system has two main options for control: to learn one controller or multiple. Firstly, a single controller could be learned that captures all potentially relevant contextual information at once, and this single controller could be altered with each new scenario experienced. However this could potentially lead to catastrophic forgetting scenarios such as those observed in deep neural network models used in machine learning (Kirkpatrick et al., 2016; McCloskey and Cohen, 1989; Ratcliff, 1990). An alternative is to learn multiple distinct controllers that can co-exist, each suitable for a different context or set of contexts which can be flexibly switched between (Wolpert and Kawato, 1998). The language we will use here reflects an implicit assumption of the latter, while in reality the implementation of controllers in the brain probably lies somewhere between these two architectures.

In order to learn a diverse range of skills, the neural representations of motor skills must be organised such that learning generalises appropriately across tasks and to new situations. What is it that makes multiple motor skills learnable, so that policies can be to some extent parcellated and protected from interference, yet accessed and updated when the right task is re-experienced? In general we are interested in how memories for these motor skills, that is *motor memories*, interact over time and across tasks, as well as when training on multiple tasks is intermixed.

In laboratory settings this has been studied extensively using paradigms that expose participants to two tasks which are in a sense opposite to each other, such as two dynamic *velocity-dependent curl force-fields*[5] which are opposite in their perturbing direction (Brashers-Krug et al., 1996; Caithness et al., 2004; Gandolfo et al., 1996; Shadmehr and Holcomb, 1997), or two oppositely directed visuomotor rotations (Hirashima and Nozaki, 2012; Krakauer et al., 2005, 1999). These perturbations can be generated by a robotic manipulandum, which participants grasp while making reaching movements. Over time, if a participant is consistently exposed to a single direction of perturbation (A), they rapidly learn to compensate for the field dynamics or visuomotor perturbation, responding to reach errors on each trial and gradually reverting their movements back towards their baseline, approximately straight trajectories to the target. This learning is thought to arise from small adjustments made to a motor memory after each trial. If learning is followed by exposure to the oppositely directed perturbation (B), adaptation to perturbation B is significantly slower than the original adaptation to A (Brashers-Krug et al., 1996; Shadmehr and Brashers-Krug, 1997; Shadmehr and Holcomb, 1997; Shadmehr and Moussavi, 2000). This is termed *anterograde interference*.

---

[5] We use these fields extensively in this thesis and often refer to them as simply curl fields, or velocity-dependent force-fields. The vector field of the perturbing force rotates clockwise or counter-clockwise as a function of the velocity (see section 1.3 for details).

Similar effects can also be observed when perturbations are randomly switched between instead of blocked, such that each adjustment to a single memory is oppositely directed and cancels out, rendering learning ineffective. In deep neural network models, the effects on learning of a switching curriculum are pronounced. While frequent task switching enables the trainable parameters (network weights) to find an intermediate solution appropriate for both tasks, blocked training results in catastrophic interference, whereby the network weights for the original task are largely overwritten when the secondary task is experienced. In contrast, humans appear to respond differently to switching training curricula, at least for the cases of opposing force field learning (Herzfeld et al., 2014a) and for trial and error learning of orthogonal task rules for complex perceptual categorisation tasks (Flesch et al., 2018). Recently, Herzfeld et al. (2014a) proposed a model suggesting that the tendency for human participants to learn faster from blocked versus interleaved training on a switching motor task, may result from adjustments in the sensitivity to error on each trial. That is, participants modified their responses relatively more after experiencing an error that was similar to those experienced on recent trials than in response to those that were different, hence leading to a greater trial-by-trial learning rate when training was blocked to yield similarly directed errors across time. Similar effects were found in the perceptual categorisation domain by Flesch et al. (2018) who demonstrated that human participants benefited from blocked training on each of two rules relative to interleaved training, even when their performance was subsequently evaluated on an interleaved session. This is in contrast to canonical learning theory which would suggest a benefit for matched training and testing conditions, and enabled the authors to cleanly isolate the effects of task-switching on learning, from the cognitive task-switching costs associated with alternating between different explicit task rules (Monsell, 2003). Hence in humans at least, while task switching imposes a performance cost, multiple distinct skills are learnable and temporal task consistency may assist with this learning.

1.2.2 Contextual rules for separating motor memories

Motor states, such as the limb position or velocity, change continuously within a movement, and the motor commands required to execute changes in the state are contingent upon them. Other parameters such as the inertia of a manipulated object, or the presence of a travelator in an airport, change more discretely, but can have marked effects on the control signals required for efficient movement. We consider such discrete changes in the environment or body as high level movement *contexts*. In order to develop distinct representations for different skills and avoid interference between them, considerable research has focused on identifying different contextual cues that can be used to partition learning for different contexts.

Many sensory cues which one may expect to be salient are ineffective. For example, when two opposing curl force-fields are randomly interleaved for reaching movements made across a single training session, associating each with a different background colour (Gandolfo et al., 1996; Howard et al., 2013) or peripheral visual cues (Howard and Franklin, 2015; Howard et al., 2012) does not reduce interference between them. In contrast, several studies have shown that if each field is associated with different states of the limb, such as when moving to spatially separate targets (Howard et al., 2013; Hwang et al., 2003, 2006), performing each with a different grasp (Gandolfo et al., 1996), or arm orientation (Yeo et al., 2015), with different motion of the contralateral arm (Howard et al., 2010) or with different inferred states of the limb due to manipulations of visual feedback (Hirashima and Nozaki, 2012; Howard et al., 2013), interference between the opposing fields is reduced and participants can learn both perturbations concurrently. The prevailing theme across these data is therefore that context is predominantly attached to the state of the limb or world during the generation of movement. However, sequential interpretations of context have also been observed.

Wainscott et al. (2005) demonstrated a small but significant reduction in interference between oppositely directed curl field perturbations, if the direction of the force field was paired with the order of the reaching movement in a two-part sequence. For example, when participants were required to reach to two sequential targets (T1 and T2) in the workspace, the first reach was always perturbed with a CW curl field, and the second reach with a CCW curl field. However, when the same reaches were made as part of a different reach pair (e.g. a reach to target T0 was made prior to the reach to target T1, where the sequence ended), the direction of the field on the reach to target T1 switched. The representation of motor adaptation was therefore shown to be at least somewhat sensitive to the temporal ordering of movements in a sequence, even when participants dwelled between successive movements for around 500 ms. The encoding of such reaches made across the same physical states was subsequently shown to depend strongly of the recency of the temporal history of sensorimotor states (Howard et al., 2012). That is, opposing force fields can be concurrently adapted to if each reach to the same target is paired with a different lead-in movement, but this effect decays away progressively as the time between successive movements increases and is virtually eliminated with dwell times greater than 600 ms. Intriguingly, pairing different force fields with different movements to be made in the future (e.g. follow-through movements), also enables participants to concurrently adapt to both (Howard et al., 2015). This final result further showed that when a follow-through movement, that is, a secondary movement after reaching through a force-field, is made consistently to the same target versus to different variable targets, faster learning is observed. This occurs despite each field being experienced across the same physical states of the limb. It remains an open question as to what features of an environment or of movement enable separate representations of motor memories to form. In Chapter 2 we isolate and test two hypotheses to address this question.

1.2.3 Learning to plan hierarchically

So far we have only considered how movements may be controlled when tasks are very simple. However, humans engage in many motor behaviours which are more complex than simply reaching from one point to another, such as drinking a cup of coffee or playing a game of basketball. It has long been argued that human behaviour, and in particular behaviour in compound tasks such as these, is not just a simple chaining together of simple stimuli and responses, but that actions are planned and this planning is hierarchical (Lashley, 1951; Miller et al., 1960). Movements are broken down into *chunks* or subtasks and these chunks concatenated, or flexibly combined and reused later. For example, the motor commands corresponding to the action ‘bounce the ball’ may be repeated many times while dribbling to shoot a hoop in a game of basketball.

Evidence for hierarchical representations of actions has largely been built around discrete sequential production tasks, in which participants learn and perform long sequences of key presses (Rhodes et al., 2004; Rosenbaum et al., 1983; Sakai et al., 2003; Verwey and Eikelboom, 2003; Wymbs et al., 2012). Behaviourally, button presses have been observed to be performed in temporal cycles, consisting of one slow button press followed by several executed much more quickly. This has led researchers to hypothesize that long motor sequences are segmented into chunks composed of small sets of sequential motor commands. These motor chunks have been hypothesized to reflect temporally integrated memory structures, such that groups of individual movements can be prepared, executed and represented together at lower computational cost. However, it is not currently clear how such discrete button press tasks would relate to the chunking of more complex movements that the motor system tends to perform.

Recently, Ramkumar et al. (2016) demonstrated that, with practice, monkeys performing sequences of centre out reaches made movements that were chunked more cohesively over time. Moreover as chunking changes, both short and long chunks appear to be performed efficiently within horizon of planning (Ramkumar et al., 2016). However, the selection of action hierarchies or subgoals is a notoriously difficult problem (Botvinick et al., 2009; McNamee et al., 2016; Solway et al., 2014), and only very recently have normative models of continuous movement chunking been developed which can predict a priori how movements should be chunked for efficient representation (McNamee et al., 2017a). Moreover, although chunks appear to extend in length with practice, it remains unclear how chunks are selected in unfamiliar environments or when the complete set of tasks to be performed is unknown. In Chapter 5 we extend a theory proposed by McNamee et al. (2017a) to predict how simple sets of trials may effect motor chunking and assess how closely behaviours reflect this planning hierarchy.

1.3 Motor adaptation in virtual reality

Motor learning refers to improvements in performance of a motor task through practice. In this thesis we study a type of motor learning called *adaptation*, typically thought of as modification of an existing internal model in order to reduce prediction errors that co-occur with changes in the sensorimotor mapping or environmental dynamics (Krakauer and Mazzoni, 2011). We study this in an attempt to reduce real-world learning behaviours to well-controlled laboratory-based tasks in which we can elicit stereotyped changes in performance over the course of an hour or two, and restrict the potential diversity in cognitive learning strategies at play. We highlight that this is a fundamental limitation of the experimental work within this thesis and we have chosen to use this approach regardless. The use of robot devices is now conventional and commonplace in the study of arm movement adaptation, enabling the fluid manipulation of environmental dynamics (Shadmehr and Mussa-Ivaldi, 1994) or sensorimotor mappings Krakauer et al. (1999), while precisely controlling sensory input and measuring behavioural responses online. Here we too use the canonical robotic reaching paradigm for testing our hypotheses.

In particular, in this thesis we focus our study on planar reaching movements performed while healthy participants grasp a robotic manipulandum called the vBOT (Howard et al., 2009) and make goal-directed reaching movements between targets (Figure 1.2A). By altering the dynamics of the manipulandum part-way through the experiment, in our case by introducing curl force fields which perturb participants with a force proportional and perpendicular to their velocity, adaptation can be assessed by monitoring incremental adjustments to participants' reaching kinematics. We have used such force field perturbations for three primary reasons,

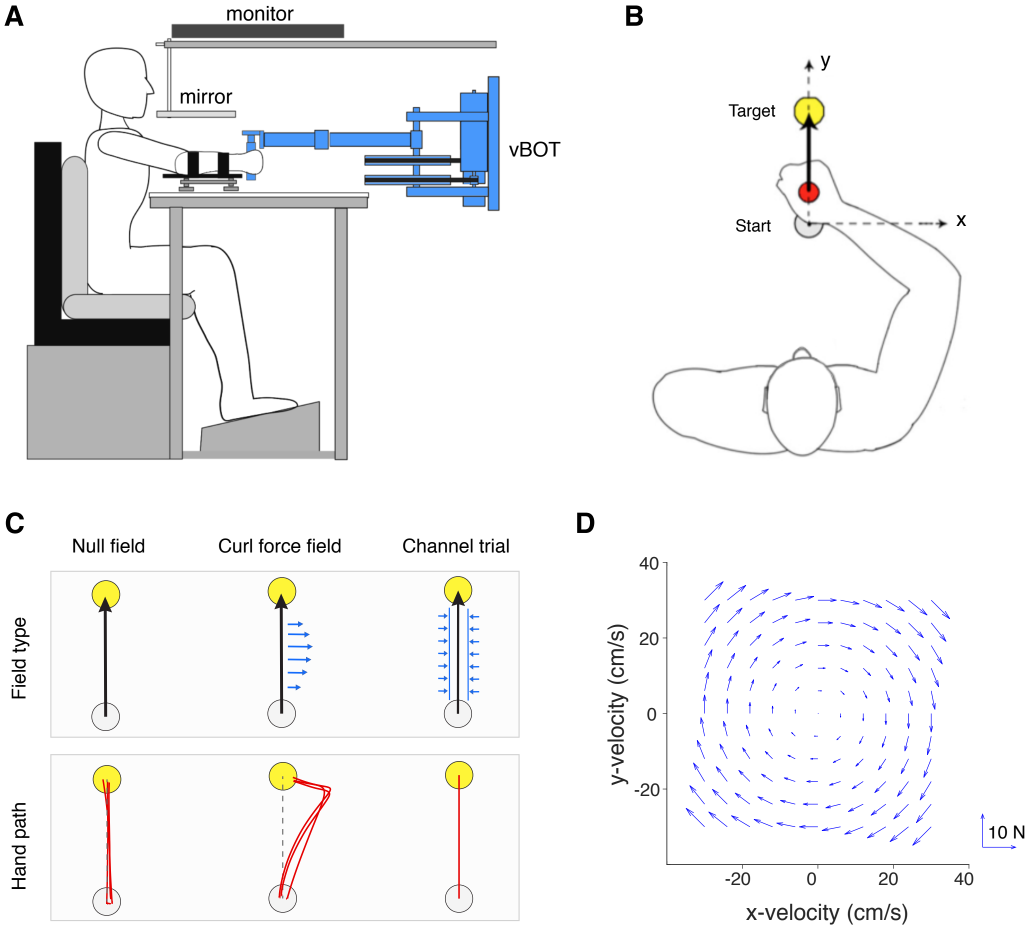

Fig. 1.2 **Virtual reality planar robotic manipulandum (vBOT) for motor adaptation paradigms.** A) Schematic of a participant interacting with the vBOT (blue), with an arm support (adapted from Sadeghi (2018) with permission). B) Participants typically reach from a start position (grey circle) to a target (yellow circle) with veridical visual feedback of a cursor (red) vertically above the hand. C) Three different types of trials are typically used, each with different dynamics (top row). Example hand paths are illustrated for each (bottom row). On null trials participants reach with the robot unperturbed, and make canonically straight movements to the target (red paths). On curl field trials participants are perturbed with a force (blue arrows) proportional and perpendicular to their velocity, and on channel trials the participant's hand is constrained to reach straight to the target and any perpendicular forces are measured by the vBOT to assess whether participants have generated compensatory feed-forward forces. D) The vector field of a clockwise curl perturbation of 15 Ns/m, the standard strength we use for the experiments in this thesis.

- Curl perturbations are unusual dynamic structures to encounter, and so when participants do experience them in an experiment, they can be presumed to present with similar baseline performance and little transferable skill.
- While curl fields themselves are unusual, changes in movement dynamics are not. Over visuomotor perturbations, movement dynamics regularly change in naturalistic environments, when interacting with tools or when muscles fatigue. As we are interested in the fundamental properties of motor adaptation, we consider understanding dynamic motor learning, which we believe to be a more naturalistic task for humans, to be the most suitable approach.
- Unlike visuomotor manipulations, by using force field perturbations we do not separate the visual and proprioceptive sensation of the participant's state of the hand. Therefore we do not have to guess at the inferred hand position which will likely be between these two locations (Wolpert et al., 1995) when we draw conclusions from our data.

The vBOT (**v**irtual reality ro**bot**) is a robotic manipulandum which is optimised for motor adaptation experiments, and which allows two-dimensional, planar movements of the handle while minimising the intrinsic dynamics of the manipulandum (Howard et al., 2009). The vBOT is therefore well suited to studying horizontal reaching movements. The vBOT can impose two-dimensional, state-dependent force perturbations on the handle end-point, enabling free, constrained or perturbed movements as desired by the experimenter (Figure 1.2C). Visual feedback of the handle location is provided by displaying the image of a cursor in a monitor mounted above the vBOT, which is reflected via a mirror back to the participant (Figure 1.2A,B). This can either be veridical, that is, located directly above the actual handle position, or altered, to induce visuomotor perturbations. Kinematic data pertaining to the handle end-point is collected from optical encoders at the joints at a rate of 1kHz. To interact with the vBOT, participants hold on to the handle with their right hand, pressing a switch which engages the robot and activates the experiment. Releasing the switch pauses the experiment and terminates any on-going trial. We attempt to minimize the effect of fatigue while interacting with the vBOT by supporting the participant's forearm arm on a low-friction air sled.

In general participants are assumed to aim for reaching movements that have straight, smooth trajectories, as has been traditionally observed (Flash and Hogan, 1985; Morasso, 1981), such that kinematic performance can be crudely condensed to scalar metrics such as the maximum perpendicular error achieved on a trial. With practice, participants learn to predict the reach dynamics, generating feed-forward compensatory forces against the perturbation which helps to make movements more direct (Shadmehr and Moussavi, 2000; Shadmehr and Mussa-Ivaldi, 1994; Thoroughman and Shadmehr, 2000). To measure this feed-forward adaptation explicitly, simulated springs can be used to construct a virtual channel that constrains execution to be straight towards the target (Scheidt et al., 2000). Forces generated by the participant which are perpendicular to this virtual channel can then be measured from the lateral deviation in the hand's position relative to the channel wall.

Finally the following studies examine healthy adult participants between the ages of 18-45 with no known neurological conditions, for the simple reason that we believe understanding motor learning behaviour in a healthy adult population will lead to the simplest and most informative theory of developed brain function. We further restrict to only right-handed participants as we are unsure how handedness may affect the learning or adaptation of control.

1.4 Structure of this thesis

Chapter 2 concerns the representation of motor skills, specifically how multiple motor memories can be learned concurrently without interference to develop a broad motor repertoire. We challenge a predominant view of motor learning which suggests that multiple perturbations can only be learned when each is associated (closely in time) with a different physical state of the body, or world. Instead, we show that the key to representing multiple motor memories is to have each associated with a different neural state (i.e. motor plan) and not differences in the physical state of the body. In Chapter 3, we extend this result by asking whether motor imagery can change the neural state so that skills which normally interfere can be learned. Our question contrasts with many studies of motor learning with imagery in which the role of imagery is to rehearse or mentally practice a movement. We discover a powerful and complementary role, in which mental imagery which is not of the skill itself, but of different movements after physically performing the skill, affects the way a motor memory is represented. In Chapter 4 we ask whether context-dependent decay, like context-dependent adaptation, may also result from the planning of different movements, rather than their execution. Surprisingly, we show that while executing the adapted physical states of a movement results in a strong contextual de-adaptation effect, just planning and initiating the same movements does not. This highlights a new disassociation between the mechanisms of motor memory formation and retention. Finally, having shown that the actions we plan can be instrumental in the representation of skills that develop, in Chapter 5, we attempt to predict *how* motor plans should be divided when task sets become complex. We develop a recent model of normative motor chunking and evaluate the extent to which the efficient representation of motor commands dictates chunking behaviour and subsequent learning.

Chapter 2

Motor planning, not execution, separates motor memories

Recent theories of limb control emphasize motor cortex as a dynamical system, with planning setting the initial neural state, and execution arising from the self-limiting evolution of the intrinsic neural dynamics. Therefore, movements that share an initial trajectory but then diverge might have different neural states during the execution of the identical initial trajectories. We hypothesized that motor adaptation maps neural states to changes in motor command. This predicts that two opposing perturbations, which interfere when experienced over the same movement, could be learned if each is associated with a different plan even if not executed. We show that planning, but not executing, different follow-through movements allows opposing perturbations to be learned simultaneously over the same movement. However, no learning occurs if different follow-throughs are executed, but not planned prior to movement initiation. Our results suggest neural, rather than physical states, are the critical factor associated with motor adaptation.

2.1 Introduction

Recent studies of neural coding in motor cortex have emphasized its operation as a dynamical system in which planning involves setting the initial neural state and execution involves allowing the transitory dynamics to evolve from this state (Ames et al., 2014; Churchland et al., 2012; Pandarinath et al., 2015). This suggests that two planned movements that share similar initial kinematics but that diverge later may have fundamentally different neural dynamics, even for the shared kinematic component of the movement. We hypothesized that motor adaptation involves mapping such neural states to changes in motor commands. This would suggest that different neural states, for the same physical limb state, could be associated with different motor memories.

Consistent with this, it has recently been shown that opposing dynamics can be learned for movements that are kinematically identical if they are part of a more extensive movement that begins with different physical states of the limb (Howard et al., 2012). That is, when participants made reaching movements through a force field whose sign depended on the direction of a prior lead-in movement, they could learn to represent both force fields concurrently across the identical component of the movement. In contrast, if the lead-in position was shown (and again associated with the field direction) but the lead-in not executed, no learning was seen (Howard et al., 2012). Similarly, two planned movements that begin with similar kinematics but subsequently diverge, may have different underlying neural dynamics during the execution of the identical initial trajectories. We hypothesized that these different neural states could therefore enable concurrent adaptation to opposing dynamics which are paired with the different follow-throughs (Howard et al., 2015). Since it is known that motor planning affects neural activity (Cisek and Kalaska, 2005; Riehle and Requin, 1993; Tanji and Evarts, 1976; Wise, 1985), it is possible that planning different follow-throughs directly engages separate neural populations or engages the same population by setting the initial neural state of the dynamical systems in motor areas that control movement (Churchland et al., 2012).

To test this, here we ask whether it is the planning and/or the execution of follow-through movements that is essential for the ability to represent opposing perturbations concurrently. We isolate the planning and execution components of the follow-through and show that simply having different plans allow multiple motor memories to be learned and expressed for the same physical state of the limb. However, no learning is seen if different follow-throughs are executed, but not planned prior to movement initiation. This suggests that the key to representing multiple memories is to have each associated with a different neural, rather than physical, state.

2.2 Methods

30 subjects (18 female, 25.3 ± 4.0 years, mean ± SD), with no known neurological disorders, provided informed written consent and participated in the experiment. All participants were right handed according to the Edinburgh handedness inventory (Oldfield, 1971) and were naive to the purpose of the experiments. The protocol was approved by the Psychology Research Ethics Committee at the University of Cambridge. Experiments were performed using the vBOT planar robotic manipulandum described in section 1.3, with associated virtual reality system and air table (Howard et al., 2009). The vBOT is a custom-built back-drivable planar robotic manipulandum exhibiting low mass at its handle. Position and force data were sampled at 1 kHz. The position of the vBOT handle was calculated from optical encoders on the motors. Endpoint forces at the handle of the robotic manipulandum are specified by sending commands to the torque motors. Participants grasped the handle of the vBOT with their right hand, with their forearm supported by an air sled (constraining movement to the horizontal plane). Continuous visual feedback of the subject's hand position was provided using a computer monitor, projected to the participant via a horizontal mirror, such that a hand cursor (0.5 cm radius) overlaid the veridical hand position in the plane of the movement.

2.2.1 Experimental paradigm

Participants were divided into four main groups and two controls (n=6 per group, n=4 execution-only control, n=2 EMG control). Participants made reaching movements in a horizontal plane from one of four starting locations to a central target, located approximately 30 cm below the eyes and 30 cm in front of the chest. The four starting locations (1.25 cm radius) were positioned 12 cm from the central target and arranged at 0° (closest to the chest), 90°, 180°, and 270° as in Figure 2.1. During the movement, the robot generated no force (null field trials), a velocity-dependent force (exposure trials), or a spring-like force constraining the hand to a straight-line path to the target (channel trials). On exposure trials, the velocity-dependent curl force field was implemented as:

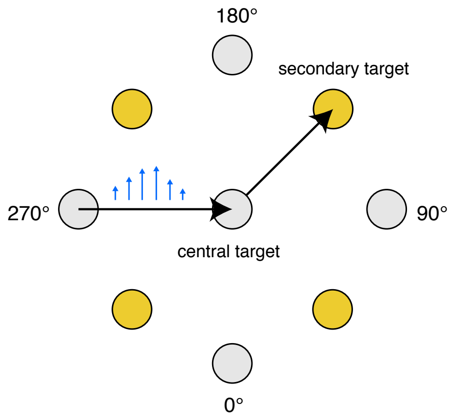

Fig. 2.1 **The four follow-through reaching orientations.** The workspace changed orientation on each trial, such that each trial started from one of four starting locations arranged at 0°, 90°, 180°, and 270°. The black arrows illustrate a full follow-through movement from the 270° start location, which is perturbed with a clockwise curl field (blue arrows).

$$F = b \begin{bmatrix} 0 & 1 \\ -1 & 0 \end{bmatrix} \begin{bmatrix} \dot{x} \\ \dot{y} \end{bmatrix} \tag{2.1}$$

where $\dot{x}$ and $\dot{y}$ are Cartesian components of the hand velocity and b is the field constant (±15 N.s/m) whose sign determined the direction of the force field (positive = clockwise and negative = counter-clockwise). Channel trials were used to measure subject-generated forces, a proxy for feed-forward adaptation (Milner and Franklin, 2005; Scheidt et al., 2000). On a channel trial, the vBOT produced a spring force field (spring constant of 6,000 N/m, damping coefficient perpendicular to the wall of 50 N.s/m) con- straining the subject's movement to a straight line to the central target. In addition to the start and central targets, on each trial one of two secondary targets could be displayed (depending on the condition) 10cm from the central target and positioned at either +45 or -45 relative to the line connecting the starting and central targets. On exposure trials, the direction of the force field applied during the movement to the central target was coupled to the position of the secondary target (e.g., +45 = clockwise; -45 = counter-clockwise). The association between secondary target position and curl field direction was fixed within a participant and counterbalanced across participants. At the end of each trial the vBOT passively moved the hand to the next starting location using a cosine velocity profile.

Group 1: Full follow-through

At the start of each trial, one of the starting locations appeared and the hand was passively moved to its location. The central target and one of the two possible yellow secondary targets were then displayed (Figure 2.2, Full follow-through). Subjects were required to remain within the start locations for 300 ms, after which they were cued by a tone to start the movement. We chose this delay period (which was used for all groups) so that the target would be displayed for 440 ms prior to movement, comparable to the shortest delay periods used in neurophysiological studies of neural dynamics (e.g., 400–1,000 ms delays in Churchland et al. (2012)). The movement between the starting location and the central target was through a null field, curl field, or channel and after reaching the central target they continued with a movement to the displayed secondary target. This secondary movement was always made in a null field. Subjects had to remain within the central target for at least 50 ms before following through on to the secondary target. For movement durations from the start position to the secondary target between 400 and 800 ms, a “correct speed” message was displayed; otherwise a “too slow” or “too fast” message was displayed. If subjects moved before the audio cue, took longer than 1.5 s to complete the movement, or took longer than 1.0 s to respond to the audio cue, a mistrial was triggered and subjects were required to repeat the trial.

A block consisted of eight field trials and two channel trials, such that a field trial was experienced at each combination of the four starting positions and two possible secondary target positions (corresponding to the two different field directions). All channel trials were performed from the 0 starting position, one for each of the secondary target positions. The order of trials within a block was pseudo-random.

Before the experiment subjects were given 30 trials of familiarization in a null field. Subjects then performed a pre-exposure phase of five blocks (40 null trials), an exposure phase of 150 blocks (1,200 exposure trials), and finally a post-exposure phase of three blocks (24 null trials). Rest breaks (1.5 min) were provided approximately every 200 trials, with a longer rest break available in the middle of the experiment if required.

Group 2: No follow-through

This group only differed from the full follow-through group in that after reaching the central target they were required to stop there, ending the trial (Figure 2.2,No follow-through). At the end of each trial, subjects were provided text feedback of “correct speed” if the movement duration was between 150–250 ms. Otherwise a “too fast” or “too slow” message was displayed.

Group 3: Execution only

In the execution-only group, we isolated the effect of executing a follow-through without planning it prior to the movement to the central target. On null and exposure trials the secondary target was not displayed at the start of a trial and, instead, the secondary target only appeared once the hand had moved 10 cm toward the central target (Figure 2.2, Execution only). In piloting we found that this allowed enough time for the participants to make a natural follow-through movement to the secondary target. Importantly, on all channel trials the secondary target appeared from the start of the trial.

Group 4: Planning only

In the planning-only group we isolated the effect of planning a follow-through without executing it. In contrast to the full follow-through group, once the hand had moved 6 cm toward the central target, the secondary target was extinguished on all null and exposure trials (Figure 2.2, Planning only). Participants were instructed that if the secondary target disappeared, they were not to execute the secondary movement but instead stop at the central target. In this sense the task performed by the planning-only group can be seen as a form of stop-signal task, commonly used in studies of response inhibition. In stop-signal tasks, participants who are trained to perform a ‘go’ task (such as a button press or saccade) in response to a particular cue, are required to inhibit their response and not execute the action if they see a secondary cue (a ‘stop’ signal), which appears only occasionally. Response inhibition is thought to rely to a large degree on reactive executive control recruiting the prefrontal cortex (Verbruggen and Logan, 2008). Therefore while we have called this group ‘planning-only’, this is simply to indicate the factorial design which separates the importance of the motor planning and execution components for the specificity of motor adaptation, and does not imply the absence of reactive processes altogether. Rather, as reaching through force perturbations requires continuous feedback control and this paradigm requires reactive stopping, there are surely reactive processes taking place within this task, although critically they do not include execution of the follow-through.

We chose 6 cm based on a pilot study so as to trade off the length that we displayed the secondary target during the movement to the central target (as planning could take place during this movement) and the ability of participants to terminate the movement and not overshoot the central target by 3 cm. Therefore, in contrast to typical stop-signal paradigms which tend to manipulate the timing of the stop signal to investigate the mechanisms of stopping, in the planning-only group, the position at which the secondary target disappeared was kept constant and chosen so that secondary reaches could always be terminated in time.

Critically, on all channel trials the secondary target did not disappear and subjects performed the full follow-through. In order to encourage participants to plan the follow-through movement, we required channel trials for all starting positions (otherwise eight out of ten trials would have been terminated and always terminated for some starting locations). Therefore, in this group we kept the total number of exposure trials the same as the other three groups, but doubled the number of channel trials, including them for each reach direction equally. Therefore a block was 12 trials with 4 channel trials. Across pairs of blocks, we included two exposure trials and one channel trial for every combination of starting location and secondary target position.

Text feedback on trial duration was provided only on channel trials in order to match overall kinematics to the full follow-through group.

2.2.2 Additional control groups

Group 5: Execution-timing control

This control was created following the results from the main four groups. To examine whether the lack of learning in the execution-only group resulted from an inability to generalize from late-appearing (exposure trials) to early-appearing (channel trials) targets we ran an additional control. In this control we included channel trials in which the target appeared at a time uniformly sampled from 300 ms before to 400 ms after the tone.

We recruited a group of 4 subjects to perform this control. We increased the size of each block from 10 (8 field trials and 2 channel trials) to 14 (8 field trials and 6 channel trials). Two of the channel trials were, as in the original experiment, with the target appearing at the start of the trial and these were now performed for the 0° and 180° targets. On the remaining 4 channel trials the target appeared at a time between the start of the trial and 700 ms later (i.e. 300 ms before to 400 ms after the tone; or at latest 10 cm into the movement). This time period covers the average appearance times in the execution only group as on exposure trials the target appeared on average 406 ms ± 14 ms after the tone. Across the experiment there were 80 of such random appearance trials for each target and secondary target location. We covered the -300 ms to 400 ms range in 80 equally spaced steps and permuted the order of the appearance times across the experiment for each target and secondary target position (640 trials in total). Across pairs of blocks we ensure that there was a channel trial with a random-appearance time for each combination of starting location and secondary target position.

Group 6: EMG planning-only control

This control was also created following the results from the main four groups. In the planning only group we found that planning but not executing different follow-through movements enabled two opposing perturbations to be learned. While pre-exposure null trial kinematics did not differ for the movement to the central target when planning but not executing different follow-throughs, it remained unclear whether the different neural states generated by each plan generated distinct activity at the periphery. In order to determine whether distinct motor commands were generated when executing movements with the same kinematics but different underlying plans, we recruited a further two participants to perform a variant of the planning only experiment. In these two additional participants we recorded electromyographic (EMG) activity from six muscles in the arm and assessed whether linear combinations of aggregate muscle activity was differentiated over the same end-point kinematic movement to the central target when planning different follow-throughs.

As in the planning only group, each block consisted of 12 trials, including 4 channel trials. In order to ensure clear measures of pre-exposure muscle activity, we increased the length of the pre-exposure phase from 5 blocks to 40 blocks, and doubled the post-exposure phase from 4 blocks to 8 blocks. We reduced the number of starting positions from 4 to 1, as this provided us with more trials of comparable muscle activity to provide a classifier. As participants therefore did not need to generalise learning across starting locations, we expected faster adaptation and so reduced the exposure phase from 150 blocks to 120 blocks. Participants were strapped to the experiment chair to avoid postural adjustments during the experiment.

Surface EMG was recorded from the bellies of six muscles: pectoralis major, posterior deltoid, biceps brachii, long head of the triceps, lateral head of the triceps, and brachioradialis. A reference electrode was placed on the posterior side of the wrist. Prior to electrode placement, the skin was cleansed with alcohol and prepared by rubbing abrasive electrode paste over the skin before removal with a cloth. EMG was recorded using pairs of silver-silver chloride surface electrodes (DELSYS Bagnoli-8) lying parallel to the muscle fibres, and a thin layer of conductive gel. EMG signals were amplified, tested for clipping (electrode pair impedance < 10 kOhm), and then digitally sampled at 2.0 kHz. As in previous experiments, movement onset was defined as the moment the hand left the start position.

2.2.3 Data analysis

Learning metrics

On null and exposure trials, we calculated the maximum perpendicular error (MPE) as the largest deviation of the hand from the straight line connecting the starting location to the central target. The sign of MPE on each trial was set such that a positive MPE indicated a kinematic error in the same direction as the force field (as would be expected in early learning). We required participants to reach the central target for a successful trial within a tight time window. This was necessary for the follow-through groups who had to pass through the central target on the way to the secondary target. Therefore, to balance the experiment we also required it for the other groups.

In order to adjust for differences in peak speed, either between groups (in particular the no-follow-through group moved faster than the other groups) or throughout the experiment as subjects fatigued, which would affect the size of the perpendicular error, we normalized the MPE by the peak speed on a trial-by-trial basis to produce NMPE (normalized MPE). For display purposes we multiplied these normalized values by the average peak speed across all groups and trials.

On channel trials we measured percent adaptation as the slope of the regression of the time course of the force that participants produced into the channel against the ideal force profile that would fully compensate for the field. To do this we extracted a 400 ms (or the maximum available) window of data centred on the time of peak velocity and calculated the force generated by the channel. We used the velocity along the channel to predict the force the vBOT would have applied on an exposure trial. We performed regression (with no intercept) on these times series and expressed the slope as a percentage (slope of 1 = 100%). As the planning only group performed half the number of channel trials at the 0° starting location we included in our analysis the channel trials at 180° as well (the inclusion of only 0° channel trials does not affect the statistical conclusions). For statistical analysis, we averaged the MPE for each subject across consecutive sets of 8 exposure trials.

To evaluate learning within and between groups, we compared differences in both the kinematic error and force compensation between two epochs, the first six blocks and final six blocks in the exposure phase. For each measure, mixed-design ANOVAs were performed to compare learning between groups, with the factors group and epoch treated as fixed effects, and subjects treated as random effects. Differences between the final adaptation of specific pairs of groups were explored post-hoc with unpaired t-tests. Learning within each group was evaluated with paired t-tests (first and final six blocks in the exposure phases) for both the NMPE and adaptation. To assess whether there were any after-effects when the force-field was turned off, we examined whether the mean post-exposure NMPE across subjects differed from the mean NMPE during pre-exposure (paired t-test).

Kinematics

To display hand paths, we extracted position data from when the hand left the starting location until 50 ms after it entered the central target position. Each path was then linearly interpolated (x and y separately) so as to sample 1000 points equally spaced in time. For each subject, we generated a mean path by averaging the sample paths over trials of interest. To generate a path for a group we calculated the average (and s.e.) of the subjects' paths and plot the mean with shading showing ± s.e (Figure 2.4).

We then examined whether the pre-exposure null trial kinematics on the movements to the central target depended on which secondary target position was displayed (±45°). The pre-exposure trials provide a fair comparison as we expect substantial differences during field trials (as the field directions are different for the different secondary targets). Five kinematic measures were extracted for each pre-exposure movement to the central target. We calculated the duration, path length and peak speed of the movement. We also calculated the signed lateral deviation from the straight line joining the starting and central target when the hand was midway to the central target. In addition, for the full follow-through and execution only groups we calculated the dwell time that the hand spent within the central target. All duration reports are mean ± s.e. across subjects.

Within each group we compared these measures for the +45° and -45° secondary targets and also compared these measures across the four groups (collapsed across targets). As some measures were not normally distributed, for each group we performed a non-parametric Wilcoxon signed-rank test for each kinematic measure as a factor of secondary target direction. We also performed a Kruskal-Wallis test for differences across groups, for each measure. Any differences were explored post-hoc using Mann-Whitney U tests with statistical significance considered at $p < 0.05$.

Electromyography

EMG signals were zero-phase bandpass filtered (25 - 500 Hz, bidirectional pass, 6th order Butterworth), and full-wave rectified. Data was aligned by movement onset time and trimmed to include 150 ms before movement onset, to 200 ms after. For each muscle, activity was normalised by the root-mean-square signal across all trials, so that baseline and adapted responses could be directly compared across muscles. EMG data were analysed in three epochs: a baseline epoch of the first 480 trials (160 null trials, per secondary target), comprising the entire pre-exposure phase; an early exposure epoch, the first 480 trials of the exposure phase (160 curl field trials, per secondary target); a late exposure epoch, the final 480 trials of the exposure phase.

To determine whether the pre-exposure muscle activity during movements to the central target depended on secondary target position, EMG data were analysed for each subject individually. For each muscle, data were gathered across baseline epoch null-field trials to generate vectors of muscle activity, one for each of the n included time samples. Each muscle and time sample therefore had two associated vectors of data, labelled for each of the two secondary target positions, where each vector represented the distribution of activity across trials at that time sample. The ability to correctly classify these time-series vectors according to their secondary target position, was assessed by computing the area under the receiver operator characteristic curve (AUROC) for a simple logistic regression classifier. This was performed for each time sample so that time series AUROC curves would illustrate at what time in a movement muscle activity differed for leftwards and rightwards secondary target positions. We performed this analysis on EMG data from each muscle separately, and on the aggregate data across muscles for each participant, to evaluate whether linear combinations of activity across muscles were specific to the secondary target direction. We repeated this procedure for field trials within the early exposure and late exposure epochs for comparison of adapted responses to baseline. An AUROC value of 0.5 represents chance classification between signals; a value of 1 represents perfect classification.

To determine the onset of linearly differentiable muscle activity between leftwards and rightwards secondary targets, we used segmented ‘dog-leg’ linear regression to fit the time series AUROC curves. We further smoothed the time series data with a running mean (window of 10ms) and identified the time sample that first delivered an AUROC value greater than 0.70. This value was chosen as a lower threshold for signal disparity than has been used previously in EMG analysis in order to increase sensitivity to differences between secondary target positions. A dog-leg regression was fit by least squares to the data, as in Weiler et al. (2015). The model consisted of a (zero gradient) line from the first included sample (-150ms) until sample i, and a linearly rising line from sample i until the sample at which the 0.70 AUROC threshold crossing was previously identified. Sample i was fit and corresponds to the time sample at which the signals began to diverge from chance discrimination.

2.3 Results

2.3.1 Reproducing follow-through-dependent learning

Participants grasped the handle of a robotic interface and made reaching movements from one of four starting locations through a perturbing force field to a central target (see Methods). The field direction (clockwise or counter-clockwise) was randomly selected on each trial. For a first group of subjects (Figure 2.2, full follow-through) we associated the direction of the force field with the location of a secondary target (at ±45°). After the target appeared there was a delay period of 300 ms before a tone cued the participant to initiate their movement. These participants were required to make a second unperturbed, follow-through movement to this target immediately after arriving at the central target. We interspersed the movements in the force field with channel trials, in which the movement was confined to a simulated mechanical channel from the start to central target. This allows us to measure predictive force compensation independently from factors such as co-contraction. As expected (Howard and Franklin, 2015), over the course of 150 blocks (1200 force field trials) participants reduced their kinematic error (Figure 2.3A blue, difference of -1.22 cm, paired t-test, $t_5 = 4.62$, $p = 0.0057$; hand paths shown in Figure 2.4) and showed substantial force compensation on channel trials (Figure 2.3B blue, difference of 37.7% full compensation, paired t-test, $t_5 = -4.75$, $p = 0.0051$) reaching approximately 40% of full compensation. In contrast, participants who had the same visual display of the secondary target (which again determined the force field direction) but who did not follow-through (Figure 2.2, no follow-through) showed no learning (Figure 2.3A & B grey; NMPE, difference of -0.35 cm, paired t-test, $t_5 = 0.67$, $p = 0.53$; force adaptation, difference of 0.07% full compensation, paired t-test, $t_5 = -0.05$, $p = 0.96$). This is in accord with many studies that have shown that static cues are insufficient to reduce interference seen when exposed to opposing force fields (Gandolfo et al., 1996; Howard and Franklin, 2015; Howard et al., 2012, 2013). To examine which features of the follow-through allowed the separation of motor memories for opposing force fields, in two new groups of participants we isolated execution and planning.

2.3.2 Isolating motor execution

In an execution only group (Figure 2.2) the secondary target was not displayed at the start of the trial. Participants initiated the movement in one of the randomly chosen force fields. However, part way through the movement to the central target the secondary target associated with the presented force field appeared (on average 406 ± 14 ms after the cue to move and 270 ± 16 ms after movement initiation), and participants were required to make a follow-through movement to this target. Therefore, subjects executed the follow-through but could not plan it prior to the initiation of the movement through the force field. This potentially allowed the participants to retroactively associate the secondary target with the force field. Critically, on the channel trials (presented throughout the experiment) the secondary target was displayed from the start of the trial, allowing us to assess whether any latent learning had taken place based on execution of the follow-through. We found that although this group showed a reduction in kinematic error (Figure 2.3A, yellow; difference of -0.73 cm, paired t-test, $t_5 = 2.71$, $p = 0.042$) this was accounted for by co-contraction as they showed no significant increase in force adaptation (Figure 2.3B, yellow; difference in 5.1% full compensation, paired t-test, $t_5 = -0.85$, $p = 0.43$) and no aftereffects in the post-exposure period when the force field was turned off (Figure 2.3A and Figure 2.4; difference of -0.08 cm, paired t-test, $t_5 = 1.18$, $p = 0.29$). This suggests that simply executing a follow-through movement to a target, that is uniquely associated with the force field direction, does not allow separation of motor memories.

For the execution only group to have shown learning, they would need to generalize from exposure trials with a target appearing late in the movement to the trials in which the target was displayed from the beginning of the trial (300 ms before the cue to move). To confirm that the lack of learning was not due to an inability to generalize from late-appearing to

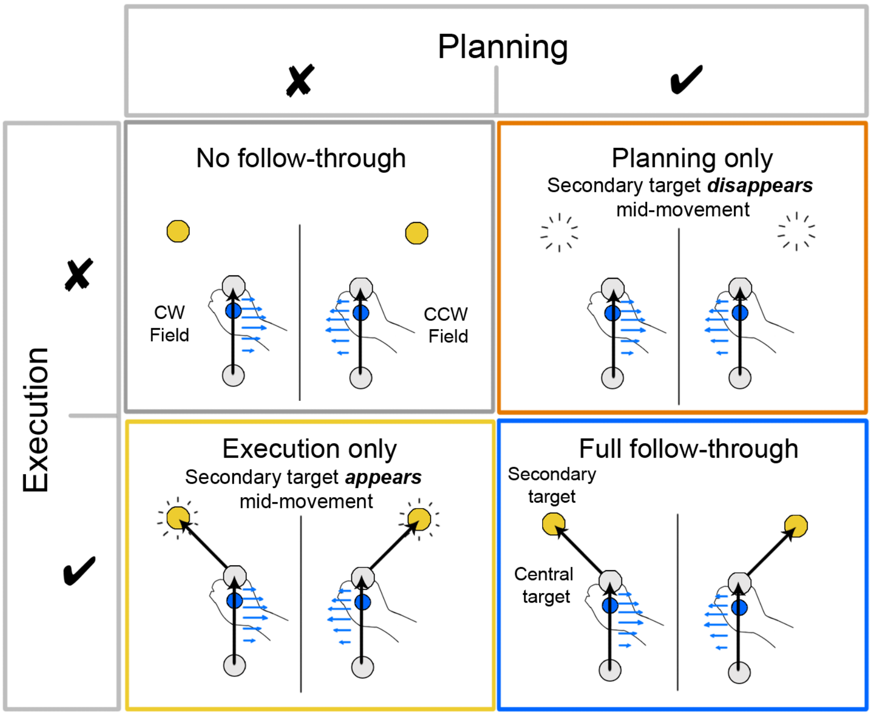

Fig. 2.2 **Experimental paradigm in which planning and execution of a follow-through movement were factorially controlled.** Participants made an initial movement from a starting location (bottom grey circle) to a central target (grey circle). During exposure trials, a velocity-dependent curl force field (force vectors shown as blue arrows for a typical straight line movement to the central target) was applied during this movement, and the field direction, clockwise (CW) or counter-clockwise (CCW), was determined by the secondary target location(at either +45 or -45 to the initial movement direction). A no follow- through group (top left) ended the movement at the central target,whereas the full follow-through group (bottom right) made a follow-through movement, thereby both planning and executing the follow-through. For the execution-only group (bottom left), the secondary target only appeared late in the movement to the central target and they were required to follow-through. Therefore, this group was prevented from planning the follow-through prior to the initiation of their movement. For the planning-only group (top right), the secondary target disappeared late in the movement to the central target and they were required not to follow-through. Therefore, this group could plan a follow-through before the initiation of the movement, but did not execute it. In all groups, channel trials were used to assess learning and for these trials the secondary target was displayed from the start of the trial. The schematic only shows one of the four possible starting locations used in the experiment.

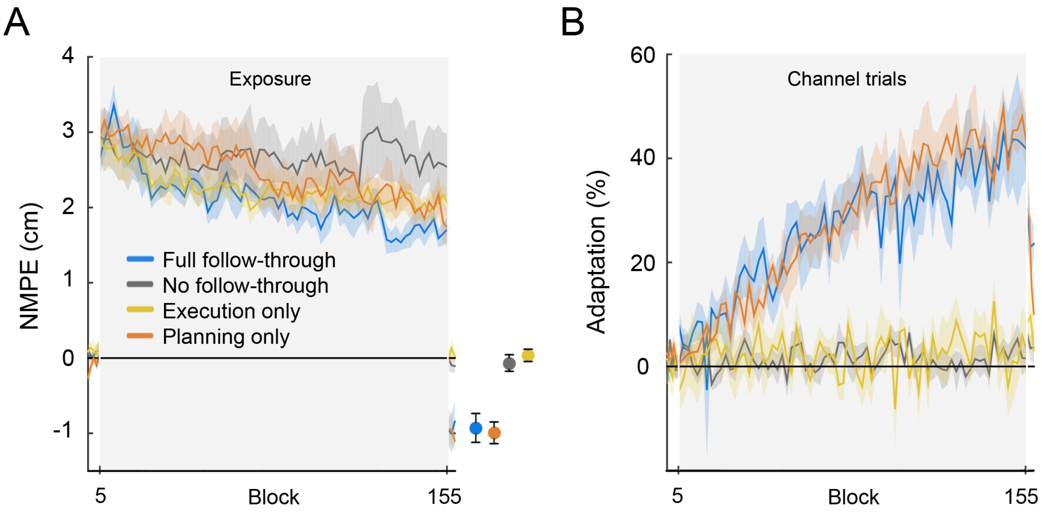

Fig. 2.3 **Planning follow-through movements reduces interference between opposing fields.** (A) The kinematic error and (B) force adaptation for the full follow-through (blue), no follow-through (grey), execution-only (yellow), and planning-only (orange) groups. Data show mean ± SE across participants for pairs of blocks in the exposure phase (grey region) and for single blocks in the pre- and post-exposure phases. In (A), we show the mean (±SE) of the aftereffects to the right of the panel (separated for clarity).

early-appearing targets, we ran a control in which we included additional channel trials throughout the experiment. On these trials the target appeared at a time uniformly sampled from 300 ms before to 400 ms after the tone, thereby allowing participant so experience a range of target appearance times which should encourage generalization. The control group showed no reduction in kinematic error (Figure 2.5A; difference of -0.01 cm, paired t-test, $t_3 = 0.64$, $p = 0.97$), no significant increase in force adaptation (Figure 2.5B; paired t-test, $t_3 = -0.08$, $p = 0.448$) and no aftereffects in the post-exposure period when the force field was turned off (Figure 2.5A; paired t-test, $t_3 = -1.70$, $p = 0.187$). This suggests that, even when exposed to the full range of secondary target appearance times, simply executing a follow-through movement to a target that is uniquely associated with the force field direction, does not allow separation of motor memories. In addition we found that in the second half of the exposure there was no obvious adaptation as a function of appearance time (Figure 2.5C). These results suggests that the lack of adaptation in the execution-only group did not result from an inability to transfer adaptation from late target-appearing exposure trials, to early target-appearing channel trials.

2.3.3 Isolating motor planning

To isolate the planning component of the follow-through, separate from execution, a fourth group of participants (Figure 2.2, planning only) made reaches in which the secondary target was displayed from the start of the movement (and as in the other groups a 300 ms delay period was imposed). However, on all exposure trials, when the subjects had reached part way towards the central target, the secondary target was extinguished (on average 301±20 ms after the cue to move and 149±6 ms after movement initiation) and participants were required to terminate their movement at the central target and not follow-through. To encourage them to plan the follow-through movement, on channel trials the secondary target remained illuminated and they were required to follow-through. We increased the number of channel trials for this group so that one third of trials were follow-through (while maintaining the same number of exposure trials as in the other groups). Even though these participants never executed a follow-through on exposure trials, they showed substantial kinematic learning (Figure 2.3A, orange line; difference of -1.11 cm, paired t-test, $t_5 = 6.24$, $p = 0.0015$), a strong aftereffect (Figure 2.3A and Figure 2.4; difference of -0.90 cm, paired t-test, $t_5 = -6.3$, $p = 0.0015$), and a concomitant increase in force compensation (Figure 2.3B; orange line; difference of 43.9% full compensation, paired t-test, $t_5 = -11.3$, $p = 9.5e-5$) to around 40%.

2.3.4 Comparisons of learning and kinematics between groups

We compared adaptation across all four groups with a mixed-effects ANOVA, with fixed effects of epoch (two levels: first and last six blocks in the exposure phase), and group (four levels corresponding to the four main groups), and a random effect of subject. There was a main effect of epoch (mixed-effect ANOVA, $F_{1,20} = 64.9$, $p = 1.05e-7$), a main effect of group (mixed-effect ANOVA, $F_{3,20} = 17.61$, $p = 7.8e-6$), and importantly a group x epoch interaction (mixed-effect ANOVA $F_{3,20} = 17.15$, $p = 9.43e-6$), suggesting that the groups demonstrated significantly different amounts of learning. We subsequently contrasted the final adaptation in the two groups who showed significant learning (full follow-through and planning only) using an unpaired t-test, and there was no significant different in final adaptation levels (unpaired t-test, $t_{10} = -0.28$, $p = 0.783$). Therefore, simply planning to follow-through leads to learning that is not significantly different from the learning that occurs when both planning and executing a follow-through.

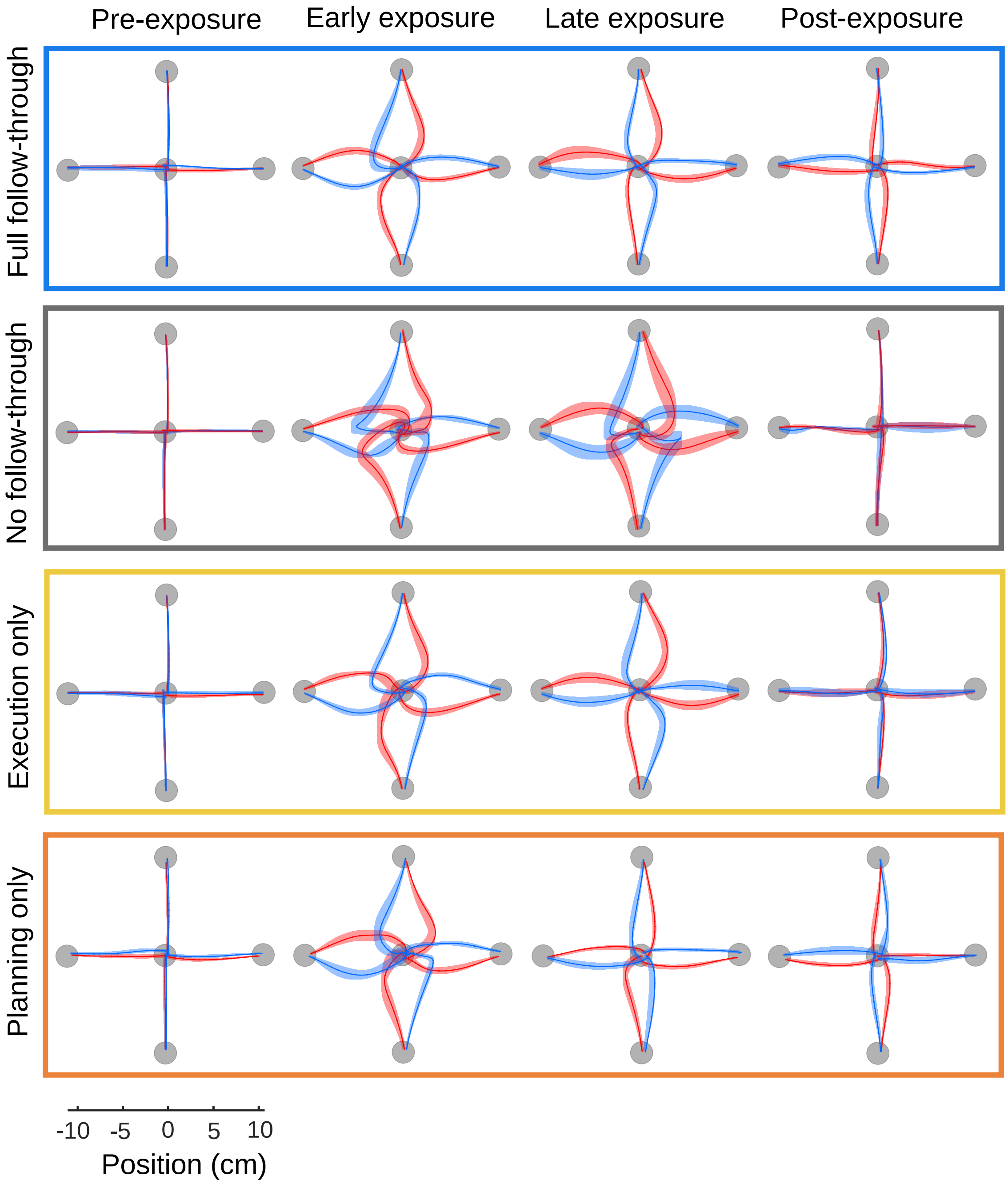

Fig. 2.4 **Kinematics across the groups for different phases of the experiment.** Hand paths are shown to the central target from the four different starting positions. Paths shown as mean ± SE across participants, for last two blocks of pre-exposure (first column), the first two blocks (second column) and last (third column) two blocks of exposure, and the first two blocks of post-exposure (fourth column). The colors indicate the field direction (blue for CW and red for CCW).

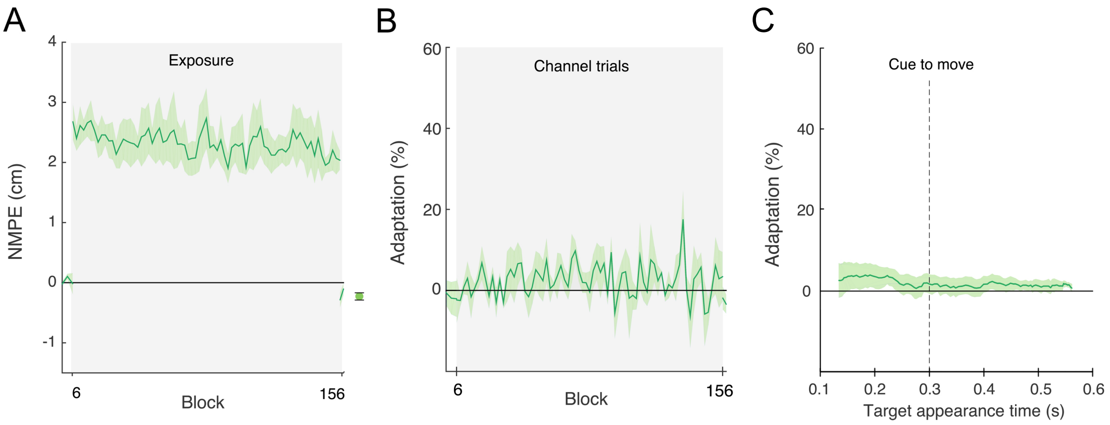

Fig. 2.5 **Varying the appearance time of the secondary target does not facilitate adaptation in an execution only control group.** (A) the kinematic error (normalized within this group) and (B) force adaptation (combining 0° and 180° early appearing channel trials). Data shows mean ± s.e. across participants for pairs of blocks. In panel (A) we show the mean (± s.e.) of the aftereffects to the right of the panel. (C) shows adaptation as a function of target appearance time for the second half of the blocks of exposure. Data shows mean (± s.e.) of separate running averages performed for each subject, each with a 150 ms smoothing window at 100 appearance times equally spaced from 0.1 to 0.6 s.

To encourage uniformity of movement kinematics, we placed constraints on several features of a trial. A trial was only deemed successful if the hand left the starting circle after the tone sounded and within 1 s; took less than 1.5 s to reach the final target and remained in the central target for at least 50 ms (success rate was $90.1 \pm 5.2\%$ and unsuccessful trials were not analyzed but were repeated). If unperturbed movements to the central target are substantially different for the two possible secondary targets this could facilitate learning (Howard and Franklin, 2015; Hwang et al., 2003). We examined the kinematics of pre-exposure movements within each group for each secondary target direction (±45°), as well as across groups. For each group and kinematic measure (see Methods), we performed a Wilcoxon signed-rank test on the pre-exposure null trial movements as a function of follow-through direction (±45°). Of the 18 tests we found only one statistically significant difference. That is, for the no follow-through group, the displayed location of the follow-through target (left or right, which they did not move to) led to a small difference in path length to the central target (Δ path length 1.9mm, $z = 4.40$, $p = 0.031$). However such kinematic differences are likely to enhance any learning and given the lack of learning in this group, such a small path length difference does not affect our conclusions.

There was no significant difference between dwell time (full follow-through and execution only groups), lateral deviation or path length. However, duration ($\chi^2(3) = 14.3$, $p = 0.0026$)

and peak speed ($\chi^2(3) = 7.9$, $p = 0.048$) were significantly different across groups. Post-hoc tests revealed that this difference was primarily due to the no follow-through group making faster movements than the other groups (pairwise comparison with 3 other groups all $p < 0.05$ for duration, and there was a difference between the full follow-through and no follow-through group in peak speed, $z = -2.16$, $p = 0.026$). However, all measurements of learning take movement speed into account and given this group is a replication of previous studies (Howard and Franklin, 2015; Howard et al., 2013), such speed differences are highly unlikely to account for a lack of learning.

2.3.5 Assessing the plan-specificity of baseline muscle activity

We found that pre-exposure null trial kinematics were not statistically different for the movement to the central target when planning but not executing different follow-throughs. However, it remained unclear whether the different neural states generated by each plan translated into distinct motor commands and subsequent activity at the periphery. As a many-to-one mapping exists between muscle activation and end-point kinematics, it was possible that different motor commands could have produced kinematically-consistent end-points when movements were planned, but not executed, to each secondary target. In order to determine whether distinct motor commands were generated when executing movements with the same kinematics but different underlying plans, we recruited a further two participants to perform a variant of the planning only experiment, while we recorded electromyographic (EMG) activity from six muscles in the arm. We assessed whether the secondary target location could be decoded from a linear combination of muscle activity on movements that were planned to different secondary targets but stopped at the central target. Compared to the previous planning only group, these participants performed the experiment from a single starting location in order to increase the number of trials with similar patterns of muscle activation. This ensured a simple logistic regression decoder had the best chance of detecting any systematic differences in muscle activity. As expected, over the course of 120 blocks (960 force field trials) both participants reduced their kinematic error (Figure 2.6A; participant 1, difference of -1.15 cm, $F_{1,7} = 11.3$, $p = 0.020$; participant 2, difference of -1.47 cm, $F_{1,7} = 118.7$, $p = 1.1e-4$) and developed considerable force compensation on channel trials (Figure 2.6B, participant 1, difference of 45.8% full compensation, $F_{1,7} = 29.2$, $p = 0.0029$; participant 2, difference of 50.2% full compensation, $F_{1,7} = 130.0$, $p = 9.1e-5$), reaching an average of approximately 50% of full compensation.

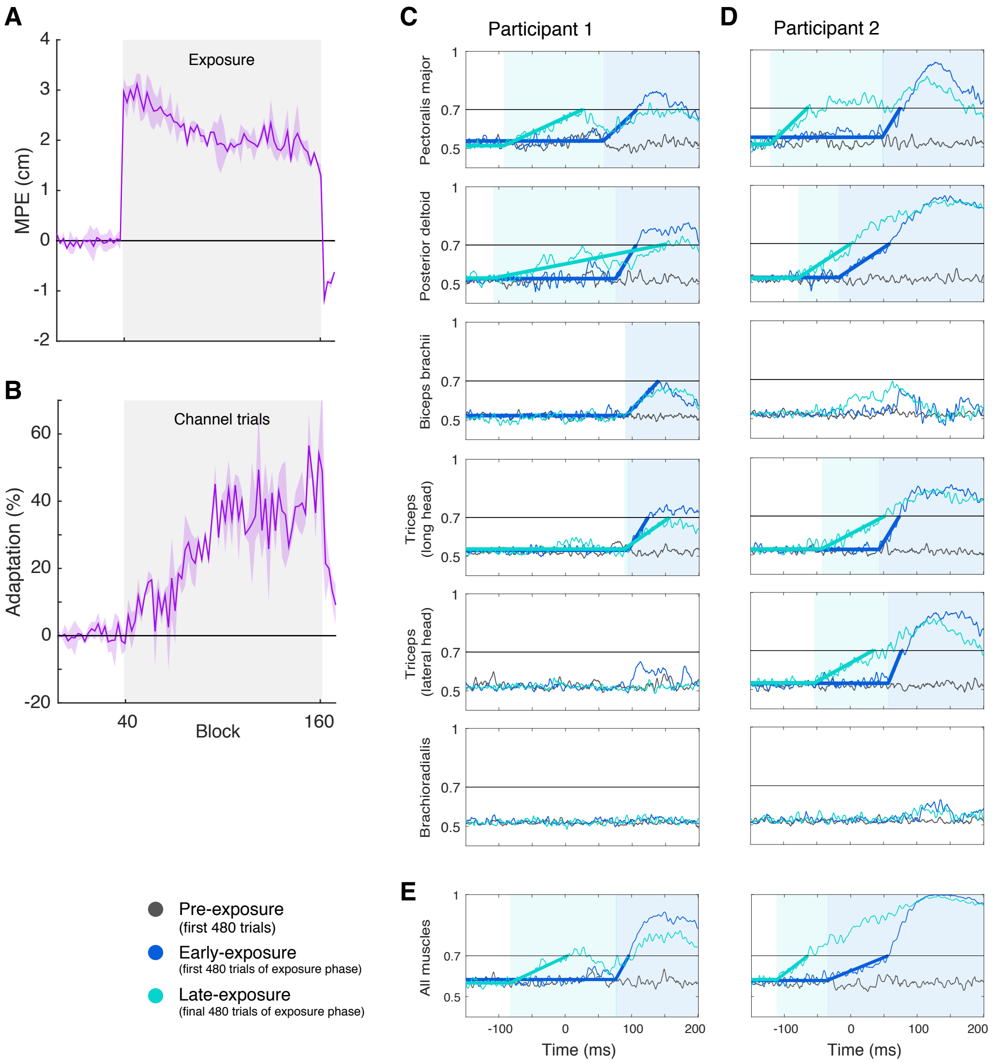

Fig. 2.6 **Linear combinations of aggregate muscle activity did not reflect planned follow-through direction in pre-exposure trials of both EMG planning-only participants.** (A) The kinematic error and (B) force adaptation for the two EMG planning-only participants (purple). Data show mean ± SD across the two participants for pairs of blocks in the exposure phase (grey region) and for single blocks in the pre- and post-exposure phases. Parts (C-E) show area under the receiver-operator characteristic (AUROC) curve of a binary classifier instructed to label the direction of planned follow-through on planning only trials, each based on 320 trials across 480 trial epochs of pre-exposure (grey), early-exposure (dark blue), or late-exposure (light blue) trial muscle activity. Classification performance is shown as a moving mean function of trial time (window of 10 ms) for each of the six muscles recorded in each participant (C-D), and for a classifier trained on the aggregate muscle data in each participant (E). Trial time is measured relative to movement onset. Chance binary classification is indicated at 0.5. Thick lines show dog-leg fits from the first moment that activity becomes decodable with AUROC greater than 0.70, and trace back linearly to find the moment at which muscle activity begins to diverge. Shaded regions indicate the time from which activity for each planned follow-through movement begins to diverge.

Table 2.1 **Movement kinematics on pre-exposure (null field) trials compared across groups.** For each kinematic measure we examined whether each of the four groups differed in their mean values. The table shows the mean ±s.e. for each group, and the Kruskal-Wallis Chi-squared value and p-values testing for differences between the groups. The comparison of dwell times instead shows the z value for a Mann Whitney U test. NA = not applicable.

Measure	Full follow-through	No follow-through	Execution only	Planning only	$\chi^2(3)$	p
Lateral Deviation (cm)	0.35 ± 0.01	0.30 ± 0.01	0.33 ± 0.02	0.32 ± 0.02	3.27	0.35
Path Length (cm)	10.94 ± 0.03	11.12 ± 0.08	10.91 ± 0.07	11.16 ± 0.13	3.34	0.34
Duration (s)	0.324 ± 0.010	0.260 ± 0.013	0.315 ± 0.014	0.302 ± 0.004	14.3	<0.01
Peak Speed (cm/s)	43.8 ± 1.9	62.7 ± 3.4	47.0 ± 2.9	51.8 ± 0.9	7.9	<0.05
Dwell Time (s)	0.098 ± 0.008	NA	0.119 ± 0.008	NA	z = -1.52	0.13

On pre-exposure movements to the central target, neither participant demonstrated detectable differences in linear combinations of activity across muscles as a function of secondary target position (Figure 2.6C and D row 7, grey; decoding accuracy gave mean AUROC time series < 0.58 for classifier trained on all muscle activity, for each participant). In contrast, by the end of the exposure phase, the direction of intended follow-through could be decoded from pre-movement muscle activity in both participants (Figure 2.6C and D, light blue shaded regions, AUROC > 0.70 before movement onset). Therefore, while the secondary target location could be predicted from muscle activity in movements made just to the central target, this difference in signal was not detectable at baseline. This suggests that linearly separable muscle activity was not produced when planning different follow-through movements that terminated at the central target, suggesting that linear combinations of aggregate peripheral activity is unlikely to be the critical factor associated with motor adaptation. However, it remains to be determined whether more flexible decoders capable of predicting with nonlinear combinations of muscle activity (such as support vector machines), might reveal pre-exposure differences in more complex multivariate activation patterns which could support adaptation.

For all of the above listed parametric tests, except where explicitly specified, Shapiro-Wilk tests could not reject the null hypothesis that the compared samples were normally distributed. For the repeated-measures ANOVAs, assumptions of sphericity were not violated as there were only two within-subjects levels (early and late exposure).

These results show that, when a follow-through movement that is predictive of the field direction is planned, even if not executed, there is substantial reduction in interference.

2.4 Discussion

Our results show that planning different follow-throughs, without subsequent execution, allows the learning of two motor skills that normally interfere. Indeed, the amount of learning was not significantly different to when the follow-throughs were both planned and executed. Moreover, executing different follow-throughs, without being able to plan them from the start of the movement, led to full interference. This suggests that the key to representing multiple memories is to have each associated with a different motor plan.

Our results can be interpreted within the dynamical systems perspective for motor cortex, which places an emphasis on motor planning (Churchland et al., 2012, 2006c) and suggests a more fundamental role for preparatory activity in motor learning. In this framework, motor preparation during an enforced delay period (400-1000 ms) involves the setting an initial state of neural activity, from which point the movement naturally evolves through intrinsic neural dynamics. If different movements are planned, delay-period firing rates will be in different initial states, and set distinct courses for the consequent evolution of neural and physical activity (Churchland et al., 2006c). A recent study recording in motor cortex from patients with Amyotrophic Lateral Sclerosis confirmed similar neural dynamics in humans compared to non-human primates (Pandarinath et al., 2015). Our results show that simply planning, but not executing, two different follow-through movements results in learning. This suggests that distinct neural states that occur in humans during a delay period for movements with different plans, lead to different neural states during the execution of the movement. These different neural states can then be linked to different force outputs, thereby compensating for the opposing perturbations affecting the same physical state of the limb.

Under our hypothesis that different neural states are critical to separate motor memories, there are several other manipulations that, by differentially altering the neural state, could also enhance the representation of multiple skills. Given that the preparatory neural state can depend not only on the planned movement itself, but on how long preparation was sustained (Ames et al., 2014; Churchland et al., 2006c) there may be some ability to differentially adapt otherwise-identical movements if some are preceded by a long delay and others are preceded by no delay. Indeed, recent studies have shown that preparation time can significantly affect the way in which motor learning proceeds (Fernandez-Ruiz et al., 2011; Haith et al., 2015). Moreover, neural activity during planning (delay period of an instructed-delay reach task) in motor regions show differential activity as a function of movement extent (Fu et al., 1993; Kalaska and Crammond, 1992; Messier and Kalaska, 2000; Riehle and Requin, 1989), hand

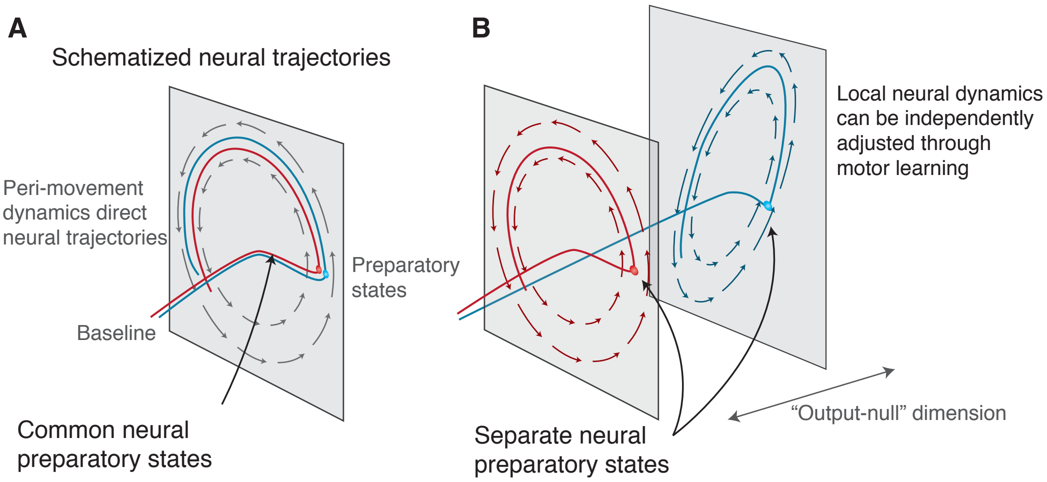

Fig. 2.7 **Illustration of neural trajectories for independent motor learning.** (A) Schematized neural trajectories for motor interference. Planning brings the neural population activity state (red and blue dots) to the same location in neural state space. Here, as is expected in the no follow-through group, the neural dynamics (grey vector field) that govern the peri-movement trajectories are shared. Consequently, adjustments to these dynamics trial-by-trial through adaptation interfere and result in no net learning. (B) Schematized neural trajectories for independent learning. In contrast to A), here planning brings the neural population activity state to separate locations in state space. The local dynamics around each neural trajectory (red and blue vector fields) can be independently adjusted, facilitating independent motor learning, as is observed in the full follow-through and planning only groups. (Image reproduced with permission from O'Shea and Shenoy (2016) commentary)

path curvature (Hocherman and Wise, 1991), and peak speed (Churchland et al., 2006b). This suggests that multiple motor memories may be separable based on other planned aspects of the movement.

Several studies have shown that it is easy to learn two opposing force fields if each is applied to a reach to different targets, such as two spatially separated targets (Howard et al., 2013; Hwang et al., 2003) . A recent study showed that you can still learn opposing force fields for two spatially separate targets even if you rotate the vision of the hand in opposite directions, so that hand kinematics are eventually identical for the two targets but appear visually different (Hirashima and Nozaki, 2012). This led the authors to suggest that planning is the important determinant of interference. However, the use of the visuomotor rotations confound the effects of state estimation and planning and, moreover, does not allow a dissociation of desired state from plans. When a visuomotor discrepancy is introduced, it leads to a state estimate of the hand's position that is somewhere between its proprioceptive and displaced visual locations. Many studies have already shown that it is simple to learn opposing perturbations if the state of the hand is different for each (Gandolfo et al., 1996; Howard et al., 2013; Hwang et al., 2003). Therefore, the study simply shows that you can learn opposing perturbations if each is associated with a different perceived state of the limb. Our study provides two significant advances on such visuomotor paradigms. First, by using a dynamic perturbation alone our study is the first to show that simply having different motor plans, without the confounding effect of dissociating the visual and physical location of the hand, allows opposing perturbations to be learned. Second, studies of visuomotor learning have not separated the concept of a plan from desired state (as noted in (Day et al., 2016)). Studies such as (Hirashima and Nozaki, 2012) show that subjects can map different desired states (i.e. left and right targets) to different force fields. However, a desired state is not synonymous with a plan. One can have the same set of desired states arising in different plans, as is the case in our experiment. We show that the same desired states (e.g. hand locations to the central target) can be mapped to two different commands (for the two force fields) when they are part of a movement which has a different overall plan, that is distinct follow-throughs (even if not performed). Therefore, previous studies have emphasized the necessity to link different desired states, or the physical or estimated states of the body, to different perturbations to reduce interference. Our results support an alternative and more fundamental hypothesis. That is, what appears to be crucial to separate motor memories is that the underlying plan, and hence neural activity during execution, must be different.

Our study fundamentally asks to what state of the body and/or brain is motor adaptation, in a sense, 'attached'. That is some contexts can tag motor memories, making them immune from interference under other contexts. When the context is the same for two opposing perturbations, adaptation under each perturbation will be driven in opposite directions leading to no net adaptation and, hence, interference. However, if the perturbations are experienced under different contexts, then there will be reduced interference and differential adaptation expressed. A fundamental question is what constitutes different contexts. We show that adaptation 'attaches' itself not to the physical situation, but to some internal state that differs in anticipation of a forthcoming movement. Consider the schematized neural trajectories depicted in Figure 2.7 (reproduced with permission from O'Shea and Shenoy (2016)). Under our hypothesis, if modifications due to each field are made around a single dynamical neural trajectory, initiated from the same preparatory neural activity state, interference to learning will occur (Figure 2.7A). In contrast, if different motor plans bring the initial neural population to a distinct point in neural state space, different consequent neural trajectories will result (Figure 2.7B). The neural dynamics local to each trajectory can therefore be associated with each force field and adapted independently in motor learning, giving rise to separate motor memories.

Based on our results, we propose that situations that lead to differential neural responses in the relevant brain areas will act as different contexts. For example, static cues (e.g., color) linked to opposing force fields have very limited ability to reduce interference (Gandolfo et al., 1996; Howard et al., 2013) suggesting that neural activity in relevant motor regions may not be affected by such cues. In contrast other contexts such as different dynamic cues (Cothros et al., 2009; Howard and Franklin, 2015; Howard et al., 2012), concurrent motion of the other arm (Howard et al., 2010; Nozaki et al., 2006; Nozaki and Scott, 2009; Yokoi et al., 2011), lead-ins (Howard et al., 2012; Wainscott et al., 2005) and follow-throughs (Howard and Franklin, 2015) often allow substantial learning. We suggest that such situations that act as contexts may simply be ones that lead naturally to different neural states in motor related regions. For example, under our hypothesis, when opposing force fields are linked to different lead-in movements performed before moving through the force field (Howard et al., 2012; Wainscott et al., 2005), different motor plans for each lead-in will bring the neural states to distinct points in neural state space before each movement through the force-field, as in Figure 2.7B. Whereas, contexts that involve shifting the physical location of the movement in the workspace, but which produce similarly directed trajectories (Hwang et al., 2003), necessitate different neural states by initiating motor plans from different physical initial conditions.

In summary, by isolating the planning and execution components of follow-through movements, we show that it is exclusively the planning component, and not execution, that allow multiple motor memories to be learned and expressed. Our results support a dynamical systems perspective for motor cortex, which emphasizes the primacy of planning, over execution, in the representation of motor adaptation. This suggests that the critical component that allows separation of motor memories is that the underlying neural states need to be different during the action, and one way this can be achieved is simply by having different plans.

Chapter 3

Overcoming interference with motor imagery

Motor imagery, that is the mental rehearsal of a motor skill, can lead to improvements when performing the same skill. Here we show a powerful and complementary role, in which motor imagery of different movements after actually performing a skill allows learning that is not possible without imagery. We leverage a well-studied motor learning task in which subjects reach in the presence of a dynamic (force-field) perturbation. When two opposing perturbations are presented alternately for the same physical movement, there is substantial interference, preventing any learning. However, when the same physical movement is associated with follow-through movements that differ for each perturbation, both skills can be learned. Here we show that when subjects perform the skill and only imagine the follow-through, substantial learning occurs. In contrast, without such motor imagery there was no learning. Therefore, motor imagery can have a profound effect on skill acquisition even when the imagery is not of the skill itself. Our results suggest that motor imagery may evoke different neural states for the same physical state, thereby enabling learning.

3.1 Introduction

The ability to acquire new motor skills without disrupting others is critical to the development of a broad motor repertoire. We have previously suggested that the key to representing multiple motor memories is to have each associated with different neural states, rather than physical states of the body ((Sheahan et al., 2016), see Chapter 2). Specifically, we proposed that when reaching in two opposing force-field environments which alternate randomly from trial to trial, the inability of subjects to learn (Brashers-Krug et al., 1996; Gandolfo et al., 1996; Heald et al., 2018; Howard et al., 2012, 2013, 2015) is due to the fact that each movement is associated with the same neural states. However, contexts which separate neural states for the same physical states should allow learning by enabling the same physical movement to be associated with different motor commands. For example, if each movement through the force-field is part of a larger motor sequence comprised of a different follow-through movement, two opposing perturbations can be learned (Howard et al., 2015; Sheahan et al., 2016). As motor preparation is thought to involve setting the initial neural state (Churchland et al., 2012), just planning different follow-through movements, without execution, results in learning of distinct representations (Sheahan et al. (2016), see Chapter 2). From this perspective, other behaviours that create different neural states for the same physical states may also enable the learning of distinct motor memories.

Many studies have suggested that imagining a movement and physically executing it may engage similar neural substrates. For example, human neuroimaging studies have shown similar motor-related activity when imagining and executing movements (Dechent et al., 2004; Hardwick et al., 2017a; Hétu et al., 2013; Mokienko et al., 2013). Moreover, simply imagining moving a body part increases the EMG response of the associated muscles to TMS over primary motor cortex, suggesting that the circuits involved in action are at least partially active during imagery (Kasai et al., 1997; Stinear et al., 2006). Similarly, direct recording of neural populations have recently revealed that when monkeys covertly control a BMI-cursor, the evolution of neural states associated with the preparation and execution of the BMI movements are similar and specific to those observed during the corresponding physical reaches (Vyas et al., 2018). Given that similar motor cortical dynamics are seen in human and non-human primates (Pandarinath et al., 2015), we hypothesized that the same overlap of dynamical neural states may also exist when humans execute or imagine movements. That is, if the neural states of a motor area involved in a physical movement can be made different (even partially) by motor imagery, then each of these neural states could be associated with learning a different motor skill.

We hypothesized that imagining movements results in distinct neural states that can drive the formation and retrieval of different motor memories. In contrast to studies of mental rehearsal in which the motor skill is imagined but not performed, here we ask whether performing the skill as part of a larger, imagined motor sequence affects its representation. Specifically, we ask whether two opposing perturbations which would normally interfere, can be learned if each is associated with an imagined follow-through movement. We show that when participants produce the same physical reach, but imagine performing follow-throughs that differ for each field, substantial learning occurs. Moreover, we find that learning under imagery transfers partially to actual movements, suggesting that motor imagery and execution engage overlapping neural states. In contrast, without motor imagery there was no learning. Our results suggest that motor imagery can have a profound effect on skill acquisition and the representation of motor memories, even when the imagery is not of the skill itself.

3.2 Methods

We recruited 58 subjects (36 female; 25.0 ± 4.1 years, mean ± s.d.), with no known neurological disorders, who provided informed written consent and participated in the experiment. All participants were right handed according to the Edinburgh handedness inventory (Oldfield, 1971) and were naive to the purpose of the experiment. The protocol was approved by the University of Cambridge Psychology Research Ethics Committee, and all experiments were performed in accordance with these guidelines and regulations.

Experiments were performed using the vBOT planar robotic manipulandum described in section 1.3. Participants received continuous visual feedback of their hand position from a cursor, as described in section 2.2.

In the fixation groups, eye movements were tracked using an SR Research Eyelink 1000 camera (sampled at 1kHz). The camera was positioned beneath a cold mirror. At the start of the experiment and after each rest break the eye tracker was calibrated over the visual work-space.

3.2.1 Experimental paradigm

Participants were divided into five groups. The number of subjects was chosen based on experience with similar motor learning experiments. Two subjects were excluded from analysis (see below) and replaced. Data from two of these groups (the Follow-through and Planning only groups) was discussed previously in Chapter 2 (n=6 in each group) and is included here for comparison. For these two groups we added two additional subjects to bring the number in each group to 8.

All participants made reaching movements in a horizontal plane from one of four starting locations to the central target (grey 1.25 cm radius disk), located approximately 30 cm below the eyes and 30 cm in front of the chest. The four starting locations were positioned 12 cm from the central target and arranged at 0° (closest to the chest), 90°, 180° and 270°, as illustrated in Figure 2.1. In addition to the start and central target, on each trial one of two secondary targets (yellow 1.25 cm radius disk) was displayed 10 cm from the central target and positioned at either $+45°$ or $-45°$ relative to the line connecting the starting and central target. The groups differed in whether they were required to continue the reach from the central target to the secondary target and what instructions they were given (see below).

During the movement to the central target the robot either generated no force (null field trials), a velocity-dependent force (exposure trials) or a simulated spring constraining the hand to a straight line path to the target (channel trials). Any movements from the central to the secondary target were made in a null field. Curl force fields and channel trials were implemented as in Chapter 2. The direction of the force-field applied during the movement to the central target was coupled to the position of the secondary target (e.g. CW for $+45°$ and CCW for $-45°$). The association between secondary target position and curl field direction was fixed for each participant and counterbalanced across participants.

Group 1: follow-through (n=8)

This experiment has been described previously in chapter 2 section 2.2.1 under the heading 'Full Follow-through group' and is re-presented in this chapter to serve as a baseline for comparison to the new results. We refer the reader to section 2.2.1 to avoid repeating the description of this experiment.

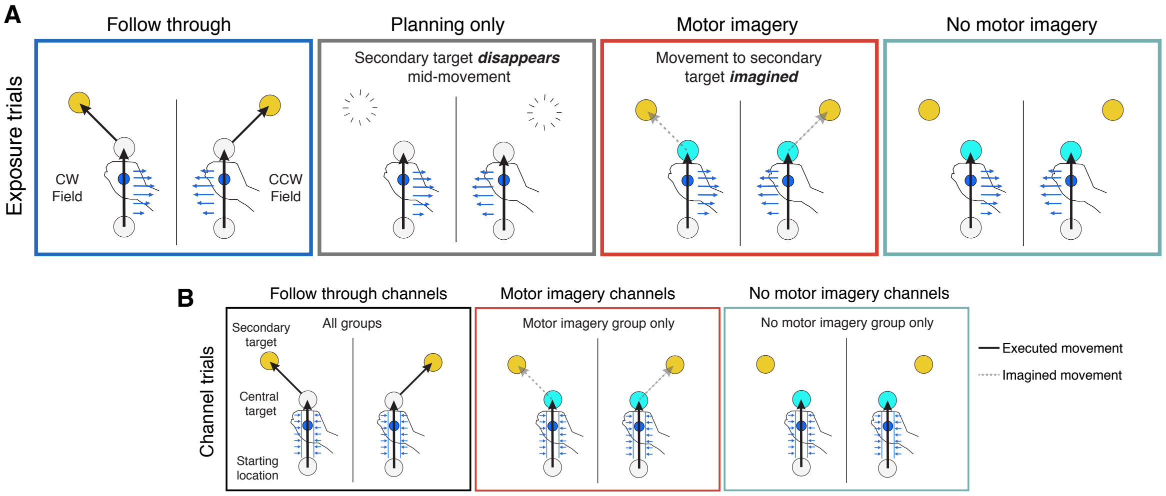

Fig. 3.1 **Experimental paradigm in which subjects imagined follow-through movements.** Subjects performed reaching movements that were either (A) exposure trials or (B) channel trials. On all trials a starting location, central target and one secondary target (at either $-45°$ or $+45°$ relative to the initial movement direction) were displayed from the start of the trial. (A) On exposure trials, a velocity-dependent curl force field (blue arrows) was applied on the initial movement. The field direction, clockwise (CW) or counter-clockwise (CCW) was determined by the secondary target location. The exposure trials varied across the groups. The Follow-through group continued the initial movement to the secondary target (null field as in channel trials). For the Planning only group, the secondary target disappeared late in the initial movement and they were required to stop at the central target. Both the Motor imagery and No-motor imagery groups were cued by a blue central target, displayed from the start of the trial, that they should stop the movement at the central target. In addition, the motor imagery groups were asked to imagine making a movement to the secondary target and press a button when the imagined movement was complete. (B) On follow-through channel trials (left), subjects made a movement to the central target followed immediately by a movement to the secondary target. A channel was applied on the initial movement, allowing an assessment of adaptation measured as the forces applied into the channel wall. A null field was applied on the secondary movement. For half of participants in the motor imagery group, we also included channels for imagined follow though trials (middle) at the end of the exposure phase. Likewise, for half of participants in the no-motor imagery group we included channels for movements just to the central target (right). Note that for clarity in all panels the trials for the two different secondary targets are shown separated, but in the experiment the starting and central targets were in identical locations so that the initial movements were the same. In the experiment there were 4 possible starting locations but for clarity we display only one.

Group 2: Planning only (n=8)

This experiment has been described previously in chapter 2 section 2.2.1 under the heading 'Planning-only group' and is also re-presented in this chapter to serve as a baseline for comparison to the new results. We refer the reader to 2.2.1 to avoid repeating the description of this experiment.

Group 3: Motor imagery (n=16)

In this group we examined the effect of imagining performing a follow-through movement, with the knowledge that it would not be executed. In contrast to the planning only group, the central target colour (blue or grey) indicated whether participants had to execute a reaching movement and stop at the central target, or reach to the central and then the secondary target. When the central target was blue, they executed a movement only to the central target, but were asked to imagine making the follow-through movement (3.1A, Motor imagery). When the central target was grey, participants planned and execute a full follow-through movement. As in the planning only group, on follow-through trials the movement to the central target was in a channel. On motor imagery trials participants were asked to press a button with their other hand to indicate when their imagined movement reached the secondary target. A single button was used for all secondary targets, so that the motor plan for this button press was not specific to the follow-through direction. This enabled us to compare the duration of imagined and executed movements. Crucially for the imagery group, the hand was unconstrained when at the central target so any net motor activity would result in movement which we could observe.

This group were required to fixate on a small white cross located on the central target during each trial. This was to ensure that participants did not make eye movements to the secondary targets. Participants rested their forehead against a headrest and were required to fixate on the cross and maintain fixation within 3 cm for the duration of the trial. If subjects broke fixation or blinked, an error was triggered and the trial was repeated. Participants could move their eyes freely between trials.

Blocks were the same as for the planning only group. At the end of the exposure phase, a subgroup (half of participants) performed the post-exposure phase, as in the planning only group so that we could compare aftereffects. The other participants performed an additional 20 blocks (termed the probe phase) in which we assessed adaptation on motor imagery trials without follow-through. In these probe blocks we kept the proportion of trials that were exposure trials the same as in previous blocks, but changed half of the full follow-through channel trials to motor imagery channel trials (3.1B, middle). Therefore, these 20 blocks consisted of 160 exposure trials, 40 motor imagery channel trials and 40 full follow-through channel trials. After the probe phase these participants performed the same post-exposure phase as the other participants.

During each rest break, participants were asked to evaluate their motor imagery in the previous set of trials (approximately 240 trials). They rated the ease with which they were able to imagine the movements (1-7, hard to easy scale, similar in style to the MIQ-RS (Gregg et al., 2010)), and how frequently they imagined the movements (1-3 scale corresponding to 'fewer than half the trials', 'most trials' or 'every trial').

All participants also completed the MIQ-RS motor imagery questionnaire (Gregg et al., 2010) prior to the start of the experiment. This questionnaire has previously been evaluated for reliability and internal consistency of visual and kinesthetic measures of motor imagery (Butler et al., 2012).

Group 4: No motor imagery (n=16)

This group was the same as the motor imagery group except that participants were not instructed to imagine making follow-through movements and did not press a button (3.1A, No motor imagery). To match the time spent at the central target with the motor imagery group, we made participants wait at the central target for the mean time it took them to execute the follow-through movements on channel trials (the average of previous follow-through trials). As in the motor imagery group, at the end of the exposure phase half of participants performed the post-exposure phase to compare aftereffects. The other half of participants performed the same probe phase as in the motor imagery group, but without the use of motor imagery. Therefore participants performed no motor imagery channel trials (3.1B, right). After the probe phase these participants performed the same post-exposure phase as the other participants.

At the end of the experiment participants were asked if they had been imagining follow-through movements on trials where they had to stop at the central target. One participant responded that they had been, and was excluded from analysis and replaced by an additional subject.

One further participant was excluded from this group and replaced by an additional subject. Midway through the experiment, this replaced subject suddenly started producing a kinematic error in the direction opposite to the field and their adaptation measured on no motor imagery channel trials was greater than 6 standard deviations from the group mean.

Group 5: Motor imagery no fixation (n=8)

This group performed the same experiment as the motor imagery group but without constraints on their eye movements. This was to make the use of eye movements in this group comparable to the follow-through and planning only groups. At the end of the exposure phase all participants immediately performed the post-exposure phase.

3.2.2 Data analysis

Metrics for learning

On channel trials we measured percent adaptation as the slope of the regression of the time course of the force that participants produced into the channel wall against the ideal force profile that would fully compensate for the field, as in Chapter 2. We analyzed all channels trials for the follow-through group, which were all performed from the 0° starting location. The other groups had channels trials for all starting locations and to match the number of channel trials analyzed we included all channels in the sagittal direction (0 and 180° starting locations). The inclusion of only 0° channel trials does not affect the statistical conclusions.

In addition, on null and exposure trials, we calculated the maximum perpendicular error (MPE) as the largest deviation of the hand from the straight line connecting the starting location to the central target, as in Chapter 2.

For statistical analysis, our key measures were adaptation during exposure (as MPE can be affected by co-contraction) and MPE during post-exposure. We averaged adaptation and MPE for each subject within a block. To assess learning we used two measures. The first measure was the difference in adaptation between the average of the pre-exposure blocks and that of the final 6 blocks of exposure. The second measure assessed the aftereffects, calculated as the difference in MPE between the average of the pre-exposure blocks and the first two blocks of post-exposure. We use averaged performance per block in our evaluations of learning, as each start locations and direction of perturbation is tested once within a single block and we wish to assess net learning across these conditions. For both measures we performed a paired t-test across subjects within each group.

Based on previous work we combined the follow-through and planning only groups into a pooled follow-through group. To compare differences across the groups, we performed a mixed-effects ANOVA across groups (pooled follow-through group, motor imagery group and the no motor imagery group), treating group and epoch (two levels: first and last six blocks of exposure) as fixed effects and participants as random effects, as in Chapter 2. We explored differences between specific groups post-hoc by comparing final adaptation on follow-through trials (average of last 6 blocks of exposure) using unpaired t-tests, and a Bonferroni-corrected α of 0.017. We compared the motor imagery group to the pooled follow-through and no imagery groups. We also compared the motor imagery group to the motor imagery (no fixation) group. As these tests compare the learning that transferred to full follow-through trials, we subsequently performed an additional two comparisons to test learning independent of transfer. We compared the learning on motor imagery channels in the motor imagery group subjects who performed the probe phase (n=8, average of first 4 blocks of the probe phase), to the learning on no motor imagery channels in the no motor imagery group subjects who performed the probe phase (n=8, also the average of first 4 blocks of the probe phase), and to the final adaptation of the pooled follow-through group. In addition, we performed unpaired t-tests comparing final adaptation between the subgroups of the motor imagery group and the no motor imagery group, to ensure subgroups were not significantly different.

Kinematics

To display hand paths (Figure 3.3), we extracted position data from when the hand left the start location until it entered the central target position. Each path was then linearly interpolated (x and y separately) so as to sample 1000 points equally spaced in time. For each participant, we considered trials at four different epochs of the experiment, which were the last block of the pre-exposure phase, the first and last blocks of the exposure phase, and the first block of the post-exposure phase. Therefore for each phase and participant we obtained a single hand path corresponding to each perturbation and start location. To generate a path for a group we calculated the average (and s.e.) of the participants' paths and plot the mean with shading showing ± s.e.

For each group and kinematic measure we performed a repeated-measures ANOVA on the pre-exposure null trials as a function of follow-through direction (±45°). Of the 20 tests (Table 1), we found one marginally significant difference (motor imagery path length, p=0.046), however the mean difference in path length between left and right secondary target positions was only 0.13cm, which other studies have shown is insufficient to drive learning (Hwang et al., 2003).

We made several between-group comparisons using Mann Whitney U tests to compare different features of behaviour that could have affected learning. We performed between-group comparisons of the percentage of imagery mistrials due to breaks in fixation (excluding blinks or breaks made before the cue to move), hand overshoots of the central target, and of the time spent at the central target.

To encourage uniformity of movement kinematics, we placed constraints on the timing of participants' reaches (see Methods). If unperturbed movements to the central target were substantially different for the two possible secondary targets, this could have facilitated learning (Howard et al., 2013; Hwang et al., 2003). Therefore, we examined whether the kinematics of pre-exposure movements to the central target within each group depended on which secondary target (±45°) was displayed. We extracted position data from when the hand left the starting location until 50 ms after it entered the central target. We tested for baseline differences in peak speed, movement duration (which covaries with peak speed), maximum signed lateral deviation and path length. Preparatory neural activity has been shown to differ as a function of peak speed (Churchland et al., 2006b), hand path curvature (Hocherman and Wise, 1991), and movement extent (Fu et al., 1993; Messier and Kalaska, 2000; Riehle and Requin, 1989), and such differential activity during planning might affect learning.

Assessments of motor imagery

For the groups who were asked to imagine the follow-through movement, the duration of the imagined movement was taken as the time from reaching the central target until the button press. We used this to assess mental chronometry in each subject (Decety et al., 1989; Sirigu et al., 1996), which compares the average imagined movement duration to the average executed movement duration on the channel trials.

We regressed the percent adaptation of each subject in the final 6 blocks of the exposure phase against the absolute time difference between executed and imagined movements, and against three different self-reported motor imagery measures: MIQ score (1-7), average ease of imagery maintenance score (1-7) and average frequency of imagery score (1-3). The MIQ-RS questions are available in the original paper by Gregg et al. (2010).

To visualise the MIQ scores we plot the distributions of the average test scores, divided into questions on kinesthetic versus visual imagery (3.5A) and total average scores (3.5B). We binned the range of possible scores (1-7) into 30 units for visualisation.

Non-parametric tests were performed in cases where Shapiro-Wilk tests yielded evidence against the data being normally distributed.

3.3 Results

Five groups of participants performed a motor learning task. Two of these groups, Follow-through and Planning only, include data from Chapter 2 as a reference and we have increased the number of participants in each. Participants grasped the handle of a robotic interface and made reaching movements from one of four starting locations through a perturbing force field to a central target (see Methods). On exposure trials, the field direction (clockwise or counter-clockwise) was randomly selected on each trial. We associated the direction of the force field with the location of a secondary target which was at ±45° relative to the movement to the central target. The groups differed in whether they were required to continue the reach from the central target to the secondary target and what instructions they were given (3.1A).

During the exposure phase, we interspersed exposure trials with channel trials, in which the movement was confined to a simulated mechanical channel from the start to central target. For all groups, on these channel trials subjects made a follow-through movement to the secondary target which was unconstrained (3.1B, left). Note that the simulated channel did not expose subjects to the force field and therefore learning was not possible on these trials. The channel trials allowed us to measure predictive force compensation (the force applied by the participant into the channel wall, expressed as percent adaptation) on the initial movement, independent from factors such as co-contraction, as in Chapter 2 (Milner and Franklin, 2005; Scheidt et al., 2000). On non-channel trials, we also calculated the maximum perpendicular error (MPE) of the hand path to the central target, which is a measure of the kinematic error of the movement.

3.3.1 Planning to execute follow-throughs

On exposure trials, the first group of participants were required to make a second unperturbed follow-through movement to the secondary target immediately after arriving at the central target (Figure 3.1A, Follow-through, same as in Chapter 2). Importantly, this follow-through movement was predictive of the field direction. The second group planned the follow-through, but never executed it on exposure trials (Figure 3.1A, Planning only, same as in Chapter 2). That is, the secondary target was displayed from the start of the trial but vanished during the initial movement indicating that the subject should terminate the movement at the central target. To encourage the planning of the entire movement, this group (like all other groups) also made full follow-through movements on channel trials (Figure 3.1B, left).

Both these groups showed significant learning of the two force fields (adaptation increases of 42.9 ± 7.5%, paired t-tests, $t_7 = 5.92$, $p = 5.9e-4$ and 41.9 ± 4.8%, $t_7 = 9.87$, $p = 2.3e-5$ for the follow though and planning groups, respectively), reaching approximately 40% of full compensation (Figure 3.2A, blue and grey). Figure 3.2B shows the MPE across the exposure blocks and Figure 3.3 shows the hand paths for key phases of the experiment for all groups. Moreover, both these groups showed significant aftereffects when the force field was removed during the post-exposure phase (difference in MPE between pre- and post-exposure; 0.94 ± 0.14 cm, paired t-tests, $t_7 = 7.28$, $p = 1.7e-4$, and 0.78 ± 0.17 cm, $t_7 = 5.05$, $p = 0.0015$ for each group respectively).These first two groups included data from six subjects from Chapter 2, together with two additional subjects in each group, to provide a baseline for the new groups. The amount of learning in our follow-through and planning only groups is similar to that observed in both a previous follow-through study (Howard and Franklin, 2015) as well as when learning opposing force fields which are associated with different contextual cues (Howard et al., 2013).

3.3.2 Motor imagery of follow-throughs

To assess whether motor imagery, like planning, is sufficient to separate motor memories, we compared a no-imagery and an imagery group (Figure 3.1A). As in the follow-through and planning only groups, on channel trials the central target was grey, and participants produced a full follow-through movement. In contrast to the follow-through and planning only groups, on exposure trials the central target was blue, such that subjects knew from the start of the trial that they were required to stop at the central target without making a follow-through movement. Both groups maintained fixation on the central target throughout each trial. Critically, the motor imagery group was asked to then imagine making the follow-through movement to the secondary target, whereas the no-imagery group was given no such instructions. Therefore, for the motor imagery group, the imagined follow-through movement was specific to the force field. To complete a motor imagery trial, these participants pressed a button with their left hand to indicate when the imagined movement reached the secondary target. Importantly, the button-press was the same for both secondary targets, and was therefore not specific to the force-field direction. In the no-imagery group, there was no button press, but we controlled the time spent at the central target by making participants wait for the average amount of time it took them to execute follow-through movements (on channel trials). Consequently, the amount of time spent waiting at the central target did not differ between the imagery and no imagery groups (difference of 72 ± 41 ms, unpaired t-test, $t_{30} = 1.72$, $p = 0.096$). After the exposure phase, a subgroup of the participants in each group (n=8) performed a post-exposure phase, identical to the two previous groups, so that we could assess aftereffects. The other participants proceeded to a probe phase of the experiment (see below).

Despite knowing prior to movement initiation that the movement would end at the central target, the motor imagery group increased their adaptation (Figure 3.2A, red; increase of 21.8 ± 3.1%, paired t-test, $t_{15} = 7.47$, $p = 2.0e-6$) and also produced significant aftereffects (Figure 3.3 and Figure 3.4C, red; 0.68 ± 0.20 cm, paired t-test $t_7 = 4.02$, $p = 0.0051$). In contrast, there was no significant increase in adaptation in the no-imagery group (Figure 3.2A, turquoise; increase of 5.1 ± 5.1%, paired t-test, $t_{15} = 1.21$, $p = 0.24$) and no significant aftereffects (Figure 3.3 and Figure 3.4C, turquoise; no motor imagery group 0.17 ± 0.11 cm, paired t-test, $t_7 = 1.83$, $p = 0.11$). Our results suggest that just imagining the follow-through movement allows the separation of motor memories.

3.3.3 Transfer of learning from imagery to execution

During exposure, adaptation was measured on channel trials with full follow-through movements (Figure 3.1B, left). In the imagery and no-imagery groups, this reflects the transfer of learning from experience of the force field on movements that stop at the central target, to full follow-through movements. In order to assess the amount of adaptation on the non-follow-through movements themselves (on which the force field was experienced), a subgroup of participants in each of the motor imagery group (subgroup n=8) and no motor imagery group (subgroup n=8) performed an additional phase in which we included

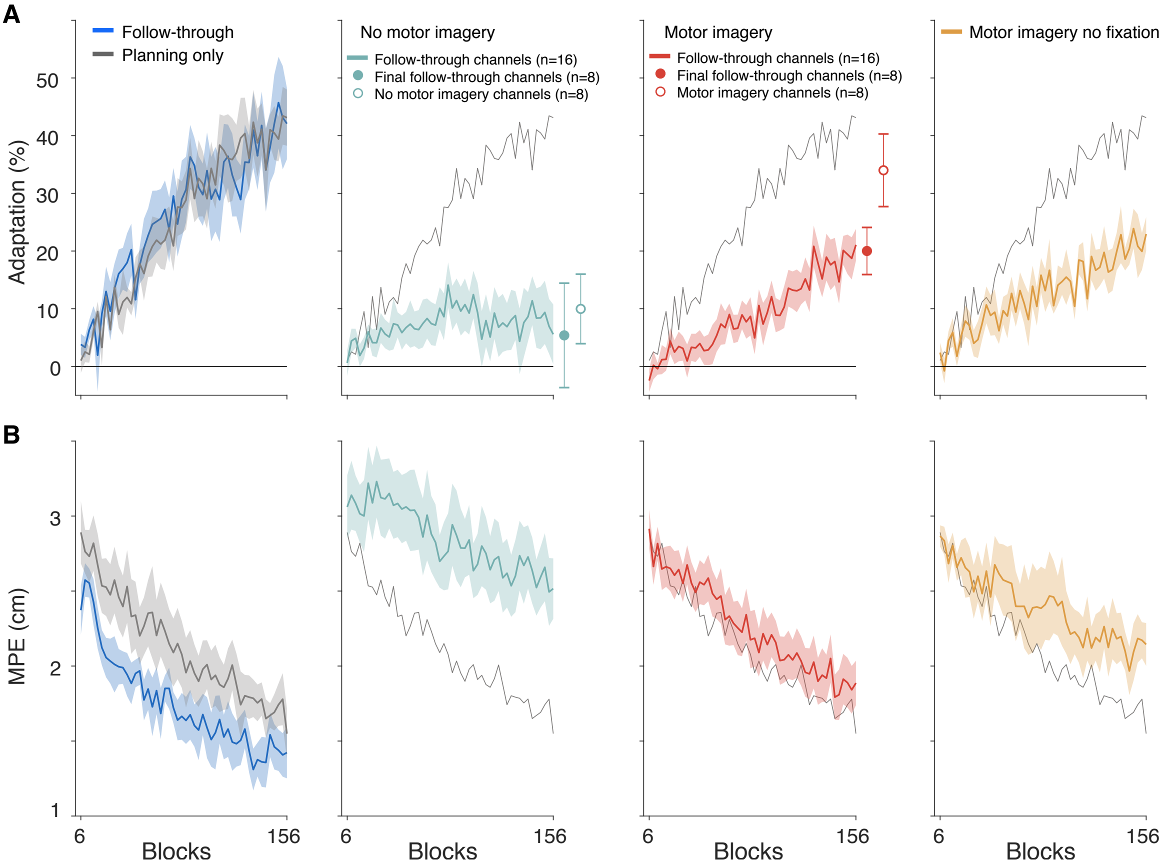

Fig. 3.2 **Motor imagery of follow-through leads to adaptation.** (A) Adaptation in the exposure phase, measured on channel trials which were full follow-through movements in all groups (Figure 3.1B, left). The solid circles to the right of the imagery and no-imagery learning curves are the final adaptation on full follow-through channel trials of the participants who subsequently performed the probe phase (half the subjects). The unfilled circles show the adaptation measured on motor imagery- or no-motor imagery channel trials (Figure 3.1B, middle and right) in the same subjects as the solid circles. (B) Maximum perpendicular error (MPE) measured on exposure trials. Data show mean ± s.e. across participants (for display the 150 exposure blocks were averaged over consecutive blocks of 3 to produce 50 bins) in the exposure phase. For comparison, the mean adaptation and MPE for the planning only group (grey) are repeated on all panels.

channels on non-follow-through trials (Figure 3.1B, middle and right). Final adaptation on follow-through trials was not significantly different between the two subgroups in either the motor imagery group (difference of 0.2%, unpaired t-test, $t_{14} = 0.04$, $p = 0.97$) or the no motor imagery group (difference of 1.7%, unpaired t-test, $t_{14} = 0.18$, $p = 0.86$). The adaptation measured on motor imagery channel trials (motor imagery group) was 34.0 ± 6.3% (Figure 3.2A red, motor imagery channels), and no motor imagery channel trials (no motor imagery group) was 10.0 ± 6.0% (Figure 3.2A, turquoise). There was a significant difference between these groups (Figure 3.4B;f 24.0 ± 8.7%, unpaired t-test, $t_{14} = 2.76$, $p = 0.015$). For comparison, we pooled the follow-through and planning only groups (pooled follow-through group) based on previous results showing their similar levels of adaptation. We compared the final adaptation in the pooled follow-through group with the adaptation measured on motor imagery channel trials in the imagery group (Figure 3.4B), and did not find a significant difference between the two (difference in adaptation of 8.9 ± 7.6%, unpaired t-test, $t_{22} = 1.20$, $p = 0.24$). This suggests that imagining follow though movements afforded levels of adaptation not significantly different to when executing or planning to execute them.

3.3.4 Controlling for eye-movements

In contrast to the motor imagery group, in the full follow-through and planning only groups we did not constrain eye movements. To examine whether potential eye movements to the secondary targets could influence learning, we repeated the motor imagery task but without constraining eye movements. This no fixation motor imagery group increased their adaptation (Figure 3.2A, orange; increase of 17.2 ± 3.1%, t(7) = 4.66, p = 0.0023) and produced significant aftereffects (Figure 3.3 and Figure 3.4C, orange; 0.75 ± 0.17 cm, t(7) = 4.98, p = 0.0016). We compared the motor imagery groups with and without fixation, and did not find a significant effect of fixation on adaptation (difference of 1.5 ± 3.6%, t(22) = 0.375, p = 0.71).

3.3.5 Comparisons of learning across groups

We compared the final adaptation levels across groups (Figure 3.4A). A mixed-effects ANOVA of adaptation with fixed effects of group (pooled follow-through, no motor imagery, and motor imagery) and epoch (first and last six blocks of exposure), and a random effect of participants, revealed a main effect of epoch (mixed-effect ANOVA, $F_{1,45} = 100.8$, $p =$

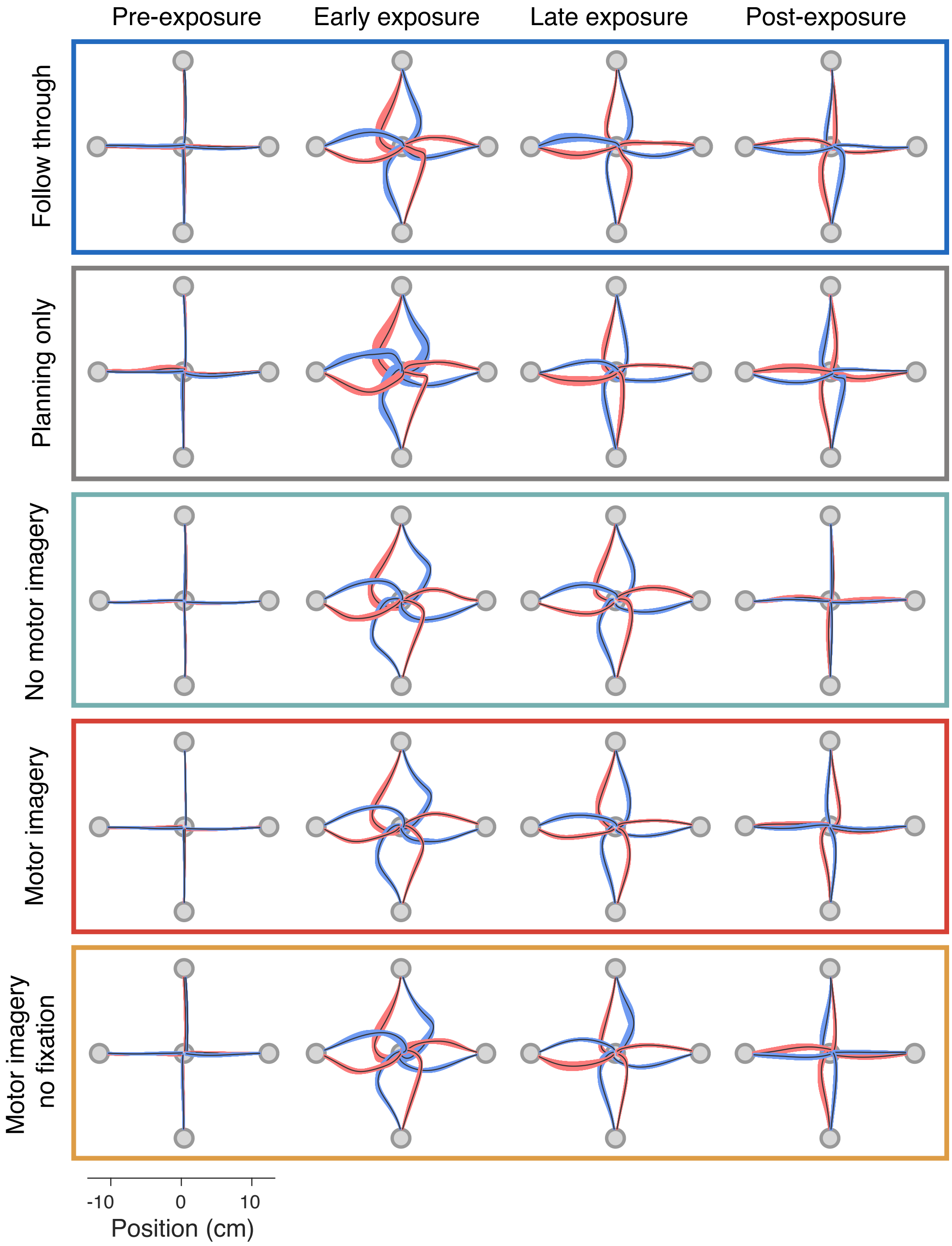

Fig. 3.3 **Kinematics across groups for different phases of the experiment.** Hand paths are shown from each starting location to the central target for all groups across four different phases of the experiment. Paths show the mean ± s.e. across participants, for pre-exposure (last block), early exposure (first block), late exposure (last block), and post-exposure (first block). The colors indicate the field direction (blue for CCW and red for CW).

$4.6e-13$), a main effect of group (mixed-effect ANOVA, $F_{2,45} = 16.3$, $p = 4.7e-6$), and significantly different learning between groups (mixed-effect ANOVA, group x epoch interaction $F_{2,45} = 23.9$, $p = 8.6e-8$). Post-hoc comparisons showed that the final adaptation in the no imagery group was significantly less (difference of 13.6 ± 5.4%, unpaired t-test, $t_{30} = 2.53$, $p = 0.017$, Bonferroni-corrected α of 0.017) than the motor imagery group, suggesting that imagining follow-through movements has an effect on learning. In addition, the pooled follow-through group had significantly greater adaptation than the motor imagery group (difference of 23.0 ± 5.0%, unpaired t-test, $t_{30} = 4.62$, $p = 6.9e-5$, Bonferroni-corrected α of 0.017) showing that learning under motor imagery does not transfer fully to actual follow-throughs. The aftereffects mirror the results seen in the measures of adaptation (Figure 3.3 and Figure 3.4C).

3.3.6 Measures of motor imagery

Comparing the chronometrics of imagined and executed movements in the motor imagery groups (Decety et al., 1989; Sirigu et al., 1996), there was no significant difference in the durations across participants (Figure 3.5C difference of 11 ± 3 ms, paired t-test, t(23) = 0.37, p = 0.71), although the variability was much higher for the imagined durations. Indeed Figure 3.5C appears to show that a subset of participants took much less time imagining than executing movements, while other participants took considerably more time imagining than executing (over 600 ms in some participants). This may indicate different approaches to the imagery part of the task across participants. However, despite the between-group differences in learning, within the imagery group none of our measures of imagery were correlated with the extent of learning. It therefore appears that variability in how participants imagined their follow-throughs did not have a meaningful impact on their learning. The absolute time difference between executed and imagined follow-throughs in each participant was uncorrelated with their final level of adaptation (r = -0.05, p = 0.802). In addition, there was no correlation between the final level of adaptation in the motor imagery groups and the self-reports from subjects as to how often they remembered to imagine follow-through movements (r = 0.24, p = 0.25), the ease of imagery maintenance (r = 0.14, p = 0.51), or the Motor Imagery Questionnaire (MIQ-RS) scores (r = -0.03, p = 0.88, for MIQ scores see Figures 3.5A and B).

Although we did not directly measure muscle activity through EMG in our experiment, we could quantify net motor activity during motor imagery by overt movement. That is, subjects were required to be stationary at the central target during motor imagery and the handle

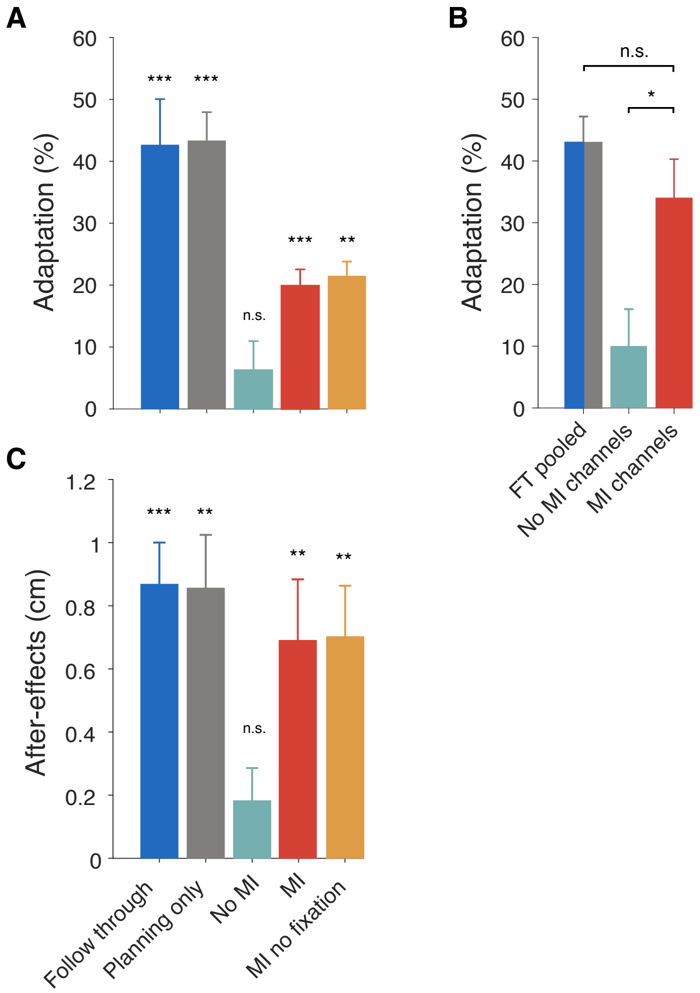

Fig. 3.4 **Adaptation and aftereffects when follow-throughs were executed, planned, imagined or absent.** (A) Final adaptation measured on follow-through channel trials for all participants (mean ± s.e. of final six blocks of exposure). (B) Comparison of the adaptation between the pooled follow-through group and adaptation measured in the subjects who performed the probe phase in the motor imagery and no-imagery groups (first 4 blocks after exposure). (C) MPE during the post-exposure phase (mean ± s.e. of first two blocks) showing aftereffects. Here we consider only the no motor imagery and motor imagery participants who did not perform the probe phase. Therefore all participants shown in (C) experienced the same number of exposure trials before after-effects were assessed. Asterisks show statistical significance of final adaptation level (A) and after-effects (C) compared to pre-exposure, and of differences between groups (B). MI = motor imagery; FT = follow-through; n.s. = not significant.

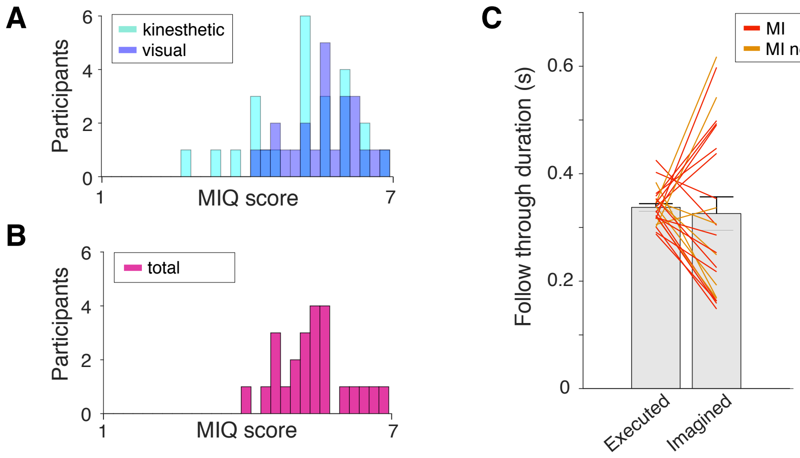

Fig. 3.5 **Measures of motor imagery.** A-B) Histograms of the MIQ scores of all motor imagery participants, divided into (A) measures of visual and kinesthetic imagery (B) and the total scores per participant. In each plot the range of possible scores (1-7) is binned into 30 units for visualisation. C) Durations of executed and imagined follow-throughs for all participants in the motor imagery groups. The coloured lines indicate individual participants; bars show mean ± s.e. across participants

of the vBOT was free to move so that any overt movement which would trigger a mistrial. During the exposure phase, the frequency of mistrials was not statistically different between the motor imagery group and the no motor imagery group for either breaks in fixation (6.0% and 5.3%, $z = 0.848$, $p = 0.39$, for each group respectively), or central target overshoots (4.0% and 4.1%, $z = -0.433$, $p = 0.66$). This suggests that neither type of mistrial was responsible for learning in the motor imagery group. We also compared various kinematic measures during pre-exposure to ensure that hand paths on the initial movement did not vary systematically with the secondary targets (see Table 3.1). For all of the above listed parametric tests, Shapiro-Wilk tests could not reject the null hypothesis that the compared samples were normally distributed. Where one-way ANOVAs were performed, a Bartlett test could not reject the null hypothesis that the compared samples were homogeneous in variance.

3.4 Discussion

Our results show that when subjects repeatedly reach in a force field whose direction can reverse from trial to trial, substantial interference occurs and there is no net learning. However, if subjects are asked to imagine making different follow-through movements for each field

Table 3.1 **Pre-exposure (null field trials) movement kinematics do not depend on secondary target position.** Data are for the movement to the central target, and from a single start position (0°). δ is the difference between mean measures for each target ($+45°$ target minus $-45°$ target).

	Follow-through			Planning only			No motor imagery			Motor imagery			Motor imagery no fixation		
Measure	δ	$F_{1,7}$	p	δ	$F_{1,7}$	p	δ	$F_{1,15}$	p	δ	$F_{1,15}$	p	δ	$F_{1,7}$	p
Lateral deviation (cm)	-0.26	0.49	0.507	-0.37	0.85	0.387	-0.12	0.93	0.350	-0.27	2.96	0.106	-0.52	3.54	0.102
Path length (cm)	-0.01	0.00	0.953	-0.45	4.76	0.065	-0.01	0.02	0.901	-0.13	4.72	0.046	0.11	0.96	0.361
Duration (s)	-0.01	0.06	0.807	-0.03	0.56	0.478	-0.00	0.55	0.472	-0.01	1.06	0.319	0.01	0.14	0.724
Peak Speed (cm/s)	-0.8	0.69	0.434	-0.6	0.15	0.711	-1.0	2.16	0.163	-0.8	2.12	0.166	0.1	0.02	0.890

direction, they show substantial learning for identical movements. Critically, the only difference between these two conditions is motor imagery. This suggests that the act of imagining different future movements, even though subjects know they will not be performed, allows two motor memories to develop for the same physical state of the limb. In contrast to previous studies of mental practice, here imagery is not a mental rehearsal of the skill itself. That is, all subjects actually make the initial movement in the field, but the mental imagery is of a future movement (the follow-through) which is separate from the skill itself. This suggests that knowing that you will imagine a subsequent movement changes the planning of the entire motor sequence so that the movement and motor imagery may be planned together prior to initiation. This supports a distinct role for mental imagery in the ability to learn novel skills.

Many studies have suggested that practicing a physical skill through motor imagery can result in improvement when subsequently performing the skill (Driskell et al., 1994; Gentili et al., 2010; Gentili and Papaxanthis, 2015; Gentili et al., 2006). Traditional theories consider that such motor imagery acts as a simulator (Grush, 2004; Jeannerod, 2001), whereby imagery can improve performance by using a forward model to predict the consequences of non-executed actions (Gentili et al., 2010). That is, a forward model allows a subject to try out different sequences of commands and compare the consequences, or to adapt a controller from the mentally simulated movement with the ensuing imagined error. The value of such a mechanism relies on the notion that, in general, forward models are easier to learn than controllers, as the desired output and the movement outcome can be compared to train a forward model during real action. In contrast the signal that is required to train a controller, that is the error in motor command, is not readily available (Flanagan et al., 2003). Crucially, these studies of motor imagery consider the effects of mentally rehearsing the skill that is to be learned and typically compare learning under actual performance to either no practice or mental practice of the skill. Our study shows that subjects are able to learn two opposing skills, not by imagining the skills themselves, but by pairing each real execution of a perturbed physical movement with subsequent motor imagery that differs for each perturbation.

We have previously suggested that the key to representing multiple motor memories is to have each associated with a different neural state, rather than physical state of the body (Sheahan et al., 2016). In this view, the interference seen in the no-imagery control group is due to repeatedly experiencing the same neural states for each reach to the central target. After each trial in an opposing field, the motor system will link these neural states to changes in the motor command, but over time these opposing adjustments cancel out, leading to no learning. Contexts which separate the neural states for the reach to the central target should allow learning by expanding the representation of the physical state to different neural states. This would then allow the same physical movement to be associated with different motor commands.

Taken together with previous results, our study suggests that distinct motor imagery and distinct motor planning can both lead to different neural states that can be used to form and retrieve different motor memories. However, this does not mean that motor planning and motor imagery are identical. Although both lead to equal amount of learning, our data suggests only partial overlap between them as we observed incomplete transfer of learning from motor imagery to motor execution.

One way to create different neural states for the same physical state, is to change the context of each movement by making the movement to the central target part of a larger motor sequence. For example, the movement in the force field to the central target could have a different movement before (Howard et al., 2012) or after it (Howard et al., 2015; Sheahan et al., 2016), enabling concurrent adaptation to force fields that would normally interfere. Alternatively, two recent studies have shown that adaptation to opposing force fields for spatially separate targets can be achieved for the same kinematic states, if visual feedback when reaching to each target is distinct. This maps the same kinematic states to different visual locations, producing different inferred states of the limb (Hirashima and Nozaki, 2012; Howard et al., 2013). Therefore, neural states that reflect different desired states of the limb (e.g. hitting spatially separated targets) or different motor plans (e.g. mappings of desired states to limb dynamics), can map the same physical states to distinct motor commands. In the dynamical systems perspective of motor cortex, planning sets an initial neural state, and execution arises from the subsequent evolution of the intrinsic neural dynamics (Churchland et al., 2012, 2006c; Shenoy et al., 2013). Therefore, planning the same kinematic trajectory (movement to the central target) as part of a larger motor sequence will lead to a different initial neural state and a different subsequent neural trajectory. We have previously shown that planning different future movements, but aborting the plans before execution, allows learning of different force-fields over the same physical states. Here our results show that even when subjects know that they will not follow-through, motor imagery of a follow-through leads to the ability to learn opposing fields. This suggests that imagining different future movements may lead to distinct neural states from the start of the movement. Our hypothesis is consistent with recent electrophysiological work in non-human primates. Recently, Vyas et al. (2018) demonstrated that when monkeys used a brain-machine interface (BMI) to covertly rehearse cursor reaching movements, they adapted their cursor movements to visuomotor rotations, and moreover this adaptation transferred reliably but incompletely to overt arm reaching. Futhermore, the initial neural states for each centre-out BMI-controlled cursor movement closely resembled the initial neural states for the corresponding physical reaches. This consistency in neural dynamics between BMI-controlled and overt movement preparation is comparable to the learning and transfer observed here in humans instructed to imagine moving. Considering that similar motor cortical dynamical features are seen in humans and non-human primates (Pandarinath et al., 2015), this suggests that human motor imagery may evoke similar preparatory neural states to physical movement. In addition, human neuroimaging and electrocorticography studies have shown similar motor-related activity when imagining and executing movements (Dechent et al., 2004; Hardwick et al., 2017a; Hétu et al., 2013; Miller et al., 2010; Mokienko et al., 2013) and similar effects on corticospinal excitability (Lebon et al., 2018; Ruffino et al., 2017).

Our results demonstrate a complementary function for motor imagery. That is, in addition to its potential use as a simulator for possible actions, motor imagery can also engage distinct motor memories when preparing for the same physical movement. We show that mentally imaging a follow-through movement can separate motor memories as well as actually performing or planning a follow-through (Figure 3.4B). Moreover, such learning under mental imagery has significant transfer to full follow-through movements that are planned and then executed, as indicated by our measures of force adaptation on full follow-through channel trials. This suggests two features of motor imagery. First, that preparatory neural activity may be different when preparing to make the same movement but imagining different subsequent movements. Second, the generalization of this learning to physical action suggests that the neural states evoked when preparing for an imagined movement are similar to the states for the corresponding planned and executed movement.

The link between imagined and executed movement is supported by the similar chronometrics of the two. For example, imagined movements are known to have similar durations to executed movements (Decety, 1996; Decety et al., 1989; Papaxanthis et al., 2002; Sirigu et al., 1996) and show a speed-accuracy trade-off (Bakker et al., 2007; Cerritelli et al., 2000; Decety, 1996; Decety and Jeannerod, 1995; Sirigu et al., 1996). While the participants in our study demonstrated similar chronometrics for imagined and executed movements, the absolute difference between the time spent imagining and executing follow-throughs was uncorrelated with final adaptation. The amount of learning seen for each subject was also uncorrelated with performance on the MIQ-RS motor imagery questionnaire, used for assessing imagery ability (Gregg et al., 2010). However, a point to point movement is almost the simplest movement one can make and may well be simple to imagine as reflected in the relatively high mean scores (all above 3.9 out of 7, Figure 3.5A and B).

It is still an open question as to what differences in neural state are necessary for the learning seen in our study. For example, it might require different activity in the same neural circuits or that different neural circuits are active. Recent studies of neural coding in motor cortex have emphasized its operation as a dynamical system in which planning involves setting the initial neural state and execution involves allowing the transitory dynamics to evolve from this state (Ames et al., 2014; Churchland et al., 2012; Pandarinath et al., 2015). In this framework, our results would be accounted for by the same circuit but with different activity for each imagined movement. However, future work will be required to fully resolve how motor imagery leads to separate motor memories.

In summary, we show that simply imagining different future movements can enable the learning and expression of multiple motor skills executed over the same physical states. Our results suggest a new role for imagining in the representation of movement: to engage distinct motor memories for different future actions.

Chapter 4

Planning and contextual decay

Current views of motor adaptation suggest that both learning and decay depend on the context of the movement. Context is thought to tag different motor memories for learning and retrieval, such that when the brain experiences an error, it updates motor commands by effecting the action that was planned in that context. However, as motor memory decay occurs in the absence of errors, how is context captured during de-adaptation? We hypothesized that, like adaptation, motor memory decay derives its context-dependence by acting on the planned motor commands, but that unlike adaptation, this occurs independently of errors. Here we adapt participants to oppositely directed perturbing dynamics which are present for just the second movement in a short motor sequence. Therefore, on trials in which participants plan and initiate the sequence, but stop prior to execution of the adapted states, the effects of planning and executing movements in different contexts on decay are separated. Our results demonstrate direct evidence against our hypothesis. We show that while executing the adapted movement results in a strong contextual decay effect, just planning and initiating the same movement does not. We further show that with execution, context-dependent decay generalises across two motor memories for oppositely directed perturbations, such that de-adaptation of one can facilitate the expression of the other. Together this suggests a novel disassociation between the computations involved in motor memory acquisition and decay.

4.1 Introduction

Human motor control requires adaptation of motor commands to changes in environments, tasks and the dynamics of our bodies. With each experience of a movement error, the brain adjusts behaviour to compensate and alters the motor commands generated on the next movement. This learning accumulates to create a motor memory that can persist for days (Criscimagna-Hemminger and Shadmehr, 2008; Joiner and Smith, 2008) or even months (Shadmehr and Holcomb, 1997). However, in theory, changes to motor commands may often be required only transiently, such as when altering a tennis stroke when playing on a particularly windy day. Persistent adaptation of the stroke under these conditions would be inappropriate for the ensuing breezeless days, while a better policy may be to create small adjustments which are temporary so that with time, the motor command reverts to its previous form. In adaptation settings such as these, many studies have observed comparable behaviour in humans. That is with time, and in the absence of errors, recently adapted motor memories slowly revert back to baseline (Cohen et al., 2004; Galea et al., 2011; Kassardjian, 2005; Kitago et al., 2013; Scheidt et al., 2000; Shmuelof et al., 2012; Smith et al., 2006; Vaswani and Shadmehr, 2013; Vaswani et al., 2015).

Classic studies of motor learning have examined such adaptation and de-adaptation by asking humans to reach under a varying dynamic force field (Shadmehr and Mussa-Ivaldi, 1994; Thoroughman and Shadmehr, 2000) or visuomotor perturbation (Krakauer et al., 2005, 2000; Mazzoni and Krakauer, 2006). For both types of perturbation, adaptation and its error-sensitivity has been studied in considerable detail. However, behaviour that reverts to baseline is often simply cast as passive exponential decay—a process operating independently of errors, which forgets some fraction of the previous motor state with each successive trial (Hosseini et al., 2017; Ingram et al., 2013; Lee and Schweighofer, 2009; Smith et al., 2006). This formalism of a de-adaptation process predicts phenomena such as incomplete adaptation to perturbations (Krakauer et al., 2006, 2000; Smith et al., 2006; Van Der Kooij et al., 2015), but fails to account for the distinct differences in de-adapation rate between the multitude of possible zero-error conditions, such as the when movements are clamped to provide perfect performance feedback (Scheidt et al., 2000), or in the absence of movement but with the passage of time (Kitago et al., 2013).

Recent studies suggest that decay is context-dependent, acting as a regulariser for learning that helps to minimise motor effort (Ingram et al., 2013; Takiyama, 2015). In this framework, these distinct rates of unlearning for different zero-error conditions may emerge as contextual effects. However, it remains unclear what constitutes a distinct context for decay, and which aspects of control drive this de-adaptation process. As adaptation has been shown to centre updates on the planned action, rather than the physically executed states (see Chapter 2, and (Day et al., 2016; Hirashima and Nozaki, 2012; McDougle et al., 2017; Schween et al., 2018; Sheahan et al., 2016), it is possible that de-adaptation may also derive its context-dependence by acting on the planned motor commands, independently of error.

To test this, here we ask whether it is the planning and initiation, or execution of different movements that is required to evoke context-dependent de-adaptation. We concurrently adapt participants to two oppositely directed perturbations, each associated with a distinct lead-in movement, and subsequently assess how decay depends on context in three zero-error conditions: 1) when the adapted motor commands are planned and executed with channel trials, 2) when they are planned and initiated but the adapted movement after the lead-in is not executed, and 3) when no movements are planned or executed so that adaptation decays with time alone. We subsequently fit a state-space model of trial-by-trial decay and show that motor memory de-adaptation is entirely independent of context, unless the adapted sensorimotor states are physically executed. This suggests a disassociation between the computations involved in motor memory acquisition and decay, lending evidence to a recent theory that unlike adaptation, motor memory decay may be model-free (Kitago et al., 2013). Finally, the data suggests that the context-dependent decay that occurs with execution can either increase or decrease the rate of motor memory de-adaptation relative to temporal decay, and this depends on the context of execution.

4.2 Behavioural methods

A total of 20 subjects with no known neurological disorders, provided informed written consent and participated in two experiments. Data from 15 out of 20 of these subjects (12 female, 23.9 ± 4.9 years, mean ± SD) were included in the analysis (see exclusion criteria below). All participants were right handed according to the Edinburgh handedness inventory (Oldfield, 1971) and were naive to the purpose of the experiment. The protocol was approved by the University of Cambridge Psychology Research Ethics Committee, and all experiments were performed in accordance with these guidelines and regulations.

Experiments were performed using the vBOT planar robotic manipulandum described in section 1.3. Participants received continuous visual feedback of their hand position from a cursor, as described in section 2.2.

At the start of a trial a start location and a central and secondary target were displayed (Figure 4.1). The central target (grey 1.25 cm radius disk) was located approximately 30 cm below the eyes and 30 cm in front of the chest. The start location could be in one of two possible locations (grey 1.25cm radius disk) 10 cm proximal to the central target at either at either $-45°$ or $+45°$. The secondary target (yellow 1.25 cm radius disk) was 12 cm directly in front of the central target). Subjects positioned their hand at the start location and after a delay period of 300 ms, a tone cued participants to initiate their movement. Participants reached from the start location to the central target (a $+45°$ or $-45°$ lead-in movement relative to the line connecting the central and secondary targets). Subjects had to remain within the central target for between 25 and 250 ms with a velocity less than 8 cm/s, before making a second reach to the secondary target, as these dwell times have previously been shown to enable concurrent field learning with contextual lead-in movements (Howard et al., 2012). During the movement from the central target to the secondary target, the robot either generated no force (null field trials), a velocity-dependent force (exposure trials) or a simulated spring constraining the hand to a straight line path to the target (channel trials). The movement from the start location to the central target was always made in a null field. For movement durations from the central target to the secondary target between 200 and 350 ms, a ‘correct speed’ message was displayed, otherwise a ‘too slow’ or ‘too fast’ message was displayed.

In order to separate the effects of planning versus execution on the contextual de-adaptation of motor memories, on some trials (planning-only trials) the secondary target disappeared when the hand had moved 6 cm from the starting location and participants had to stop at the central target. Therefore on these trials participants planned, but did not execute the secondary movement. On planning-only trials, the secondary target disappeared on average 350 ± 21 ms after the cue to move and 127 ± 3 ms after movement onset, mean ± s.e. As these trials were identical to the lead-in trials until the secondary target disappeared, subjects were encouraged to plan the full movement sequence on all trials.

On exposure trials the velocity-dependent curl force field was implemented as in Chapters 2 and 3. The force field direction (clockwise or counterclockwise) was determined by the start location, i.e. the direction of the lead-in ($\pm 45°$, Figure 4.1). Therefore, the lead-in direction constituted a contextual cue which could be used to adapt to each force-field (Howard et al., 2012). The association between the field direction and lead-in direction was counterbalanced across the subjects. Channel trials were used to measure feed-forward adaptation as in Chapters 2 and 3 (Milner and Franklin, 2005; Scheidt et al., 2000).

If subjects moved before the audio cue, took longer than 1.5 s to complete the movement, or took longer than 1.0 s to respond to the audio cue, a mistrial was triggered and subjects were required to repeat the trial. Before the experiment subjects were given 40 trials of familiarization in a null field. Rest breaks (1.5 min) were provided approximately every 175 trials, with a longer rest break available in the middle of the experiment if required.

We classified planning-only trials as overshoot mistrials if subjects moved past the central target by more than 3 cm. On these trials, subjects received a “moved too far” error message.

4.2.1 Concurrent adaptation

Subjects performed blocks of trials. Short blocks consisted of 10 exposure (or null) trials, 2 channel trials and 2 planning-only trials. Long blocks consisted of 26 exposure trials, 2 channel trials and 12 planning-only trials. For both blocks the trials were balanced across the two start locations (and therefore across the two force-field directions when applied). The order of trials within a block was pseudo-random.

Subjects first performed a pre-exposure phase of 6 short blocks with null fields. The exposure phase then consisted of a combination of 40 short blocks (400 exposure trials) followed by 16 long blocks (416 exposure trials). Long blocks were used in the later phase of the exposure to incorporate a higher percentage of planning-only trials, before moving into the probe phase. We did this in order to ensure subjects were well-practiced at stopping at the central target on planning-only trials without overshooting. We anticipated that by the end of the exposure phase, participants would have developed two different motor memories (one for each force-field). We subsequently examined how these adapted motor memories de-adapted back towards baseline.

4.2.2 Inducing context-dependent decay with probe blocks

To quantify motor memory de-adaptation, we used *probe blocks* of 14 trials. The first and last two trials of each probe block were channel trials on the movement to the secondary target to

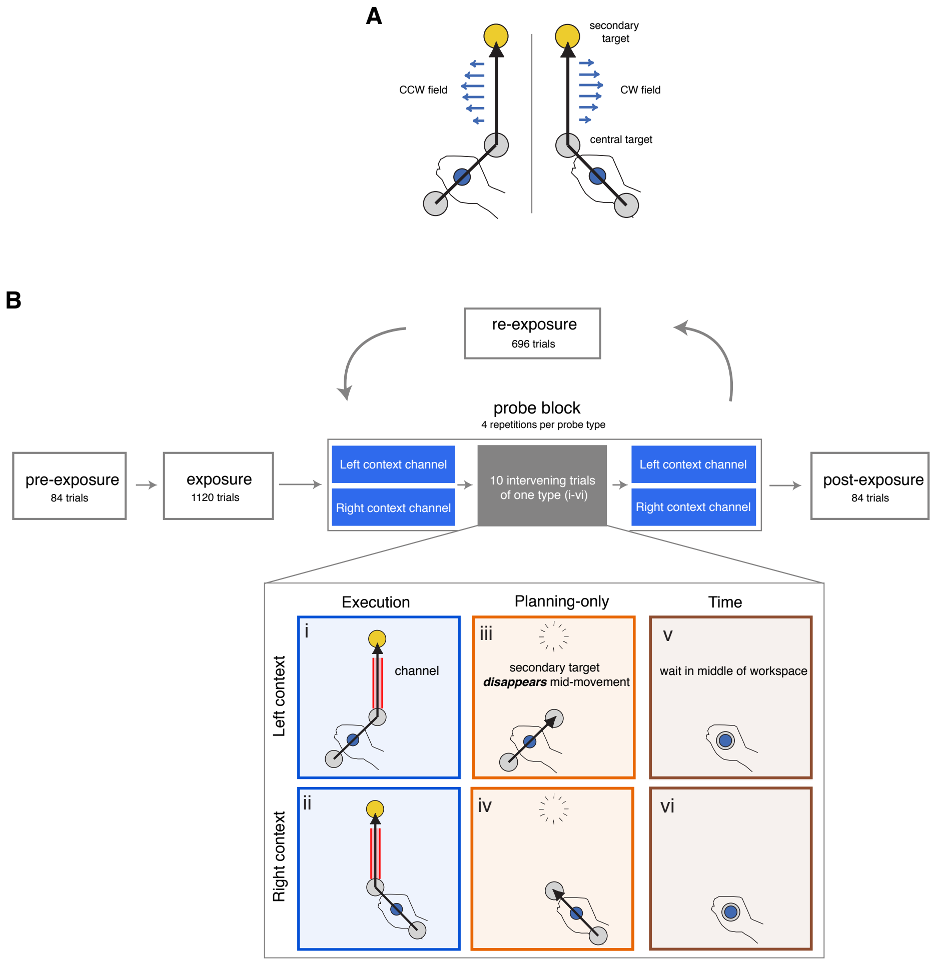

Fig. 4.1 **Experimental paradigm to isolate how planning and execution of lead-in movements affects de-adaptation in different contexts.** A) Participants made an initial movement from a starting location (bottom gray circle) to a central target (middle gray circle), and then immediately moved to a secondary target (yellow circle). On exposure trials, a velocity-dependent curl force field (force vectors shown as blue arrows for a typical straight line movement to the secondary target) was applied during this second movement, and the field direction, clockwise (CW) or counter-clockwise (CCW), was determined by the start location (either +45° southeast or -45° southwest of the primary target). Note that the secondary movement was over the same space for both lead in and only shown separately here for clarity. B) In the probe and re-exposure phase, we tested how performing probe blocks containing different trial types affected de-adaptation of the two adapted motor memories. Each probe block began and ended with a channel trial in each context (a left and right lead-in). We assessed de-adaptation under six different types of intervening probe trials (i-vi). Participants performed one of the six trial types for 8-10 trials and we tested the level of adaptation before and after each block to measure de-adaptation. Participants were then re-exposed to force-field perturbations to restore their adaptation level prior to the next de-adaptation block, in which another trial type was tested. In the planning-only probe blocks we included in the intervening trials two intermixed channel trials which were made in the same context, to encourage planning of full two-part movements. We also included these in the wait time probe blocks to control for their effect on net de-adaptation.

assess the level of adaptation for each of the two contexts (±45° lead-ins in a balanced order across repetitions). The intervening 10 trials consisted of one of 6 different probe types: i) 10 channel trials in the left context, ii) 10 channel trials in the right context, iii) 8 planning-only trials and 2 channel trials both in the left context, iv) 8 planning-only trials and 2 channel trials both in the right context, v) 8 trials in which subjects waited passively midway between the start locations and 2 channel trials in the left context vi) 8 trials in which subjects waited midway between the start locations and 2 channel trials in the right context (Figure 4.1). The two channel trials were included so as to encourage planning of full movements in the planning-only probe blocks.

The wait probe blocks were included to contrast the effects of intervening trials and time, on de-adaptation. On wait 'trials' the subject's hand position was maintained midway between the two start positions for the average duration of the previously executed trials. No targets or auditory cues were made between wait time trials. The two channel trials were included in wait probe blocks to match the planning-only probe blocks. These conditions allowed us to assess how de-adaptation depends on context (same or different) and on planning or execution.

Therefore, a set of intervening trials was either (primarily) channel trials, planning-only trials, or wait time trials, for each of the two start locations. On planning-only trials we increased the duration of the inter-trial interval so that the total duration of each planning-only or wait time trial was equal to the average duration of a full lead-in trial. This enabled us to isolate the effect of trial type from that of time.

Each probe block therefore consisted of a total of 43% channel trials, a similar ratio to the 33% channel trials we used previously in a follow-through task in which planning alone led to learning of opposing force fields (Sheahan et al., 2016).

After each probe block there was a short re-exposure period of between 26 and 32 exposure trials. We probed de-adaptation using 4 repetitions of each of these 6 conditions (336 de-adaptation trials plus 696 re-exposure trials) with each condition presented in a pseudorandom order between each rest break. Finally a post-exposure phase of 6 blocks (60 null trials) was performed.

4.2.3 Data analysis

Assessments of learning

We assessed learning using two measures across the pre-exposure and exposure phases.

On channel trials we measured percent adaptation as the slope of the regression of the time course of the force that participants produced into the channel wall against the ideal force profile that would fully compensate for the field. To do this we extracted a 400 ms (or the maximum available) window of data centred on the time of peak velocity and calculated the force generated against the channel. We used the velocity along the channel to predict the force the vBOT would have applied on an exposure trial. We performed regression (with zero intercept) on these times series and expressed the slope as a percentage (slope of 1 = 100%), termed adaptation, as in Chapters 2 and 3. In addition, on null and exposure trials, we calculated the maximum perpendicular error (MPE) as in previous chapters.

We averaged adaptation and MPE separately for each participant within a block. We evaluated the difference for each measure between the average of the first 5 short exposure blocks and the final 3 long exposure blocks using Wilcoxon signed rank tests across subjects, due to violations of normality on some measures.

To display hand paths (Figure 4.2), we extracted position data from when the hand left the central target until it entered the secondary target position. Each path was then linearly interpolated (x and y separately) so as to sample 1000 points equally spaced in time. For each subject, we generated a mean path by averaging the sample paths over trials of interest. To generate a path for a group we calculated the average (and s.e.) of the subjects' paths and plot the mean with shading showing ± s.e.

Assessments of decay

To examine how contextual de-adaptation depends on planning, execution and time, we evaluated de-adaptation as the difference in adaptation for the left and right lead-in channel trials before and after the intervening trials of each type. That is, because one channel trial for each lead-in start location was performed both at the start and end of every probe block, a single probe block provided two pre-post measures of how de-adaptation depended on each context (same or different), for the particular type of intervening trials assessed (planning, execution, or time). For example, a set of channel trials originating at the left start location provided a measure of de-adaptation for the ‘same context, execution’ condition when the pre-post adaptation levels for the left start location were evaluated, as well as a measure of de-adaptation for the ‘different context, execution’ condition when the pre-post right start location was evaluated. We averaged the pre-post difference in adaptation across all included probe block repetitions for each participant and probe type, and then averaged across participants.

As some measures of de-adaptation were slightly non-normal, we performed Wilcoxon signed rank tests to evaluate de-adaptation within each condition. To compare across conditions we first performed a Friedman test of de-adaptation (pre-post difference) across all probe conditions (6 levels). We then investigated de-adaptation differences post-hoc for specific pairs of conditions using Wilcoxon signed rank tests.

We took the decay duration of a probe block to be the time from the end of the first two channel trials, to the start of the final two channels, and compared the decay duration of each probe block type (execution, planning-only or wait) collapsed across both contexts using a Friedman test with 3 levels (one for each probe type).

Exclusion criteria

To avoid conflating de-adaptation from executing overshoot mistrials with that of planning different movements, we analysed only probe blocks in which no planning-only trials overshot. This resulted in planning-only probe block data from 15 out of 20 subjects remaining for analysis in the final dataset. As our primary aim was to compare de-adaptation under planning with that of execution, we therefore excluded all data from the 5 subjects who did not manage to complete any planning-only probe blocks without overshoot (total of 48 out of 120 planning-only block repetitions included for the remaining 15 subjects). Of the remaining 15 participants, they overshot the central target at least once on an average of 60.0 ± 5.6% out of the 8 planning only probe blocks (range 25.0 - 87.5%) and these probes blocks were excluded. Across subjects, the overshoot over the 8 planning-only blocks occurred at an approximately constant rate (mean of 10% of planning-only trials per block) suggesting that subjects continued to plan movements to the secondary target across the experiment.

Non-parametric tests were performed in cases where Shapiro-Wilk tests yielded evidence against the data being normally distributed. Statistical significance was generally considered at $p < 0.05$. When performing posthoc comparisons of de-adaptation between conditions, we used the Bonferroni-corrected α threshold of $p < 0.0055$ to take into account all $3\binom{3}{2}$ possible pairwise comparisons. That is, pairwise comparisons for the two different contexts within a probe type, and pairwise comparisons across probe types within a single context. Similarly, when performing pairwise comparisons of GLM decay rates, we used the Bonferroni-corrected significance threshold of $p < 0.0083$ (6 comparisons), as there was just a single decay rate for time.

4.3 Modeling motor memory decay

In order to assess how de-adaptation depends on context (same or different), planning, execution and time, we assessed how the rate of de-adaptation differed as a function of intervening trial type within each probe block. State-space models of motor learning typically treat de-adaptation as a fractional loss of the previous adaptive state with each successive trial (Hosseini et al., 2017; Ingram et al., 2013; Lee and Schweighofer, 2009; Smith et al., 2006). The trial-by-trial evolution of adaptive state is therefore modeled as

$$x_{t+1} = \alpha x_t + \eta e_t \tag{4.1}$$

where x_t is the *adaptive state* of a motor memory on *trial* $t \in 0, 1, ..., T$. In practice, this adaptive state is measured by proxy on channel trials (see section 4.2.3 for the calculation of adaptation). In all of our conditions, *performance error* e can be approximated to zero, as in channel trials, movements are executed straight to the target, while on planning-only trials and wait trials, the adapted portion of the movement is not executed and so no performance error accrues. The two parameters which determine the adaptive state are the learning rate η, and the retention factor α. Here, we will instead call α the *decay rate*, due to the absence of performance errors in our test conditions.

4.3.1 Capturing context in a model of decay

We modeled de-adaptation in our experiment using a similar state-space model in which x_t corresponds to the adaptive state for a particular direction of lead-in. Consider the case of a decaying motor memory for a leftwards lead-in. The motor memory for a leftwards lead-in de-adapts according to whether the experienced *trial type* j, was i) executed in the same context as the motor memory being updated (i.e. was a leftwards lead-in), ii) executed in a different context (rightwards lead-in), iii) planned in the same context (leftwards), iv) planned in a different context (rightwards), or v) a 'wait' trial which resulted in passive temporal decay. Therefore we defined decay rate parameters α_j, for the $j \in 1,...,5$ trial types. Therefore, in our model the dynamics of a single motor memory evolves according to

$$x_{t+1} = \alpha_{j_t} x_t \tag{4.2}$$

Considering a single step forward in a trial sequence of arbitrary trial types, we see that within our model, de-adaptation operates recursively

$$x_{t+2} = \alpha_{j_{t+1}} (\alpha_{j_t} x_t) \tag{4.3}$$

Thus, looking backwards over a sequence of trial indices $p \in 1,...,t$ of mixed types that have led up to trial t, we can obtain an expression for the resulting adaptive state which is independent of the ordering of each trial type j. To consider de-adaptation under a mixed sequence of trials in a probe block under different decay rates α_j, the adaptive state on trial t can be expressed as

$$x_t = x_1 \prod_{p=1}^{t-1} \alpha_{j_p} \tag{4.4}$$

where j_p is the trial type j on trial $p \in 1,...,t$ in the sequence of trials leading up to trial t. We fit this model to the channel trials from all subjects and from both contexts simultaneously.

In order to fit the decay rate parameters, Equation 4.4 can be transformed to be linear in log-space. This enables us to separate the adaptive state data x_t which we obtain from each different channel trial $t \in 1,...,14$ in a probe sequence, from the unknown decay rates, and the adaptive state at the start of the sequence x_1. For each context, the adaptive state at the start of the sequence is known only 50% of the time, that is when the first trial in the sequence is a channel trial in that context. In this case x_1 is obtained from the data. For blocks where the first trial in the sequence is a channel in the other context, x_1 constitutes a free parameter per block.

$$log(x_t) = log(x_1) + \sum_{p=1}^{t-1} log(\alpha_{j_p}) \tag{4.5}$$

One option would be to fit the unknown initial states and decay rates using simple linear regression, such that the log-transform of the data $z = log(x_t)$ is fit to solve for parameters $B_{0,\ldots,5}$. These parameters would capture the log of the initial adaptive states for each probe block, and the decay rates.

$$z = B_0 + \sum_{p=1}^{t-1} XB_{j_p} \tag{4.6}$$

However, directly fitting this function with an ordinary least-squares cost function will weight estimation errors in proportion to the log of the data, under-penalising large estimates that are far from our measures of adaptation. Instead, we can define our adaptation data $y = x_T$, a design matrix N containing the predictor trial sequences n_j for all j, and a vector β of unknown parameters, composed of α_j and the initial adaptive state, x_1. This allows us to fit to the adaptation data directly with a generalised linear model (GLM) of the form

$$log(y) = N\beta \tag{4.7}$$

We fit this GLM to the adaptation data y from channel trials in all probe blocks for all participants, for both motor memories together. For the predictor N, we used the real trial sequence performed by each subject. This enabled us to infer the adaptive state of participants on planning-only and wait time trials for which we had no adaptation data.

4.3.2 Model fitting and hypothesis testing

We fit this GLM using a gamma distribution for the response variable y and a log-link function. Channel trials showing a negative adaptive state (subjects pushing in the same direction as the force-field) were excluded from the dataset (0.4% of non-overshot probe block trials), as their log-transforms yield complex numbers. We simulated data by rolling out the actual trial sequence performed by each subject, using the best-fit GLM decay rates for the group and the initial adaptive state estimates for each subject-specific probe block. To compare our simulations to the raw data, we plot the mean ± s.e. across simulated subjects (Figure 4.3).

To assess whether the GLM fits give significantly different decay rates when participants planned movements under different contexts, we performed four planned comparisons using general linear hypothesis testing on the best-fit decay rate parameter estimates. We compared the decay rates when executing movements under different contexts (executed, same context versus executed, different context), when planning but not executing movements under different contexts (planning-only, same context, versus planning-only, different context), and compared the temporal decay rate with planning under each context (planning-only, same context versus time; planning-only, different context versus time).

4.4 Results

Participants grasped the handle of a robotic manipulandum and made reaching movements from one of two starting locations. On most trials two targets were displayed. After a 300 ms delay period, a tone cued participants to initiate a movement first to the central target, and then to a secondary target immediately after reaching the central target (Figure 4.1). While the first movement was always performed in a null field (unperturbed), during exposure trials the movement from the central target to the secondary target was made in a curl viscous force field which perturbed participants with a force perpendicular to their direction of movement (see section 4.2). The force field direction (clockwise or counterclockwise) was determined by the trial starting location, i.e. the direction of the lead-in to the central target (±45°). This starting location, and hence force field direction, was chosen pseudorandomly on each trial. The association between force-field and lead-in direction was consistent within a participant and counterbalanced across participants. These force field trials were interspersed with channel trials, in which the movement from the central target to the secondary target was confined to a simulated mechanical channel. This allowed us to measure predictive force compensation independently from factors such as co-contraction (Milner and Franklin, 2005; Scheidt et al., 2000).

4.4.1 Adaptation to opposing dynamics with contextual lead-ins

Over the course of 816 exposure trials, the contextual lead-in movements led participants to adapt to both force-fields concurrently, as has been shown previously (Howard et al., 2017, 2012; Sarwary et al., 2015). Participants reduced their maximum perpendicular kinematic error (MPE, Figure 4.2A and C, decrease of 2.49 ± 0.26 cm, $z = 3.41$, $p = 6.55e-4$), and increased the forces they generated on channel trials to approximately 80% of that required to completely compensate for the perturbations (adaptation, Figure 4.2B, increase of 57.0 ± 3.5%, $z = 3.41$, $p = 6.55e-4$). Given recent evidence for plan-centred updating in motor adaptation (Hirashima and Nozaki, 2012; McDougle et al., 2016; Schween et al., 2018; Sheahan et al., 2016), we hypothesized that trial-by-trial de-adaptation may also progress by acting on the internal model for the planned movement, even if the adapted portion of the movement is not subsequently executed.

4.4.2 Context-dependent decay with execution

In order to assess how motor memories decay as a function of planning or executing movements in different contexts, participants subsequently performed probe blocks followed by re-exposure. We assessed how a set of intervening trials, which was either (primarily) channel trials, planning-only trials, or wait time trials, affected de-adaptation for each of the two contexts.

Across all within-subjects de-adaptation conditions, a Friedman's test revealed that participants de-adapted by significantly different amounts in probe blocks as a function of the intervening trial type ($\chi^2(5) = 13.7$, $p = 0.018$). We subsequently investigated the extent of de-adaptation under each condition. As expected (Ingram et al., 2013; Kitago et al., 2013; Vaswani and Shadmehr, 2013; Vaswani et al., 2015), when participants executed probe blocks of intervening trials that were primarily channels, there was substantial de-adaptation of the motor memory corresponding to the context of the channel trial Figure 4.3A and B, blue solid, reduction of 22.6% of full force compensation, $z = 3.41$, $p = 6.55e-4$). In contrast, the motor memory for the other context decayed only marginally (Figure 4.3A, blue unfilled, reduction of 3.5% of full force compensation, $z = 2.04$, $p = 0.041$). This is despite both adapted motor memories having the same training history and levels of adaptation that were not significantly different from each other at the end of exposure phase (mean difference of 6.7 ± 4.7%, $z = 0.85$,$p = 0.394$). Motor memory de-adaptation was therefore

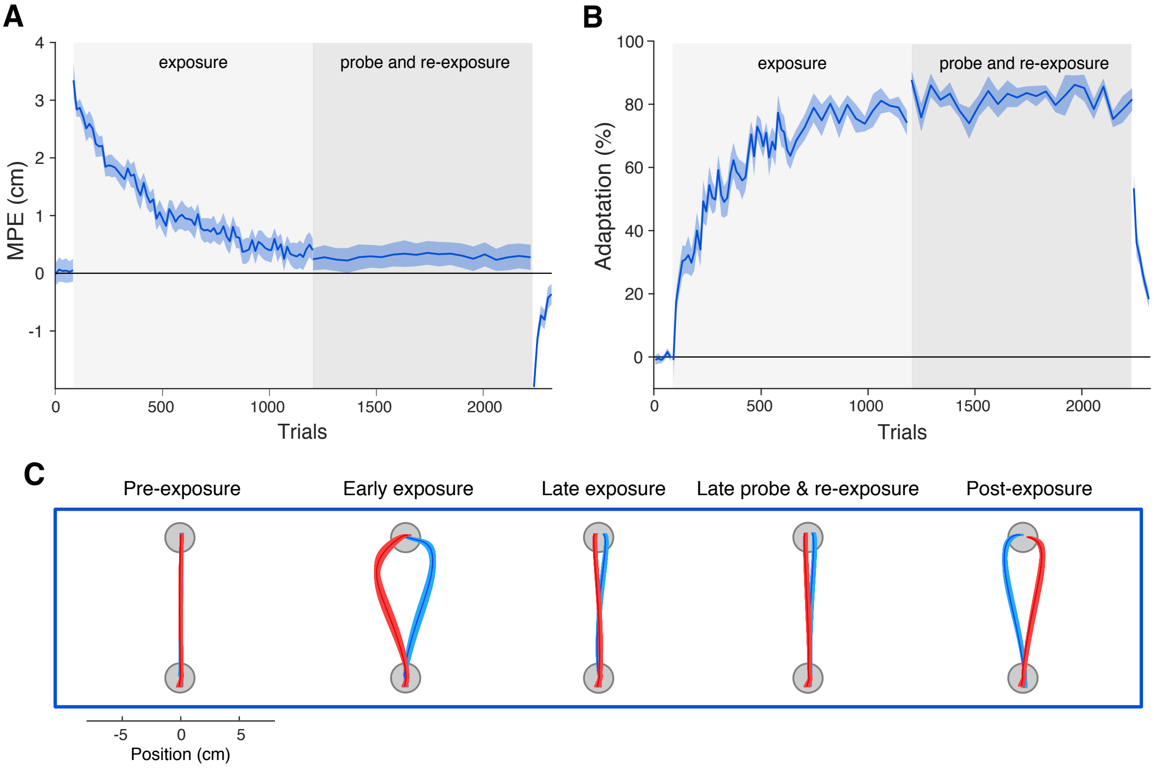

Fig. 4.2 **Concurrent learning of two force fields to subsequently assess contextual de-adaptation of each.** Pairing different lead-in movements with opposing force-fields enabled differential concurrent adaptation of two motor memories. (A) The maximum perpendicular kinematic error and (B) force compensation for n=15 participants making lead-in reaching movements which were coupled to different force-field directions. Adaptation levels remained steady throughout the probe phase due to re-exposure trials after each probe block. Data show mean ± SE across participants for pairs of blocks in the pre-exposure, exposure and post-exposure phases, and for each set of re-exposure trials in the probe phase. (C) Hand paths are shown from the central target to the secondary target for five different phases of the experiment. Paths show the mean ± SE across participants, for the first or last 20 trials (two blocks) at the start of the pre-exposure phase (pre-exposure), the start (early exposure) and end (late expsorure) of the exposure phase, the final re-exposure in the probe phase (late probe & re-exposure), and the start of the post-exposure phase (post-exposure). The colors indicate the field direction (blue for CW and red for CCW).

highly context-dependent when executing channel trials (mean difference in decay of 19.1% adaptation, $z = 3.18$, $p = 0.0015$, Bonferroni-corrected $\alpha = 0.0055$), decaying more when trials were executed in the same context as the probed motor memory and less when executed in the other context, as expected (Ingram et al., 2013).

4.4.3 Context-independent decay with planning

In contrast to when executing full movements in channel trials, when participants only planned the secondary movement, motor memories for both the same (Figure 4.3A, orange solid; reduction of 18.1% of full force compensation,$z = 2.89$, $p = 0.0038$) and different (Figure 4.3A, orange unfilled; reduction of 20.2% of full force compensation, $z = 3.41$, $p = 6.55e-4$) contexts decayed. The amount of decay did not differ with context (mean difference of -2.0%, $z = 0.28$, $p = 0.776$). This suggests that while motor memory de-adaptation depends strongly on context when adapted movements are executed, simply planning and initiating different recently adapted movements results in de-adaptation that is contextually independent. Surprisingly, when participants planned but did not execute the secondary movement for one context, the motor memory for the other context de-adapted more than if the planned movements were actually executed (Figure 4.3A, mean difference of -16.7% of full force compensation, $z = -2.78$, $p = 0.0054$) although this was marginally significant (Bonferroni-corrected $\alpha = 0.0055$).

4.4.4 Decay with time

While error-clamps (channel trials) which artificially eliminate movement errors are known to elicit de-adaptation (Ingram et al., 2013; Lago-Rodriguez and Miall, 2016; Scheidt et al., 2000; Vaswani and Shadmehr, 2013), de-adaptation can also occur simply with the passage of time (Criscimagna-Hemminger and Shadmehr, 2008; Kitago et al., 2013). On wait probe blocks participants remained still for the average time it took them to execute on full movements to the secondary target. Consequently, there was no difference in duration between execution, planning and wait probe blocks (mean duration of 20.1 s; $\chi^2(2) = 0.53$, $p = 0.766$). To match each planning-only probe, these wait time probe blocks included two channel trials executed in one of the two contexts, and these were positioned pseudo-randomly within the block. We therefore consider each wait time probe type separately, as shown in Figure 4.3A. We found that passive temporal decay blocks that included channels

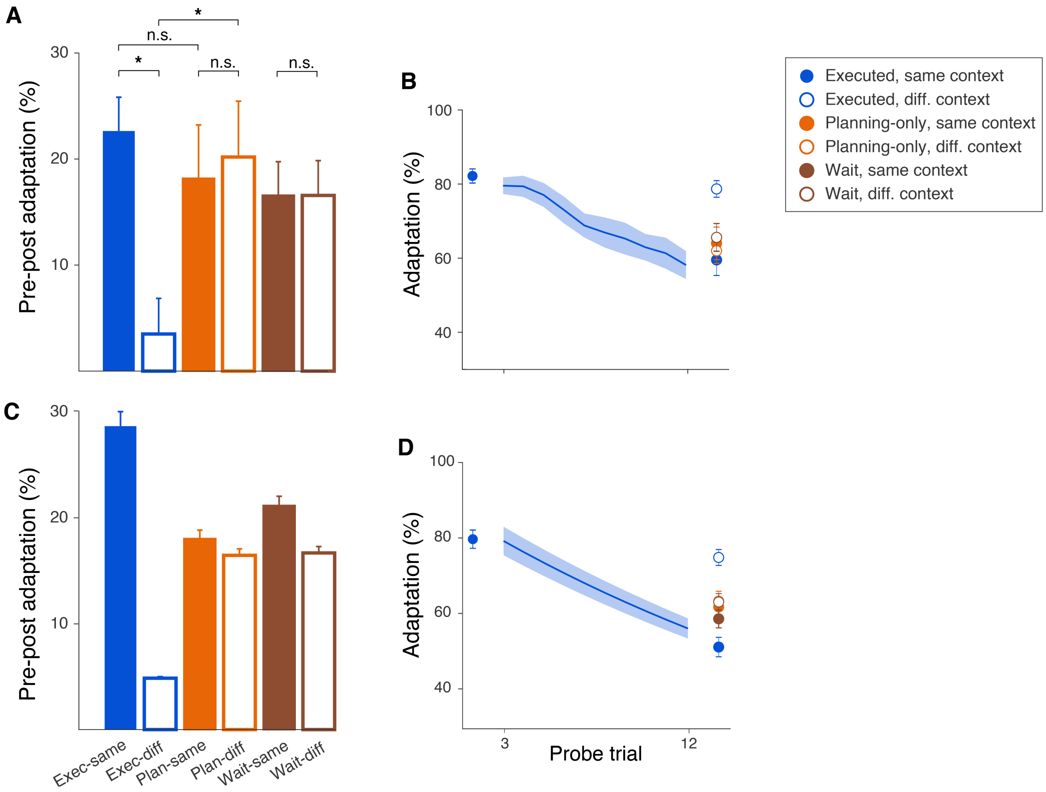

Fig. 4.3 **Motor memories de-adapted independently of context when movements were planned but not executed.** (A) De-adaptation from probe blocks of trials that were either executed lead-in channels (blue), planned lead-ins that stopped at the central target (orange), wait time trials (brown), in the same (solid) or different (unfilled) contexts as the pre-post test. De-adaptation was strongly context-dependent when lead-in movements were executed through channel trials, with the greatest de-adaptation when movements were executed in the same context as the probe. However, no difference in adaptation was seen when movements were just planned for different contexts and abruptly terminated at the central target. Data show mean ± s.e. across subjects. (B) Trial-by-trial de-adaptation within a probe block of executed channel trials. Dots show pre- and post- probe adaptation under different intervening trials. The post-probe means for each condition have been offset by the amount required to align the pre-probe adaptive states, and so these are for display purposes only. (C-D) Simulated data using best-fit parameter values from the GLM, displayed same as (A-B), showing mean ± s.e. across simulated subjects.

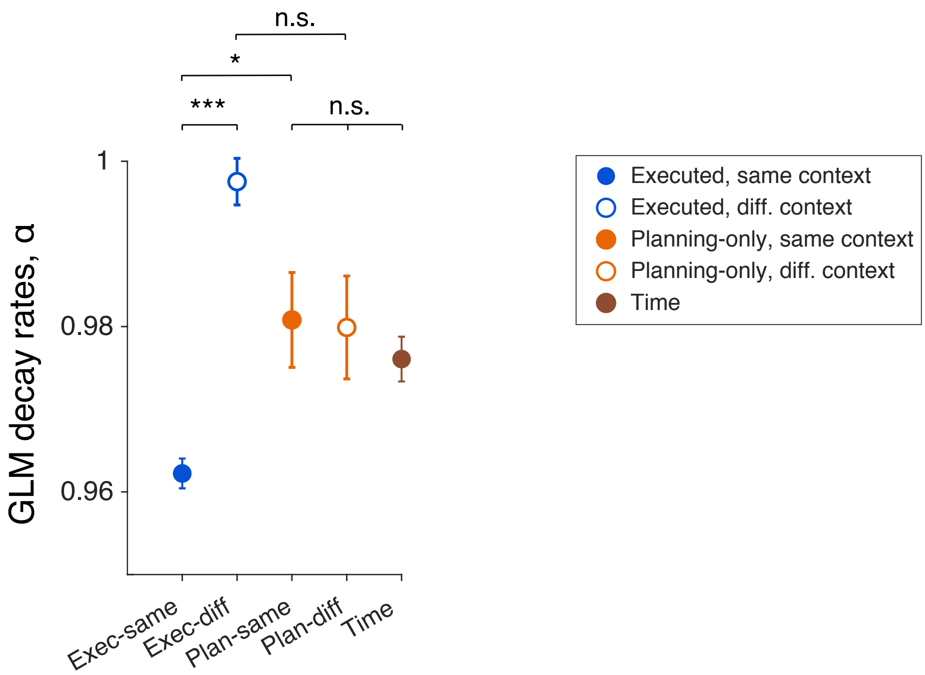

Fig. 4.4 **Best-fit decay rate parameter values for the GLM.** Each decay rate corresponds to one α_j in Equation 4.4. Figure shows mean ± s.e. of the best-fit parameter estimates.

in the same (Figure 4.3A, brown solid, reduction of 16.6% of full force compensation, $z = 3.24$, $p = 0.0012$) and different (Figure 4.3A, brown unfilled, reduction of 16.6% of full force compensation, $z = 3.41$, $p = 6.55e-4$) contexts both resulted in significant de-adaptation. This suggests, that not only was execution of the adapted states required for context-dependent de-adaptation, planning and initiating movements under different contexts had no measurable effect on de-adaptation compared to waiting alone.

After each probe block, we re-adapted participants with a short set of exposure trials under both contexts to ensure that each probe block was initiated from a similar adaptive state. Participants successfully maintained this initial adaptive state across the probe phase (Figure 4.2A, B and C).

Taken together, these results show that just planning and initiating contextual movements, even from different sensorimotor states, does not result in context-dependent de-adaptation. Instead, our behavioural data demonstrate that for de-adaptation to be context-dependent, the adapted states of a motor sequence must be executed.

4.4.5 Modeling context-dependent decay under planning, execution and time

To characterise the distinct effects of execution, planning and time on de-adaptation, we fit the trial-by-trial de-adaptation process with a state-space learning model (see section 4.3). We fit our model to the channel trials from all subjects and from both contexts simultaneously. The best fit parameters are shown in Figure 4.4E and the fit had a R^2 of 0.66.

Simulated data using best-fit parameter values are displayed in Figure 4.3C and D in the same format as (Figure 4.3 A and B. In accordance with our pre-post block measures, the model fit demonstrated significantly different decay rates for executing movements in the same context compared to when executing movements in the other context (Figure 4.4, difference in parameter estimate of 0.035, $F_{1,2384} = 103.36$, $p = 9.85e-24$, Bonferroni-corrected α of 0.0083). In contrast, the decay rate estimates when just planning movements did not differ significantly by context (Figure 4.4, difference in parameter estimate of -0.00091, $F_{1,2384} = 0.012$, $p = 0.913$), and each rate estimate was not different to the rate for passive temporal decay (Figure 4.4, same context planning versus time, difference of 0.0047, $F_{1,2384} = 0.575$, $p = 0.448$; different context planning versus time, difference of 0.0038, $F_{1,2384} = 0.331$, $p = 0.565$). This suggests that even when accounting for the inclusion of channel trials within planning-only and wait time probe blocks, simply planning and initiating different contextual movements de-adapts motor memories at a rate that does not differ significantly by context or from temporal decay. Executing channel trials did however, produce different rates of de-adaptation to when just planning the same movements. This was true when planned or executed movements were of the same context (difference in parameter estimate of 0.019, $F_{1,2384} = 9.16$, $p = 0.0025$, Bonferroni-corrected α of 0.0083) but was not significantly different when planning or executing different contexts (difference in parameter estimate of -0.018, $F_{1,2384} = 5.93$, $p = 0.015$, Bonferroni-corrected α of 0.0083).

For all of the above listed parametric tests, Shapiro-Wilk tests could not reject the null hypothesis that the compared samples were normally distributed. Non-parametric tests were used in cases of non-normal samples.

The central result of this study was that planning and initiating different contextual movements did not result in context-dependent de-adaptation, unless the adapted portion of the movement sequence was executed. Curiously, we also found that executing movements out of context reduced the amount of de-adaptation relative to any other condition, including decay with time (Figures 4.3 and 4.4). This shows that the context a movement is made under can cause motor memory de-adaptation to either increase or decrease relative to temporal decay, even when these movements are made without error.

4.5 Discussion

Different contexts can tag motor memories such that distinct skills are modified independently and made immune from interference. In motor adaptation, context is thought to achieve this tagging by affecting the motor plan, such that it is the planned motor commands that are modified with each experience of an error (Hirashima and Nozaki, 2012; McDougle et al., 2016; Schween et al., 2018; Sheahan et al., 2016). Recently, motor memory decay has also been observed to depend on context, and this context-dependence subsequently theorized as an effective mechanism to support effort minimization in learning (Ingram et al., 2013; Takiyama, 2015). However, under the prevailing belief that de-adaptation is an error-independent process, it has remained unclear what processes drive de-adaptation and how these processes capture the relevant context. Our results show that for de-adaptation, context-dependence emerges only when the adapted sensorimotor states of a motor memory are physically executed. That is, executing recently adapted movements in the same context as the de-adapting motor memory results in significantly greater de-adaptation than when executing movements in a different context. However, when identical movements are just planned and initiated in each context but not executed, this dependence on context disappears and de-adaptation is no different to passive temporal decay. We therefore demonstrate that de-adaptation requires execution of the adapted physical states to capture any dependence on context. This suggests a new distinction between the processes underlying motor memory adaptation and retention.

Several recent studies have begun to distinguish the roles of planning from execution in the modification of motor memories. Interference experiments have demonstrated that distinct internal models of opposing dynamic perturbations can be developed for the same physical state of the limb (Hirashima and Nozaki, 2012; Sheahan et al., 2016, 2018), leading to the hypothesis that it is the underlying neural, rather than physical, state that motor adaptation attaches to. Therefore by simply having distinct motor plans, different motor memories may be formed, retrieved and updated. Moreover, patterns of motor adaptation generalisation, which are thought to reflect how the brain represents what it learns, indicate results consistent with these findings. By experimentally separating the task goal, physical movement and explicit direction of aim, recent studies have shown that participants adapting to visuomotor rotations implicitly centre their adaptation on the angle of the planned movement, with adaptation generalising locally about this (Day et al., 2016; McDougle et al., 2017; Schween et al., 2018). Here, we hypothesized that motor de-adaptation, that is, the reversion of recently adapted motor behaviour back to baseline, may similarly derive its context-dependence by acting on the motor plan. We show that just planning and initiating different recently adapted movements evokes no sign of context-dependent decay. This suggests that unlike motor adaptation, which is thought to be highly model-based and cerebellar-driven, de-adaptation appears to be entirely model-free, having no dependence on context unless the adapted sensorimotor states are physically executed.

Indeed, Kitago et al. (2013) recently showed that de-adaptation of a single motor memory can operate under several different conditions (time, executed channel trials, executed movements in null dynamics, and executed movements without visual feedback) with different decay rates, and only some of these conditions lead to savings, that is faster re-learning when the perturbed dynamics are re-experienced. They hypothesized that de-adaptation that gives rise to such savings may reflect a gradual reversion to habituated movements, resulting in performance shifts back towards baseline behaviours. By examining the specificity of de-adaptation under different contexts, our results confirm that when movements are just planned, but not executed, unlearning indeed is shown to be plan-independent, or model-free, and this results in distinct amounts of de-adaptation to when the same motor sequences are executed. We also show that motor memories can also de-adapt in a way that strongly depends on context, suggesting the presence of multiple distinct de-adaptation mechanisms, as is observed in multi-rate learning models (Smith et al., 2006).

Our results suggest that when contexts change, motor adaptation and de-adaptation adjust motor commands in fundamentally different ways. While error-driven adaptation relates context to learning by updating the planned motor commands, just planning and initiating the same actions results in de-adaptation that is entirely independent of the current context. How might one reconcile these results? One possibility is that the distinct effects of planning on motor adaptation versus retention, is paralleled in the neural structures that subserve these functions. Neuroimaging studies have indicated the engagement of a distributed network of cortical-subcortical areas during skill acquisition (Diedrichsen et al., 2005; Doyon and Benali, 2005; Seidler, 2010), however different areas or processes performed within this network may make different contributions to the learning process. For example, it has long been suggested that the cerebellum is well-structured to support supervised, error-based learning (Albus, 1971; Ito, 2006; Marr, 1969), and patients with cerebellar damage exhibit marked impairments in learning during sensorimotor adaptation tasks (Criscimagna-Hemminger et al., 2010; Smith and Shadmehr, 2005). Other studies have recently suggested that different brain regions may have disassociated effects on motor learning and retention. Galea et al. (2011) showed that when anodal transcranial direct current stimulation (tDCS) was applied over primary motor cortex, the rate of adaptation to a visuomotor rotation was unaffected, however retention was markedly improved. In contrast, multiple studies have now shown that when the cerebellum is stimulated by anodal tDCS, this causes faster adaptation, but does not affect retention (Galea et al., 2011; Herzfeld et al., 2015). Moreover, consolidation is disrupted when TMS is applied to motor cortex during force-field adaptation (Hadipour-Niktarash et al., 2007).This supports the hypothesis that while model-based adaptation is posited as a (at a least partly) cerebellar function (Smith and Shadmehr, 2005; Tseng et al., 2007; Wolpert et al., 1998), unlearning, or de-adaptation, may be controlled elsewhere and by distinct mechanisms.

When interpreting our results, we make the important assumption that participants continue to plan full lead-in movements throughout each assessment of ‘planning-only’ probe blocks. While this is difficult to assess behaviourally, we have previously shown that with a similar rate of aborted planning-only trials (33% executed), as was used here in each probe block (42% executed) participants do plan full two-step sequential movements, as indicated by their concurrent adaptation to distinct perturbations (Sheahan et al., 2016). While the effect of distinct plans was not observed in de-adaptation, we expect that participants in lead-in and follow-through studies plan two-part sequential movements with a similar horizon. Here, participants adapted to both opposing force fields which were associated with different lead-in movements, and additionally demonstrated regular overshooting behaviour on planning-only trials throughout the probe phase and within probe blocks. This serves to indicate continued planning of full two-part movements from each contextually-associated starting point, and lends support to our central claim that planning and initiating recently adapted movements from distinct contextual starting points, does not on its own evoke context-dependent decay.

In summary, by isolating the roles of planning and execution in motor de-adaptation, we show that decay is entirely independent of context, unless the adapted sensorimotor states are physically executed. Our results suggest that eliminating performance errors yields distinct effects on decay under different contexts, such that de-adaptation of one motor memory can lead to increases in expression of its oppositely-adapted competitor.

Chapter 5

Planning as compression of motor commands

In previous chapters we found that planning or imagining different motor sequences fundamentally shapes the motor repertoire that is learned. In practice, goal-directed actions often display hierarchical structure: movements can be segmented into shorter, discrete components and later concatenated to give rise to fluid motor sequences. Given the importance of planning to the way we learn, what is it that determines how motor plans are segmented? Here we approach this problem by considering the brain as a resource-constrained controller. We test that hypothesis that the humans may chunk movements so as to represent them efficiently. This suggests that in trial sets containing movement components which are often repeated, a memory resource-conscious planner could exploit this redundancy by chunking plans into sub-policies that can be flexibly recombined for later use. Here we simulate normative chunking of an optimal feedback controller operating within this compression framework for three trial sets, and test these chunking predictions against human behaviour in both familiar (null field) and altered (curl field) dynamics. While our simulations suggest different optimal chunking schemes for each trial set we considered, these predictions of the hypothesis appear inconsistent with the behavioural data. Specifically, neither initial chunking over a short course of null trials, nor altered chunking after thousands of curl field trials, reflected the differences between trial sets that we predicted. Instead, chunking behaviour varied considerably across participants in all groups, but correlated with chunking and subsequent learning when environmental dynamics were altered. Together this suggests that, while chunking behaviour in short motor sequences may reflect more than simply the encoding efficiency captured in our model, motor planning in familiar environments may scaffold chunking when environment dynamics change.

5.1 Introduction

Humans perform many complex motor behaviours, such as drinking a cup of coffee, or shooting a hoop in a game of basketball. Controlling movement in compound sequential tasks such as these requires identifying the best ordering of goal/s, and structuring motor commands to reach them as efficiently as possible. Most computational theories conceive of such planning as an exhaustive simulated search over a tree of possible future states and actions that might achieve these goals. Consequently, with each additional step in the planning horizon, determining the right course of action incurs an exponentially increasing computational cost. Given the complexity of planning, and the time constraints within which real world plans must be made, how do humans manage to plan such advanced sequential actions in natural environments?

An appealing approach to reduce the cost of planning is the formation of modular representations of actions (Sutton et al., 1999). In biological planning, humans have long been theorised to break compound movements down into a series of chunks, each planned over a shorter horizon, rather than planning each interim step en route to a goal with equal consideration (Lashley, 1951). More recently, human neuroimaging work has begun to characterise the neural correlates of learned hierarchical action-values (Gershman et al., 2009) and plans in navigational settings (Balaguer et al., 2016; Javadi et al., 2017). Yet, computational theories that formalize what constitutes a ‘good’ task or environment decomposition, or predict how actions should be segmented, have only recently begun to emerge (McNamee et al., 2016; Solway et al., 2014). While evidence mounts that the brain uses hierarchies in planning, the computational principles that underlie exactly how humans structure and segment sequential actions remain unclear.

We have previously demonstrated that the movements that humans plan play a key role in motor adaptation, determining how the representations of motor memories are formed (see Chapters 2 and 3, Sheahan et al. (2016, 2018)). According to this theory that motor adaptation is plan- or neural state-specific (Day et al., 2016; Hirashima and Nozaki, 2012; McDougle et al., 2017; Sheahan et al., 2016, 2018), chunking motor plans into distinct sub-sequences may automatically segment learned representations. Therefore, the sub-goals, or chunks that are selected early in learning may have a substantial effect on the ability of participants to learn or adapt to different motor skills. Here we extend a normative metric for determining how motor plans should be chunked, in an attempt to predict planning and the subsequent ability of participants to learn distinct representations for different motor control tasks. We build on a recent hypothesis (McNamee et al., 2017a) that the brain generates motor chunks so as to minimize the complexity of representing a controller. That is, we propose that an efficient neural coding scheme will generate motor commands that are optimised for encoding their average information-theoretic description length, not just within a single motor sequence, but across an entire trial set. This predicts that in trial sets in which movement components are often repeated, the brain may exploit this redundancy by chunking plans into smaller sub-policies that reduce the complexity of planning each movement, and can also be flexibly recombined for later use.

We first generate predictions based on this hypothesis by evaluating the description lengths of control signals from an optimal feedback controller that trades off achieving target end-point states with motor effort, and which chunks with different spatio-temporal horizons. This model yields different, testable predictions regarding the chunking of movements under different sets of trials. To test the hypothesis that motor chunking exploits redundancy across a finite trial set, we examine the planning horizon of sequential movements in three different sets of trials, both under familiar, unperturbed (null field) environment dynamics, and subsequently when the dynamics of the tasks change (curl fields). Under an elemental chunking framework, movements that traverse the same physical states can be planned by 'recycling' the same plan segments trial to trial. Therefore, under the hypothesis that motor adaptation is plan-specific, when opposing force-fields are experienced over movements made with the same elemental motor plan, substantial interference will occur. In contrast, a cohesive planning scheme that couples movements across the same initial physical states to different subsequent movements (e.g. follow-throughs) may evoke different neural states for the same physical states and result in distinct motor memories that can be differentially adapted. We compare our theoretical predictions for chunking to human behaviour in both null and curl field dynamics, and subsequently to whether participants learn separate motor memories for movements that traverse the same physical states.

Varying the trial sets, we find that our normative chunking model is unable to capture empirical reaching behaviour for short, unperturbed motor sequences, or the subsequent learning behaviour that emerges when dynamics change. Instead, participants were highly variable in how they chunked movements at baseline, and this behaviour had no clear dependence on the required set of trials to be performed. Dwell times when chunking movements in familiar dynamics were maintained for over a thousand trials after the environment's dynamics had been altered, and correlated marginally with the amount of concurrent learning of opposing fields. This suggests that, while chunking behaviour may reflect more than simply the encoding efficiency proposed by our hypothesis, motor planning in familiar environments may provide a scaffold for motor chunking when environment dynamics change.

5.2 Theory

The neural circuits that control movement can be considered as a channel that transmits motor commands downstream, and can thus be studied using the principles of information theory. We extend a recent model proposed by McNamee et al. (2017a) for chunking movements, based on the hypothesis that chunks should be selected to efficiently compress motor commands[1]. That is, to minimise their information-theoretic description length. This corresponds to selecting a chunking scheme that exploits regularities in the motor task, to plan motor commands that can be encoded with less neural resource.

More formally, for discrete probabilistic signal x, taking on values in the set $A_x = \{a_1, a_2, ...a_i, ...a_I\}$ with probabilities $P(x = a_i) = p_i$, the amount of computational resources required to represent x depends on the entropy $H(x)$:

$$H(x) = \sum_i p_i \log_2 \frac{1}{p_i} \tag{5.1}$$

In our theory we will take the time series of the motor commands u over a movement as samples drawn from the distribution $P(u)$ and use this to estimate the entropy of u. Intuitively, as $H(u)$ decreases, the same amount of neural resource can be reallocated in order to better represent the less complex signal u. Figure 5.1 provides an intuition for this calculation. Four example time-series of motor commands lead to four distributions $P(u)$ of u (calculated by binning u). From these distributions, the associated entropy can be approximated. For example, if u is constant then only a single number is needed to represent it and it has low (zero) entropy. In contrast if u takes on a limited range of values or some values tend to be

---

[1] In contrast to standard minimum description length (MDL) methods and efficient neural coding approaches in the sensory domain, which typically seek the selection of a model or representation that best compresses data that is *externally* generated, here the 'data' to compress are internally generated motor commands.

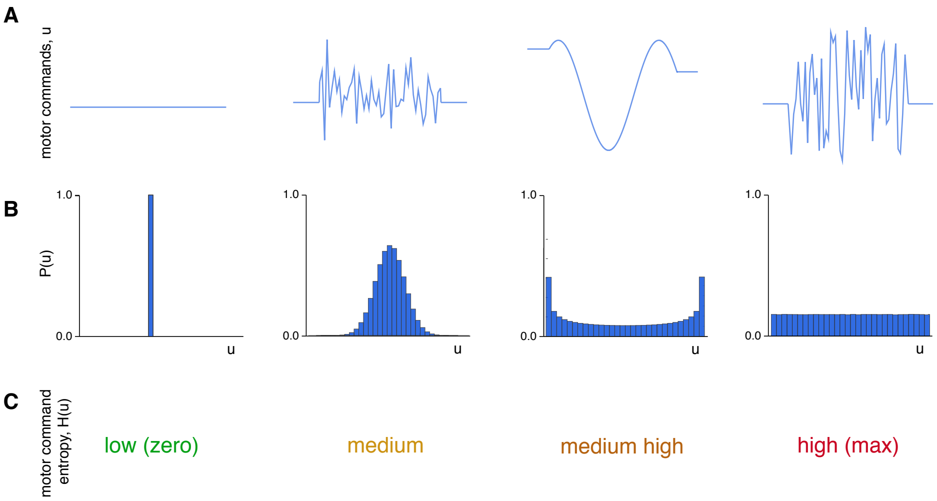

Fig. 5.1 **Schematic of how different motor command time-series have different corresponding probability density functions and associated entropy.** (A) Four example time-series of motor commands, u, illustrating (from left) constant motor commands, commands drawn randomly from a standard Gaussian distribution, commands taking the shape of a sinusoidal time-series, and command drawn randomly from a uniform distribution. (B) Histograms of the associated probability density functions, and (C) indications of the relative magnitude of the entropy associated with each distribution, ranging from zero for a delta function (left), up to maximum entropy for a uniform distribution (right).

more common then others it will tend to have slightly more entropy, but less than motor commands which take on many values with equal probability.

Although the entropy measure is agnostic with respect to the details of the neural circuit, it is a reasonable assumption that it may correlate with the number of neurons required in a population code (McNamee et al., 2017b). Thus we consider the control variable entropy, which is the expected amount of information carried in the motor control commands, to serve as a measure of the representational complexity of a motor memory.

5.2.1 Chunking optimal feedback control policies

To predict normative motor chunking, we consider voluntary arm movements to be controlled by a stochastic optimal feedback controller (Liu and Todorov, 2007; Todorov, 2005; Todorov and Jordan, 2002). Optimal feedback control (OFC) is regarded as the dominant normative theory of voluntary movement, in which the motor system deals with uncertainties in estimates of state, motor commands (Todorov and Jordan, 2002) or model dynamics (Izawa

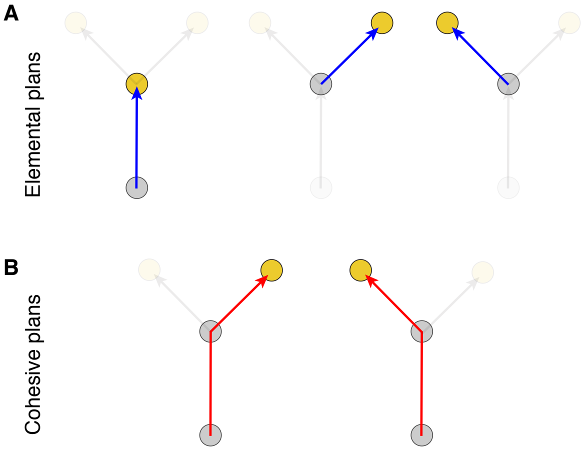

Fig. 5.2 **Follow-through movements could be decomposed into elemental or cohesive chunks].** (A) Elemental chunking of follow-through movements into discrete segments that are planned and executed separately. (B) Cohesive chunking of the same follow-through movements traverse two targets in sequence using a single plan.

et al., 2008) by making sophisticated use of online sensory feedback. In this sense, planning under OFC can be considered the optimisation of a feedback control law L_t which will be used during execution to map the estimated current state of the limb $\hat{x}_t$ at time step t of a movement to the corresponding motor command u_t.

$$u_t = L_t \hat{x}_t \tag{5.2}$$

Therefore, although the control law or policy L_t is pre-determined or planned, the optimal motor commands are evaluated online to respond intelligently to feedback-derived estimates of the current state of the limb (see Figure 1.1 in Chapter 1 for a discussion).

To determine the best policy, OFC optimises a cost function which trades off motor effort and task success, determined by the set of task goals in a given movement and their relative importance to the controller (Equation 5.6). The optimal motor commands therefore critically depend on the horizon over which the feedback policy is planned. That is, which goals are considered within the optimisation process. In compound movements consisting of multiple goals or via-points, OFC produces different control laws depending on how far into the future movements are planned. That is, one may consider all goals in a task separately, or plan to reach them all in a single optimised sweep. Planning to reach each goal with a different elemental movement requires multiple successive controllers to produce each reach. In contrast, considering all goals as part of a single motor chunk will produce a different single controller that is globally optimal. Different chunking schemes can therefore produce different motor commands, which may give rise to distinct control variable entropies. Consequently, optimising the encoding quality of motor memories may influence the chunking of sequential movements (McNamee et al., 2017a).

Here, we suggest that when encoding a set of trials, an efficient system will chunk the representation of these movements so as to minimise the complexity of encoding the motor commands across the entire set of trials. That is, different chunking leads to different sequences of motor commands (arising through the optimal feedback control law) and therefore different complexity of encoding. Here we consider the case in which movements or sub-movements often repeat from one task to another. For example, the two-part follow-through movements from Chapters 2 and 3 require motor commands which bring the hand from the same initial states, towards the same central target, before trajectories diverge. Motor commands may therefore be planned either elementally, as separate movements between successive targets (3 chunks; Figure 5.2A, or as cohesive motor sequences, that is leftwards and rightwards full follow-throughs (2 chunks; Figure 5.2B). In cases such as these, an agent can reduce the cost of representing the motor memories it needs by learning short, chunked policies that can be recycled and recomposed into different motor sequences in the future (assuming straightforward composability, with no additional costs of concatenating policies). Conversely, actively stopping and replanning movements at each sub-goal requires a greater variety of motor commands (to produce greater accelerations and decelerations) that can increase the total entropy (description length) of a motor sequence.

To compare the different ways of chunking, movements were simulated with optimal feedback control in familiar (null field) dynamic environments to find the optimal motor commands for executing three different trial sets, planned under different chunking schemes. We calculated the entropy for each trial set by concatenating the motor commands for all movements under a given chunking scheme and from this calculate the associated entropy. We propose that the chunking scheme which produces the lowest motor command entropy may be the optimal chunking.

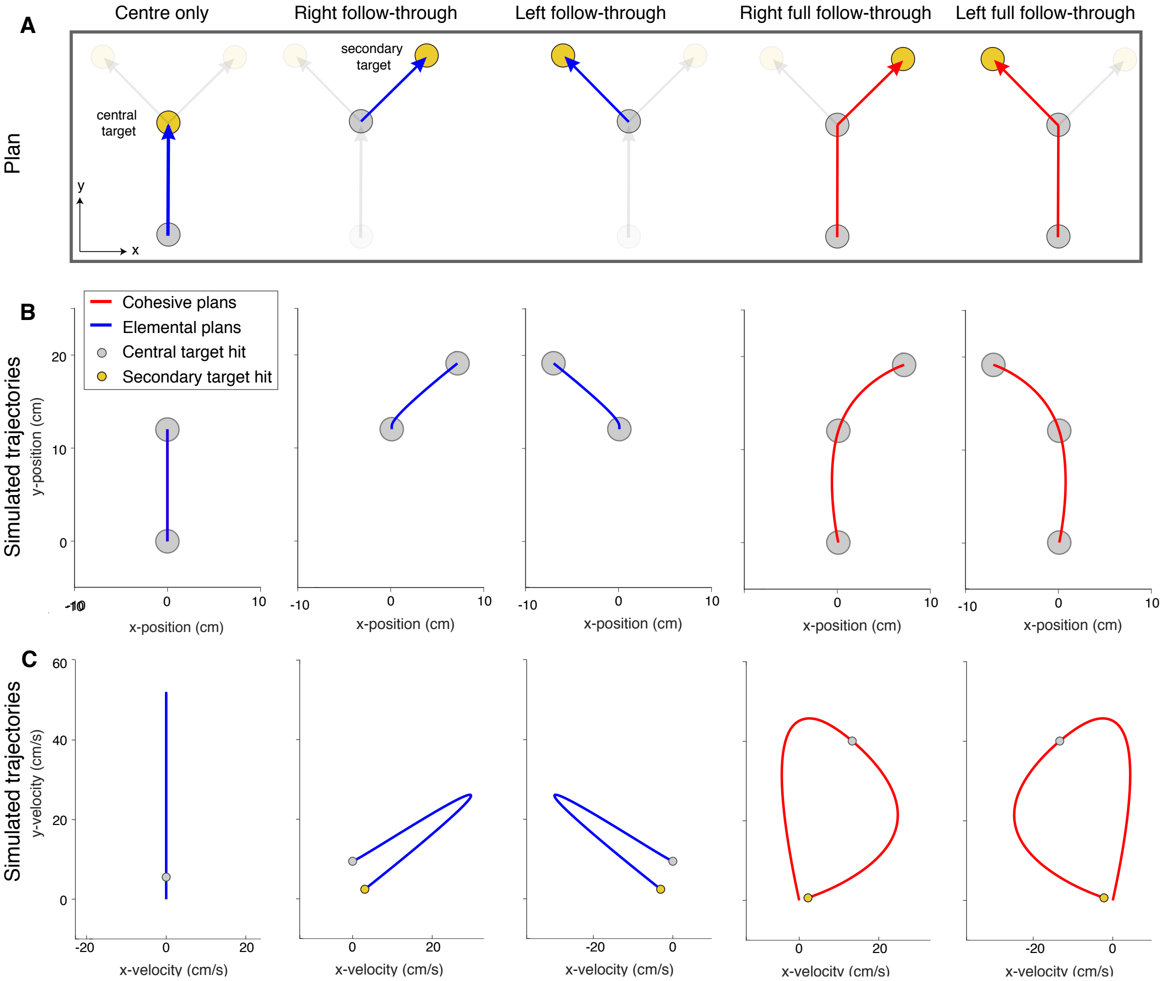

Fig. 5.3 **Optimal feedback control trajectories for elemental and cohesive chunks.** (A) Possible elemental (blue) and cohesive chunks (red). (B-C) Simulated optimal feedback control state-space trajectories (zero noise) of (B) position and (C) velocity, corresponding to the chunking in (A).

5.3 Simulations

5.3.1 Optimal feedback control policies

Optimal feedback control theory posits that when there is uncertainty in state variables or noise in the motor commands, the optimal strategy is to response intelligently to errors online through the use of a feedback control policy (see section 1.1.2 for a review). The optimal control solution has previously been derived by Todorov and Jordan (2002). We implemented an optimal feedback controller using minor modifications suggested by Liu and Todorov (2007) and obtained noisy feedback control signals under the inclusion of different task goals in the cost function (different planning horizons). To obtain the OFC-derived motor commands $u = [u_x; u_y]$, we considered the following linear dynamical system

$$\text{Dynamics}: \quad x_{t+1} = Ax_t + Bu_t + M(u_t)\varepsilon_t \tag{5.3}$$

$$M(u_t) = \begin{bmatrix} c_1 u_x(t) & c_2 u_x(t) \\ -c_2 u_y(t) & c_1 u_y(t) \end{bmatrix} \tag{5.4}$$

$$\text{Feedback}: \quad y_t = Hx_t + \omega_t \tag{5.5}$$

$$\text{Cost}: \quad 0 \leq x_t^T Q_t x_t + u_t^T R u_t \tag{5.6}$$

where x_t is the state of the system at time t comprising the instantaneous (x,y) position p, velocity v, and force f, as well as the desired positions (indicated by *) of the two targets to be reached (to be hit at times T_1 and T_2).

$$x(t) = \left[p_x(t); p_y(t); v_x(t); v_y(t); f_x(t); f_y(t); p_x^*(T_1); p_y^*(T_1); p_x^*(T_2); p_y^*(T_2)\right] \tag{5.7}$$

The state of the system is observed through noisy online sensory feedback y_t, a 6-dimensional vector comprising information about the current position, velocity and force, which are mapped to the corresponding system state using the observation matrix H, which we use to implement a sensorimotor delay of 50 ms.

$$y(t) = \left[p_x(t); p_y(t); v_x(t); v_y(t); f_x(t); f_y(t)\right] + \omega_t \tag{5.8}$$

This sensory feedback has been corrupted by noise ω_t, which are independent zero-mean Gaussians with standard deviations, which were chosen as in (Todorov and Jordan, 2002) by the reasoning that each of the position, velocity and force terms in this task are of different orders of magnitude ((velocities are an order of magnitude larger than distances, and forces an order of magnitude larger than velocities).

$$\sigma_\omega = \sigma_s\left[0.1\mathrm{cm}; 0.1\mathrm{cm}; 1\mathrm{cm/s}; 1\mathrm{cm/s}; 1\mathrm{N}; 1\mathrm{N}\right] \tag{5.9}$$

The control signal input u_t to the system is selected based on the state goals, the noise in the system and the dynamics of the controlled system which are described by the time-invariant matrices A, B. The matrix A describes the uncontrolled discrete-time system dynamics, and so relates the current position, velocity and force to those at the next time step by implementing the following equations together with the matrices B and $M(u_t)$, which we show just for the x-component of the kinematics but are similarly applied to the y-component of each term:

$$\begin{aligned}
p_x(t+\Delta t) &= p_x(t) + v_x(t)\Delta t \\
v_x(t+\Delta t) &= v_x(t) + m^{-1} f_x(t)\Delta t \\
f_x(t+\Delta t) &= (1-\frac{\Delta t}{\tau})f_x(t) + \big(\frac{\Delta t}{\tau} + c_1\varepsilon_x(t) + c_2\varepsilon_y(t)\big)u_x(t) \\
f_y(t+\Delta t) &= (1-\frac{\Delta t}{\tau})f_y(t) + \big(\frac{\Delta t}{\tau} - c_2\varepsilon_x(t) + c_1\varepsilon_y(t)\big)u_y(t)
\end{aligned} \tag{5.10}$$

The matrix B relates the control input u to the force f by implementing a first-order linear muscle filter such that B is a 10×2 matrix with elements all zero except $B_{5,1} = B_{6,2} = \frac{\Delta t}{\tau}$.

The signal-dependent noise terms $M(u_t)\varepsilon_t$ inject uncertainty in motor commands parallel (with scaling, $c_1 = 0.15$) and perpendicular (with scaling, $c_2 = 0.05$) to the control vector (Liu and Todorov, 2007). ε_t are independent standard normal random variables.

The optimal feedback control problem is to find a control law L_t which acts on the best estimate of the current state $\hat{x}_t$ to minimize the total expected cumulative cost over the duration of the movement $E_{\varepsilon,\omega}\sum_{t=1}^{T}(x_t^T Q_t x_t + u_t^T R u_t)$, that is total effort plus task error. The weighting R of effort in the cost function $R = rI$ is summed across time so that the scalar r sets the tradeoff between effort and error.

$$\text{Total effort} = r(\sum_{t=1}^{T} u_x(t)^2 + \sum_{t=1}^{T} u_y(t)^2) \tag{5.11}$$

The weighting matrix Q_t, introduces task errors into the cost function at times T_1 and T_2 when the two targets are to be reached, and is zero otherwise, thus leaving flexibility in how each goal is to be reached. Task errors are weighted in the cost function according to their relative importance to the task, and are scaled to account for the different orders of magnitude of position p, velocity v and force f terms in our reaching task.

$$\text{Task error} = \sum_{i=x,y}\sum_{t=T_1,T_2}\left(w_p(p_i(t)^* - p_i(t))^2\right) + \sum_{i=x,y}\left(w_v v_i(T_2))^2\right) + \sum_{i=x,y}\left(w_f f_i(T_2))^2\right) \tag{5.12}$$

We increased the weight of positional errors w_p in the cost function relative to Todorov and Jordan (2002), as in our behavioural task, participants were required to hit the targets in order to successfully complete a trial, but were not required to completely stop at the secondary target (see Appendix A for parameter values). Asterisks indicate the target positions.

Simulations of control laws for elemental movements used initial and final states that defined movements either from the start position to the central target, or from the central target to one of the follow-through targets. Simulations of cohesive follow-through movements used the start position as the initial state, the central target as the first goal (treated as a via-point), and one of the follow-through targets as the second goal (final state). Elemental movements were each to be performed in 400 ms, and cohesive movements were allocated goal times of 400 ms and 800 ms for reaching the first and second targets respectively. This approximates the timing requirements in subsequent behavioural experiments which required the follow-through target was reached in under 800 ms from movement onset. Additional parameters for the optimal feedback control simulations are provided in Appendix A.

5.3.2 Estimating the encoding complexity of a controller

To calculate the entropy we have to estimate the distribution of the motor command. To do this we binned the motor command signal into 32 bins for both u_x and u_y, $A_{u_x} = \{a_1, ...a_i, ...a_{32}\}$, $A_{u_y} = \{b_1, ...b_j, ...b_{32}\}$, and calculated the joint probabilities $P_u = \{p_{1,1}, p_{1,2}...p_{i,j}, ...p_{32,32}\}$, where $p_{i,j} = P(\mathrm{u}_x = a_i, \mathrm{u}_y = b_j)$.

As we take the joint probability $p_{i,j}$ of each motor command outcome to be invariant across time and state, the probability mass function of a randomly selected motor command can therefore be approximated by aggregating the trajectory of noisy samples from the optimal feedback control simulations of a given trial. For each motor task we generate 10,000 samples of the optimal feedback control trajectory response to the stochastic system described by Equations 5.3-5.6, and flatten these trajectories across time (using simulations of 10 ms temporal resolution and T time steps) to produce $10,000 \times 2\,(dimensions) \times T$ samples of a randomly selected motor command u_t. To evaluate the encoding complexity for control signals in a randomly ordered trial set, we used Monte Carlo samples of the joint probability density $p_{m,k}$ of all possible motor commands produced in the set, flattened across time and across all N trials in an experiment As the behavioural experiments which follow contain equal numbers of trials for each motor task, in our estimates of $p_{m,k}$ we assume each task occurs with equal probability. We therefore obtained $10,000 \times 2\,(dimensions) \times T \times N$ samples across time and tasks, and estimate $H(U_t)$ the entropy of a randomly selected motor command, using Equation 5.1.

To assess the robustness of our estimates of control trial set entropy, this process was repeated 20 times for each motor trial set and chunking scheme to gauge the robustness of our measures to under-sampling. The control entropy estimates were subsequently compared with unpaired t-tests to determine if cohesive or elemental chunking representations would be more efficient to encode. Note that the exact control entropy of each trial set is of less importance here than the relative magnitude of control entropy under cohesive or elemental chunking schemes. Therefore, while we are probably undersampling our estimates of $p_{m,k}$, this is not critical so long as repeating this procedure demonstrates consistent description lengths relative to alternative chunking schemes. It is an open question as to how different the encoding complexity of a signal would have to be to influence chunking behaviour, if indeed it is a variable determining chunking behaviour at all.

5.4 Behavioural methods

A total of 32 subjects (15 female; 24.5 ± 3.9 years, mean ± s.d.) with no known neurological disorders, provided informed written consent and participated in the experiment. All participants were right handed according to the Edinburgh handedness inventory (Oldfield, 1971) and were naive to the purpose of the experiment. The protocol was approved by the University of Cambridge Psychology Research Ethics Committee, and all experiments were performed in accordance with these guidelines and regulations.

Experiments were performed using the vBOT planar robotic manipulandum described in section 1.3. Participants received continuous visual feedback of their hand position from a cursor, as described in section 2.2.

5.4.1 Experimental paradigm

Participants were divided equally into four groups (8 per group). Data from one of these groups (group 1 who performed trial set 1) was presented previously in Chapters 2 and 3 and was part of the motivation for this study.

All participants made reaching movements in a horizontal plane from one of four starting locations to the central target (grey 1.25 cm radius disk), located approximately 30 cm below the eyes and 30 cm in front of the chest. As in Chapters 2 and 3 the four starting locations were positioned 12 cm from the central target and arranged at 0° (closest to the chest), 90°, 180° and 270°, as illustrated in 2.1. These different starting locations were not modelled explicitly but included to slow any learning and minimise cognitive associations between force field directions and different trials. On some trials, in addition to the start and central target, a secondary target (yellow 1.25 cm radius disk) was displayed 10 cm from the central target and positioned at either $+45°$ or $-45°$ relative to the line connecting the starting and central target. If a secondary target was displayed, participants were required to continue the reach from the central target to the secondary target.

During the movement to the central target the robot either generated no force (null field trials), a velocity-dependent force (exposure trials) or a simulated spring constraining the hand to a straight line path to the target (channel trials). Any movements from the central to the secondary target were made in a null field. On exposure trials the velocity-dependent curl force field was implemented as in Chapters 2 and 3.

The direction of the force-field, if applied, during the movement to the central target was coupled to the position of the final target to be reached to on that trial. Channel trials were used to measure subject-generated forces, as in previous chapters. Subjects had to remain within the central target for at least 50 ms before following through to the secondary target. Subjects were encouraged to make the entire follow-through movement between 400 and 800 ms. They received text feedback “correct speed”, “too slow” or “too fast” as appropriate. No text feedback was given on movement just to the central target, to avoid providing conflicting timing feedback metrics on different movements, which might affect chunking behaviour. If subjects moved before the tone, took longer than 1.5 s to complete the movement, or took longer than 1 s to initiate movement after the tone, a mistrial was triggered and subjects were required to repeat the trial. At the end of each trial the vBOT passively moved the hand to the next starting location using a sinusoidal velocity profile.

Before the experiment subjects were given 30 trials of familiarization in a null field. They then performed a pre-exposure phase (null trials and channel trials), an exposure phase (curl field exposure trials and channel trials) and a post-exposure phase (null trials and channel trials). Rest breaks (1.5 min) were provided approximately every 200 trials, with a longer rest break available in the middle of the experiment if required.

The trial structure varied between the 4 groups. Our primary manipulation was to alter the frequency of a particular movement portion (the reach to the central target) in the set of total movements to be performed. This was chosen as our theoretical framework performs a compression which utilises this redundancy in the set of total movements, to yield different predictions for how movements should be chunked. Groups 1 and 2 were constructed to test this hypothesis. However, in the follow-through experimental setting, not all movements between targets are perturbed (the follow-through movement is always unperturbed), and so the manipulation of the distribution of movements in groups 1 versus 2, also produces some movements which are perturbed but do not require follow-through movements. In theory, it was possible that perturbations on these no-follow-through movements may have been more or less easy to differentially adapt to than full follow-through movements for reasons beyond chunking, thus our movement frequency manipulation was conflated with the type of movement (follow-through or not) in the set which was perturbed. Groups 3 and 4 were created to act as controls for the groups 1 vs 2 comparison. Groups 3 and 4 contain the same distribution of movements as each other (and so unlike groups 1 and 2, our theory says they should be chunked similarly, see Figure 5.4B), but the portion of each movement which is perturbed is matched to groups 3 and 4. This allowed us to determine whether any differences in chunking of groups 1 and 2 (our critical manipulation) were due to the distribution of movements as we hypothesized, or due to other factors.

Group 1

This experiment has been described previously in Chapter 2, section 2.2.1 under the heading 'Full Follow-through group' and is re-presented in this chapter to serve as a baseline for comparison to the new results. We refer the reader to section 2.2.1 to avoid repeating the description of this experiment. Critically subjects only make follow-through movement to left and right targets (Figure 5.4, Trial set 1). Each block was 10 trials in length and consisted of 8 exposure (or null) trials and two channel trials which were on movements from the 0° starting location.

Group 2

In this experiment, in contrast to group 1, we replaced one of the two follow-through movements with a movement made just to the central target. Therefore, one field direction was associated with a follow-through movement and the other with a single movement to the central target (Figure 5.4, Trial set 2).

Group 3

Group 4 was identical to group 1 with the addition of channel trials on single movements to the central target (Figure 5.4, Trial set 3). To make the probability of performing each trial type in the experiment equal, we increased the length of each block and balanced the number of trials of each trial type across pairs of blocks. Pairs of blocks consisted of a total of 27 trials, made up of 16 exposure (or null) trials and 11 channel trials. There were 9 trials for each of the three trial types, such that each movement which was associated with a force field had 8 exposure trials and one channel trial, and the other movement of the three was always made in a channel. To match the total number of exposure trials to groups 1 and 2, and keep pairs of blocks balanced, the experiment was therefore 6 pre-exposure blocks, 150 exposure blocks (1,200 exposure trials), followed by 4 post-exposure blocks used to assess after-effects.

Group 4

Group 4 performed the same trial structure as group 3, except that different trial types in the set were associated with the opposing force fields. In this group the trial in which subjects only moved to the central target, and one of the two follow-through tasks (either $+45^\circ$ or -45°) were perturbed (Figure 5.4, Trial set 4). The other follow-through trial was always made with a channel trial on the movement to the central target, including during the pre-exposure phase. Blocks were the same as for group 3.

5.4.2 Behavioural data analysis

Metrics for learning

We have previously shown that such opposing force fields can be learned concurrently if each is associated with a different motor plan (see Chapter 2, Sheahan et al. (2016)). Therefore, concurrent adaptation can serve as an indicator of motor planning. That is, if participants adapt to two opposing force fields concurrently, we can infer that each movement is executed under a distinct motor plan, that is, movements are planned as cohesive follow-throughs. Conversely, elemental motor planning will cause each movement to the central target to be executed under the same plan for both opposing fields, and will therefore result in full interference.

Two metrics were used to evaluate learning from exposure to force fields. We analysed MPE on movements originating from all starting locations and adaptation on channel trials originating from just the 0° starting location. We evaluated adaptation only on movements that were associated with force field perturbations. These metrics were obtained using the same analysis methods as described in Chapter 2. We averaged MPE for each subject over 8 consecutive field trials, and adaptation corresponding to the same epoch, measured only on the channel trials which were nominally associated with a force field. Learning within a group was assessed using a within-subjects repeated-measures ANOVA with a fixed effect of epoch, to compare adaptation between the average of the pre-exposure blocks and adaptation corresponding to the final 48 exposure trials (approximately 6 blocks). Similarly, we also assessed the aftereffects, calculated as the difference in MPE between the average of the pre-exposure blocks and the first two blocks of post-exposure.

To compare learning between groups, we performed a mixed-effects ANOVA on the adaptation data, as assessed on just those trials which were nominally associated with a force field, and using a fixed effect of epoch (same two epochs of trials, pre-exposure vs late exposure), a fixed effect of group, and a random effect of participants, as in Chapters 2 and 3. We explored differences between groups post-hoc using reduced mixed-effects ANOVAs of a similar structure but with pairs of groups.

Central target dwell times

A measure of chunking which is common in the literature is the time between the end of one movement and the start of the next in a motor sequence (Rosenbaum et al., 1983; Sakai et al., 2003; Verwey, 1996; Verwey and Dronkert, 1996; Wymbs et al., 2012). That is longer dwell times are associated with movements which form part of separate chunks and shorter dwell times for movements which are part of the same chunk. Motor chunking was therefore assessed using the time between successive movements within a trial. For each participant this was calculated as the time between entering and leaving the central target on follow-through movements which were not artificially constrained by channel trials. We call this the *dwell time*, and calculated it using follow-through null trials in the final 40 trials of the pre-exposure phase (corresponding to approximately 4 blocks) to assess chunking under null field dynamics for each trial set. We performed a one-way ANOVA on these pre-exposure phase dwell times, using a fixed effect of group and a random effect of participant, to compare our model predictions of chunking against baseline behavioural differences between groups. We subsequently evaluated how chunking of follow-through movements changed across the experiment for the four groups by performing a mixed-effects ANOVA of dwell-times as the response variable, using a within-subjects fixed effect of epoch (three levels: pre-exposure trials, the first 40 trials during the exposure phase and the final 40 trials during the exposure phase), a between-subjects fixed effect of group (4 levels, one for each group) and a random effect of participant. Within-subjects differences were explored post-hoc across groups with reduced mixed-effects ANOVAs of similar structure but with two levels of epoch.

Movement initiation times

As response times have been shown to scale with navigational plan complexity (Balaguer et al., 2016), and the depth of planning shown to reduce when response times are restricted (Keramati et al., 2016), we additionally used movement initiation times as a measure of planning complexity. This was assessed from the go cue to the time the hand exited the start position.

We first assessed how baseline movement initiation times differed across the groups using a one-way ANOVA, with a between-subjects fixed effect of group and a random effect of participants, as for dwell-times. We subsequently assessed how movement initiation times changed across the experiment for the different groups with a mixed-effects ANOVA, using a fixed effect of group, a fixed effect of epoch (using the same three trial epochs as for the dwell time assessments) and a random effect of participants. In our experiments, the same movements are repeated hundreds of times and so response (movement initiation) times may decrease with learning, or may become at least partly habitual (Haith and Krakauer, 2018; Hardwick et al., 2017b). To separate generic decreases in response time from changes in chunking behaviour across the experiment, we evaluated the difference between response times on central target-only trials (which can only be planned as a single movement), and response times on follow-through trials (which may be planned as far as the central target, when planned elementally, or as a full follow-through movements requiring more planning depth). We assessed how these differences in movement initiation times for different trials changed across the experiment with a similarly structured mixed-effects ANOVA, again with a fixed effect of epoch with three levels consisting of the same three epochs as previously (pre-exposure, early exposure and late exposure), a random effect of participants and a fixed effect of group, this time with only the three groups that performed both follow-through and centre-only movements (Groups 2, 3 and 4).

Correlations in chunking when dynamics changed

We subsequently evaluated whether pre-exposure null field chunking scaffolded chunking in curl fields by assessing the correlation between the participants' mean dwell times in the pre-exposure (final 40 trials) and early exposure (first 40 trials) epochs.

To assess whether baseline (pre-exposure phase) chunking of follow-through movements were correlated with subsequent opposing force field adaptation across all trial sets, we assessed the correlation between participants' dwell times during the final 4 blocks of the pre-exposure phase with the final adaptation across the final 4 blocks in the exposure phase.

5.5 Theoretical results

5.5.1 Different trial structures predict different optimal chunking

To test how chunking might influence the complexity of encoding a set of motor tasks we solved OFC for 5 possible movements (Figure 5.3A): single movements: start → center, center → left target, and center → right target, and for two compound movements: start → center → right target, and start → center → left target. Then based on the trial structure we calculated the entropy for different ways of chunking to select the optimal chunking scheme.

The first trial set comprised movements from the full follow-through task in Chapter 2 (Figure 5.4, Trial set 1). Each follow-through trial required a movement which originated from the same starting position and passed through the same central target before diverging to different secondary targets. Simulating the optimal feedback controller for this trial set yielded a significantly less complex control signal when each movement was planned as a cohesive follow-through movement, than when planned as elemental movements between each target (Figure 5.4 and Table 5.1, difference in control set entropy $H(U)^{\wedge} - H(U)^{\vee} = -0.074 \pm 0.014, t(38) = -5.4, p = 3.8e-6$). This is consistent with the results of Chapters 2 and 3, which suggest that, even when movements to the central target are perturbed, participants plan movements to both the central and secondary targets prior to movement initiation.

In contrast, when one of these two follow-through tasks is replaced by a movement only to the central target, as in trial set 2 (Figure 5.4), it becomes more efficient to encode control signals for movements that are planned in elemental components than in cohesive follow-through trajectories (Figure 5.4 and Table 5.1, difference in control set entropy $H(U)^{\wedge} - H(U)^{\vee} = 0.369 \pm 0.017$ bits, $t(38) = 21.7, p = 5.2e-23$). As leftwards and rightwards follow-through movements are symmetric (in the y-plane) with respect to a movement just to the central target, requiring symmetric control signals, the theoretical encoding complexity of making a leftwards or rightwards follow-through in this trial set did not differ (mean difference between trial sets with a single leftwards versus rightwards follow-through $H(U)^{\wedge}_{L} - H(U)^{\wedge}_{R} = 0.008 \pm 0.009$ bits, $t(38) = 0.89, p = 0.38$; $H(U)^{\vee}_{L} - H(U)^{\vee}_{R} = 0.024 \pm 0.022$ bits, $t(38) = 1.1, p = 0.29$).

The final two trial sets comprised three different movements. That is, full follow-through movements in both directions, and a movement made only to the central target (Figure 5.4,

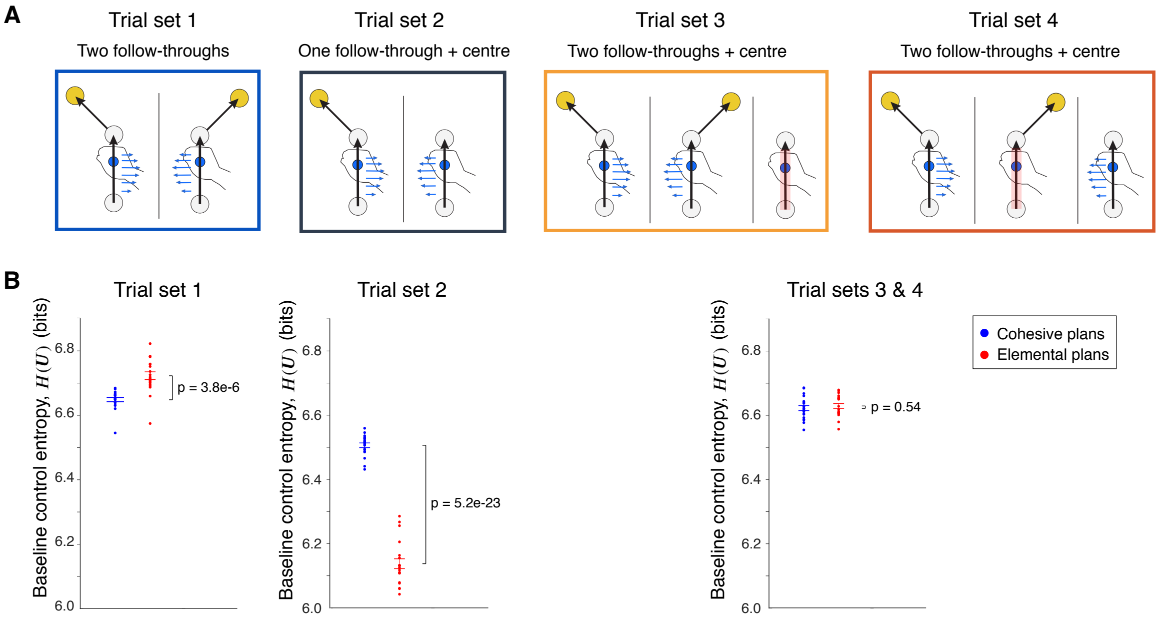

Fig. 5.4 **Four sets of trials for assessing motor chunking.** (A) All four trial sets required at least a movement to the central target, either made as part of a full follow-through movement or on its own. We assessed chunking for each of these trial sets at baseline (in simulation) and behaviourally when different movements in the set were perturbed with a curl force field (blue arrows) from the start position to central target, or made in virtual channels (shaded red in trial sets 3 and 4). Each trial set was subsequently performed by a different group of participants and adaptation was assessed as a measure of planning horizon. Trial sets 3 and 4 differed only by which movements were associated with force-fields. As we simulated encoding complexity for null fields, we predicted that these two trial sets would be chunked identically. The same two trials in the set were associated with force fields in trial sets 1 and 3, and sets 2 and 4 to control for any effects specific to the perturbation-movement pairing. Trials are shown visually separated but the movements to the central target was always made over the same physical space. (B) Estimation of trial set control entropy for unperturbed (null field) movements. Encoding optimal feedback control signals for each trial set required different average amounts of information (control entropy, $H(U)$), and these critically depended on whether the movements were planned as cohesive (blue) or elemental (red) sequences. Each dot is a single simulated estimation of entropy (20 dots per condition); bars show mean ± s.e.

trial sets 3 and 4). We created these sets to assess whether the encoding efficiency of planning full follow-through movements in trial set 1 could be modulated by introducing an additional movement to the set which was just to the central target, and so could only be planned in a single chunk. Introducing the additional movement just to the central target increased repetition in the set, which in theory, should decrease the set entropy by making some control signals more probable than others (MacKay, 2003). Indeed simulations demonstrated that the encoding cost of planning cohesive versus elemental motor chunks in these sets became more similar than when encoding trial set 1, such that for the same number of simulations, no difference in control entropy was observed (Figure 5.4 and Table 5.1, difference in control set entropy $H(U)^{\wedge} - H(U)^{\vee} = -0.007 \pm 0.011$ bits, $t(38) = -0.61, p = 0.54$). Moreover, across all three trial sets, controller entropy decreased as repetition in the set increased (Table 5.1), reflecting our predictions. We additionally included trial set 4 to control for any effects specific to the force field-movement pairing (trial sets 1 and 3, and sets 2 and 4 both associate the same movements in the set with different force-fields).

As expected, the total expected cost-to-go (the cumulative cost, as defined in Equation 5.6) across all movements in the trial set were consistently lower when movements were planned cohesively than when segmented (Table 5.1). This is due to the wider optimisation window for planning across, enabling each optimal feedback control law to reach a global optimum.

Together, these theoretical results make two behavioural predictions for movement chunking in unperturbed dynamics environments. First, that planning of trial set 1 will be more cohesive than trial set 2, and second, that chunking of trial sets 3 and 4 will on average be less cohesive than trial set 1 (as the relative benefit of cohesive planning is reduced), and more cohesive than trial set 2.

Table 5.1 **Cumulative cost of executing each trial set and the encoding costs of motor commands.** The total $E[\text{cost}]$ indicates the total expected cost for execution from the start of the movement, summed over all movements in the trial set. Entropy data are measured in units of bits and show mean ± s.e. across 20 estimates of entropy, with each estimate based on 10,000 simulated noisy movement trajectories per task.

	Trial set 1: Two follow-throughs		Trial set 2: One follow-through + centre		Trial sets 3 and 4: Two follow-throughs + centre	
	Total $E[\text{cost}]$	$H(U)$	Total $E[\text{cost}]$	$H(U)$	Total $E[\text{cost}]$	$H(U)$
Cohesive	237.3	6.65 ± 0.01	372.0	6.51 ± 0.01	490.7	6.62 ± 0.01
Elemental	673.9	6.72 ± 0.01	590.3	6.14 ± 0.01	927.3	6.63 ± 0.01

5.6 Behavioral results

5.6.1 Motor chunking in familiar dynamics

Our model suggests that trial set 1 can be encoded more efficiently when movements are planned as cohesive follow-throughs than when planned in distinct motor segments. We therefore predicted that participants would adopt a more cohesive chunking scheme performing trial set 1 than trial set 2, where elemental movements are more efficient to encode (Figure 5.4). Furthermore, the same model led us to predict that groups 3 and 4 who both perform trial set 3, but who are constrained on different movements by mechanical channels, would adopt the same chunking scheme.

We evaluated chunking in all four groups during both a pre-exposure phase in which environmental dynamics were familiar to participants (null fields) and subsequently during an exposure phase (curl fields).

Counter to our predictions for efficient chunking, a one-way ANOVA of pre-exposure dwell times revealed no effect of group (Figure 5.5A, one-way ANOVA, $F_{3,28} = 1.79$, $p = 0.17$), on chunking patterns. Furthermore, when pre-exposure movement initiation times were compared across groups using a one-way ANOVA, there was also no effect of group (one-way ANOVA, $F_{3,28} = 0.78$, $p = 0.51$). Taking these dwell time and initiation time results together, this suggests that chunking behaviours in unperturbed dynamics (null fields) could not be accounted for by model predictions for efficient representations of control.

5.6.2 Motor chunking in perturbed dynamics

We attempted to predict how participants would adapt to different dynamics which were experienced over the same physical states, based on normative predictions for how participants might chunk motor plans at baseline. Therefore, we predicted that pre-exposure chunking would scaffold chunking when dynamics changed. To test this, we compared central target dwell and response times across null and curl field dynamics, and the degree to which participants were able to concurrently adapt to opposing perturbations.

Across participants in all groups, dwell times at the end of the pre-exposure phase correlated with those at the start of exposure (Figure 5.5B, r = 0.55, p = 0.0011, slope of 0.67),

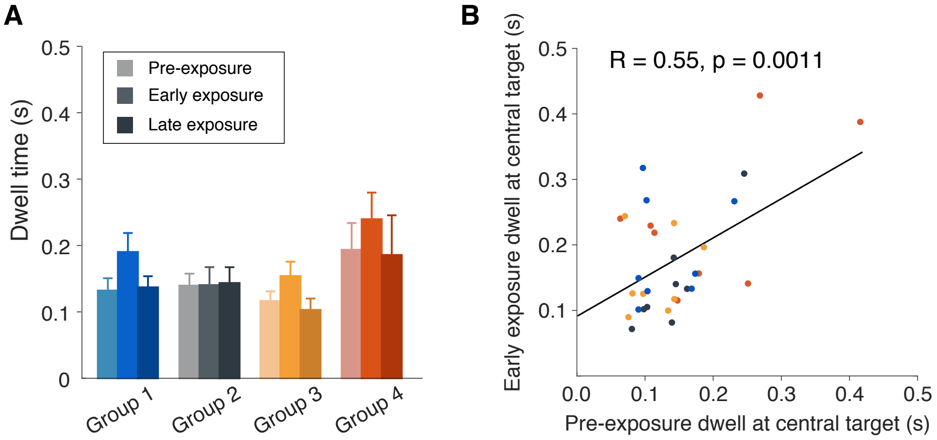

Fig. 5.5 **Central target dwell time in follow-through movements did not depend on trial set.** A) Central target dwell time on unconstrained (null field) follow-through movements during the final 40 trials of the pre-exposure phase (lightest colour), on perturbed (curl field) follow-through movements during the first 40 trials of the exposure phase (middle colour), and the final 40 trials of the exposure phase (darkest colour) for each trial set. Model predictions for motor chunking in familiar dynamics were not reflected in these dwell times. Bars show mean ± s.e. across participants. B) Central target dwell times at the end of the pre-exposure phase (final 40 trials) were correlated with dwell times at the start of the exposure phase (first 40 trials). Dots show individual participants.

suggesting a tendency for participants to adapt an existing chunking scheme, rather than adopt a completely new one when switching from baseline to perturbed environmental dynamics. However when dwell times across groups for different phases of the experiment were compared, a mixed-effects ANOVA with a fixed effect of epoch (three levels: 40 trials in each of pre-exposure, early exposure and late exposure), a fixed effect of group and a random effect of participants showed that there was a main within-subjects effect of epoch (Figure 5.5A, mixed-effects ANOVA, $F_{2,56} = 4.55$, $p = 0.015$), although there was no between-subjects effect of group (mixed-effects ANOVA, $F_{3,56} = 1.98$, $p = 0.14$) or an interaction (mixed-effects ANOVA, $F_{6,56} = 0.60$, $p = 0.73$). Therefore while individual participants' dwell times were correlated when transitioning from unperturbed to perturbed dynamics, this change in dynamics did affect how long participants waited at the central target before following through. Specifically, post-hoc reduced mixed-effect ANOVAs revealed that participants increased their dwell times when the dynamics initially changed (mixed-effects ANOVA, $F_{1,28} = 6.41$, $p = 0.017$), and subsequently decreased dwell times as the exposure phase continued (Figure 5.5A, mixed-effects ANOVA, $F_{1,28} = 6.67$, $p = 0.015$).

For all groups, the time taken to initiate a response decreased across the experiment (Figure 5.6A and B; mixed-effects ANOVA, main effect of epoch, $F_{2,56} = 22.8$, $p = 5.7e-8$; no

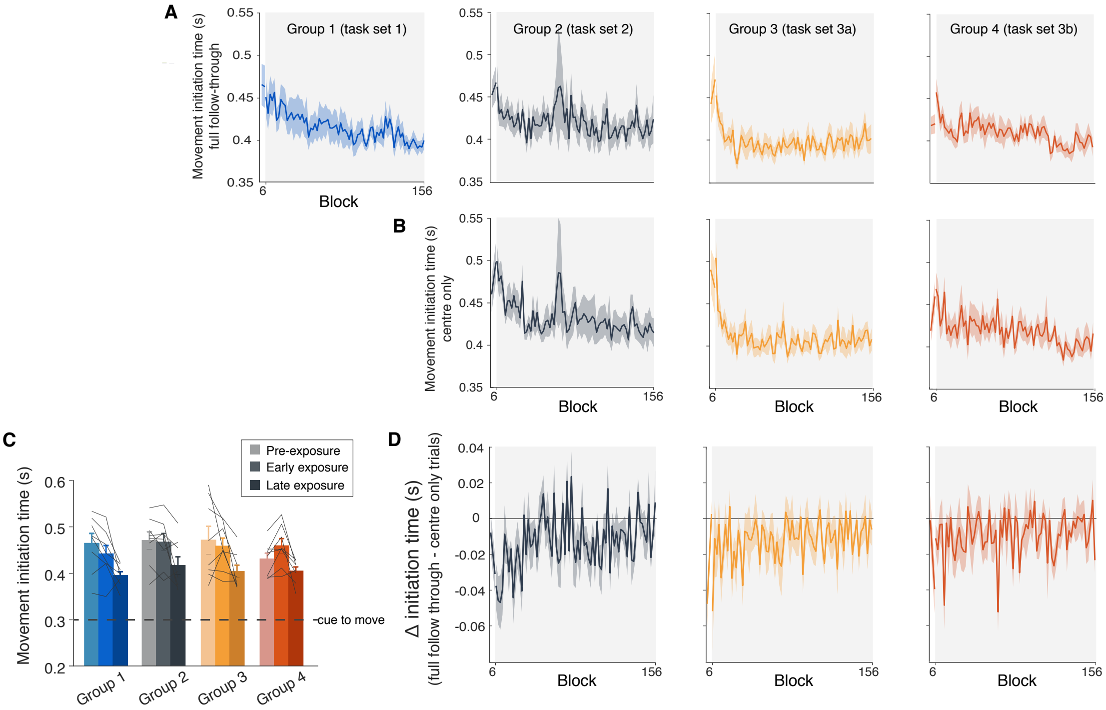

Fig. 5.6 **Movement initiation times for centre only and follow-through trials in each trial set.** A) Initiation times in follow-through trials, which could be planned as either cohesive or segmented movements, and B) initiation times to central target only trials, which can only be planned as a single chunk. Group 1 experienced only follow-through trials. Data shows mean ± s.e. across participants for pairs of blocks and includes just the final 4 blocks of the pre-exposure phase. C) Initiation times for all movements performed by individual participants across three different epochs, separated for each group. Epochs shown are for null field follow-through movements during the final 40 trials of the pre-exposure phase (lightest colour), for perturbed (curl field) follow-through movements during the first 40 trials of the exposure phase (middle colour), and for the final 40 trials of the exposure phase (darkest colour). Lines show individual participants; bars show mean ± s.e. across participants. D) The difference in response times between follow-through and central target only trials show that participants consistently waited longer before initiating a movement just to the central target. Movement response times became marginally more similar between trial types as the exposure phase continued. Data show mean ± s.e. across participants for pairs of blocks and includes just the final 4 blocks of the pre-exposure phase. Grey shaded blocks show the exposure phase.

effect of group, $F_{3,56} = 0.41$, $p = 0.74$; no interaction, $F_{6,56} = 0.92$, $p = 0.49$). This decrease in response time could reflect improvements in timing the response with the predicted go cue, or the learning of a direct stimulus-response association between the visual target stimuli and a pre-computed policy (Haith and Krakauer, 2018; Hardwick et al., 2017b), rather than reflecting the computation of a less complex motor plan. To isolate changes in motor planning time, from generic reductions in reaction time with practice, we also compared how response times changed across the exposure phase for central target trials (which can only be planned in a single element), versus follow-through trials (which can be planned elementally or cohesively), (Figure 5.6C). Unexpectedly, despite requiring a greater, or least equal planning depth, trials requiring follow-through movements took less time for participants to initiate a response to, than central target-only trials (Figure 5.6A and D). The difference in response times between the two trial types decreased across the experiment, such that, while both movements came to be initiated more rapidly, they also came to be initiated at more similar times to each other (Figure 5.6C, mixed-effects ANOVA, main effect of epoch ($F_{2,42} = 6.0$, $p = 0.0051$), no effect of group ($F_{2,42} = 1.41$, $p = 0.27$) and an interaction ($F_{4,42} = 3.08$, $p = 0.026$).

5.6.3 Motor adaptation as an indicator of chunking

Finally, we assessed how well participants in each group concurrently adapted to opposing perturbations. Over the course of 1,200 exposure trials, all four groups significantly adapted to both force fields across the same physical states. Participants in all groups increased their force compensation (Figure 5.7B; group 1: $F_{1,7} = 38.6$, $p = 4.4e-4$); group 2: $F_{1,7} = 15.5$, $p = 0.0057$; group 3: $F_{1,7} = 28.4$, $p = 0.0011$; group 4: $F_{1,7} = 15.4$, $p = 0.0057$), and displayed significant after-effects (Figure 5.7A; group 1: $F_{1,7} = 8.3$, $p = 7.4e-5$; group 2: $F_{1,7} = 4.3$, $p = 0.0035$; group 3: $F_{1,7} = 6.9$, $p = 2.18e-4$; group 4: $F_{1,7} = 4.4$, $p = 0.0031$). This suggests that, in contrast to our predictions, on average participants in all groups planned distinct movements for trials with differently directed perturbations, instead of simply recycling the same initial motor plan to the central target on each trial. Across participants, the final adaptation level was also negatively correlated with pre-exposure dwell time at the central target (Figure 5.7C, $r = -0.50$, $p = 0.0032$), such that participants who planned more cohesive follow-throughs adapted more to the force fields that were later presented.

Finally we contrasted the adaptation in the four groups using a mixed-effects ANOVA with fixed within-subject effects of epoch (two levels: pre-exposure vs. late in the exposure

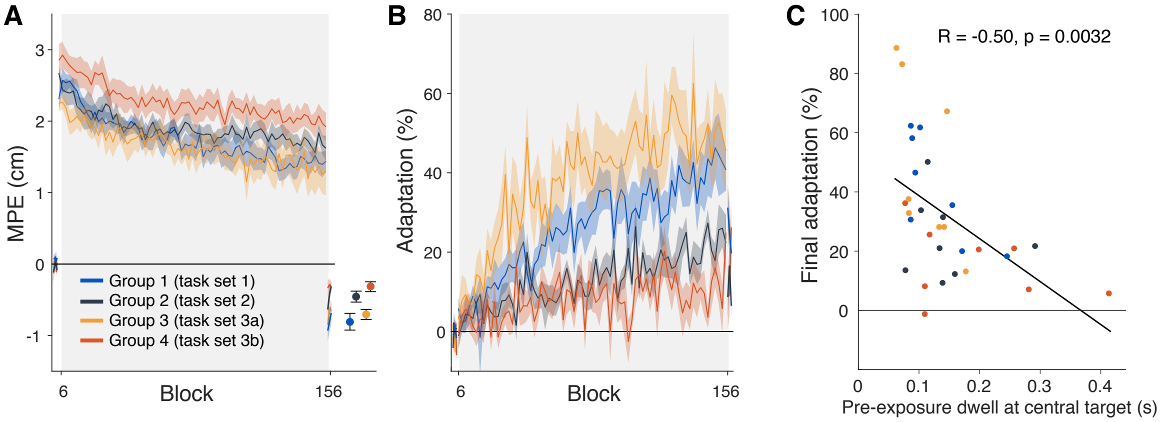

Fig. 5.7 **Adaptation to opposing perturbations** A) Maximum perpendicular kinematic error and B) force adaptation for group 1 (blue), group 2 (green), group 3 (orange), group 4 (red). C) Correlation between pre-exposure (last 40 trials) dwell time at the central target on unconstrained follow-through trials and the final adaptation (final 80 trials of the exposure phase). Dots show individual participants; bars show mean ± s.e. across participants. In A) we show the mean (± s.e.) of the aftereffects to the right of the panel (separated for clarity).

phase), a fixed between-subjects effect of group, and a random effect of participants. As expected, there was a main effect of epoch ($F_{1,28} = 93.0$, $p = 2.12e-10$), however there was also a main effect of group ($F_{3,28} = 5.6$, $p = 0.0039$) and an interaction ($F_{3,28} = 5.4$, $p = 0.0046$). Therefore, while all groups demonstrate concurrent adaptation, some groups learned more than others. Unexpectedly, perturbing different movements in trial set 3 and trial set 4 had a significant effect on adaptation. A posthoc comparison of adaptation between groups 3 and 4 with a reduced mixed-effects ANOVA revealed a main effect of epoch ($F_{1,14} = 41.7$, $p = 1.51e-5$), main effect of group ($F_{1,14} = 11.9$, $p = 0.0039$) and an interaction ($F_{1,14} = 11.1$, $p = 0.0049$). Furthermore, if participants in the four groups were instead grouped by which movements in the trial set were perturbed, such that participants in groups 1 and 3 (performing trial sets 1 and 3, with both follow-through movements perturbed, Figure 5.8A, dark green), were combined and participants in groups 2 and 4 (performing trial sets 2 and 4, with one follow-through and one central target movement perturbed, Figure 5.8A, mustard) were combined, this yielded a clear effect of perturbed movement on adaptation. Specifically, a mixed-effects ANOVA with a fixed effect of epoch and a fixed effect of group (where participants were combined across pairs of groups based on which movements were perturbed in the set), showed a main effect of epoch, as expected ($F_{1,30} = 95.3$, $p = 7.9e-11$), but also a main effect of group ($F_{1,30} = 14.6$, $p = 6.3e-4$), and an interaction ($F_{1,30} = 15.4$, $p = 4.8e-4$) (Figure 5.8B). Therefore, pairing opposing perturbations with movements that each had unique and distinct components to their plans (i.e.

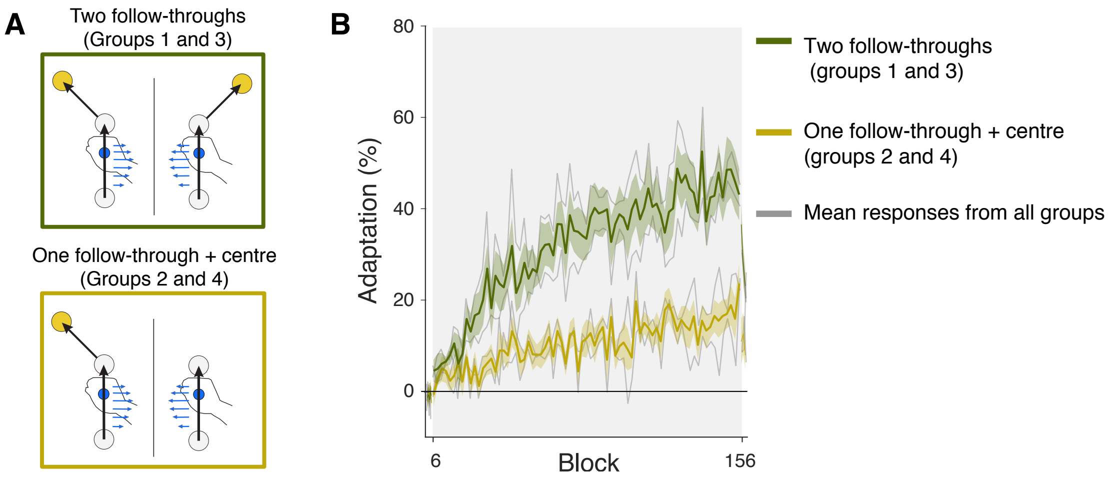

Fig. 5.8 **The amount of adaptation to opposing force fields depended on which movement in the set was perturbed.** A) In groups 1 and 3, two follow-through movements were associated with distinct force field directions (dark green), compared to in groups 2 and 4 where a movement to the central and a single follow-through were associated with each force field (mustard). B) Force field adaptation for participants combined across groups 1 and 3 (dark green), and groups 2 and 4 (mustard). Grey lines indicate the mean responses from groups 1-4 shown in Figure 5.7B. Data shows the mean ± s.e. across subjects.

different follow-throughs), yielded significantly more net adaptation than pairing opposing perturbations with plans that did not. This suggests that, while at least a small amount of learning was observed for each group, the amount of interference between opposing fields appears to depend not only on the way movements are chunked and recycled, but also on how distinct the underlying plans that generate them are.

For all of the above listed parametric tests, Shapiro-Wilk tests could not reject the null hypothesis that the compared samples were normally distributed. Where ANOVAs were performed, Bartlett's tests could not reject the null hypothesis that the compared samples were homogeneous in variance.

Taken together, our normative encoding model predicted chunking that was refuted by both empirical pre-exposure behaviour, and the subsequent ability of participants to adapt to different perturbations across the same physical states. Model simulations predicted distinct chunking for each of the three trial sets, yet four groups of participants who performed these different sets of trials demonstrated similar dwell and response times to each other, and all groups subsequently demonstrated at least partially cohesive motor planning, as demonstrated by concurrent adaptation to dynamic perturbations. Interestingly, when the dynamics of the environment initially changed, participants did alter the amount of time they paused at the central target before following through with the second movement component, possibly reflecting a change in planning depth. Moreover, dwell times indicated that chunking in familiar, null dynamics correlated with chunking early in the exposure phase, and also correlated marginally with the total amount of subsequent field adaptation.

Together this suggests that while our model did not successfully predict motor chunking on these short motor sequences, baseline chunking behaviours appear to, at least partially, persist when dynamics change, and may be able to predict the subsequent motor adaptation that develops.

5.7 Discussion

We developed a model that optimised the efficiency of encoding control signals to predict how reaches within a trial set should be chunked. In contrast with existing motor control formulations which consider the production of individual movements in isolation, our framework extended the notion of control optimality to consider the temporal context in which each movement was made. That is, the horizon of optimisation was extended to capture the entire set of movements to be made, predicting how movements within the set should be structured for efficient representation. We contrasted the behavioural predictions from this model across four groups of human participants and found that our predictions for chunking behaviours were not borne out in the data. Specifically, neither early chunking over a short course of pre-exposure trials, nor late chunking after thousands of trials of altered dynamics, reflected the considerations of the trial set that we predicted. However, while dwell times early in the experiment varied across participants in all four groups, these early dwell times positively correlate with chunking in the presence of altered dynamics (as measured by both subsequent dwell and adaptation behaviour). Together this suggests that, while short sequence chunking behaviour may reflect more than simply the encoding efficiency captured in our model, motor planning in familiar environments may scaffold chunking when environment dynamics change.

5.7.1 Behavioural chunking and adaptation

Our results demonstrated that participants who paused less at the central target early in the experiment (i.e. had shorter dwell times), adapted marginally more to the ensuing opposing dynamics. This is consistent with previous results which showed that when opposing force fields were associated with different lead-in movements, the amount of interference observed between them grew progressively as the dwell time between the lead-in movement and the movement through the field increased (Howard et al., 2012). In the study by Howard et al. (2012), this effect emerged when these different dwell times were required by different groups of participants throughout the task, and were interpreted as reflecting a dependency of motor memory encoding on recent sensorimotor states. In contrast, here we show that in similar two-part contextual motor sequences, the dwell behaviour participants naturally adopt at baseline, may correlate with the amount they subsequently adapt to different dynamics.

While we predicted that motor chunking would reflect the statistics of the trial set independent of perturbations, we observed significantly different amounts of adaptation between two groups that performed the same set of trials (groups 3 and 4). Moreover, when participants were grouped by which movements in the trial sets were perturbed (that is, fields were paired with either the movement just to the central target and a single follow-through, or paired with two distinct follow-throughs), there was a significant interaction between the amount of learning and which movements in the set experienced a change in dynamics. Exactly what determines how plans are represented and how learning generalises between them remain unclear, but these results suggest that different dynamics may be more easily learned for movements traversing some of the same physical states, if each is is planned as part of a sequence involving distinct components. That is, part of the motor plan involves executing (or possibly, imagining to execute, see Chapter 3) mutually exclusive physical states.

How the brain develops efficient representations of the world and the timescales over which this occurs are open questions. In our experiments, it is possible that the number of pre-exposure trials were simply too few to allow participants to form efficient representations, but that over a more extended exposure to these sets of trials, motor commands may have adapted more to the trial set statistics. Indeed during pre-exposure, individual participants across all groups varied in the amount of time they dwelled at the central target. A study by Sosnik et al. (2004) showed that the executed trajectories on four-target reaching sequences changes qualitatively across days from the production of more elemental movements to more cohesive sweeps. This yields a ‘smoothing’ of trajectories around via-points, similar to those yielded by a minimum jerk optimisation (highlighted by the authors), and which would also be predicted by optimal feedback control trajectories, planned over progressively longer spatiotemporal horizons (which was used in our framework). Indeed these results are also consistent with behavioural changes observed in macaques performing centre out reaching movements (Ramkumar et al., 2016). In the Sosnik et al. (2004) study, on each day participants performed up to 400 trials, and differences in the timing and number of velocity peaks were observed after 3-5 days of training (1200-2000 trials), which although spread over a much longer period and between sleep cycles, is similar to the total amount of training we provided our participants. Given their results on a more complicated task (four targets, compared to the 2 targets in ours), it is conceivable that changes in performance with chunking may have emerged by the end of training on our tasks given the similar total timeframe. However, this may also indicate that the pre-exposure period (under familiar dynamics) in our task may have been too brief to support the development of chunks that would thoroughly test our predictions.

The tasks we considered here were also for short, simple two-part sequences and so the benefit of segmenting chunks may have been less significant than for the more extended discrete sequences of finger movements (e.g. button presses) (Acuna et al., 2014; Rosenbaum et al., 1983; Sakai et al., 2003; Verwey, 1996; Verwey and Dronkert, 1996) or point-to-point movements (Ramkumar et al., 2016) typically considered in the chunking literature. Therefore, the differences between our model predictions and behavioural chunking on different trial sets should not necessarily be taken as evidence against the plausibility of coding constraints affecting motor chunking. Rather, trial set command entropy is just one potential measure of chunking efficiency, and this chapter is therefore intended to serve as a starting point for further exploration of the factors underlying chunking. Of particular interest for future work is how the selection of chunks in longer motor sequences may be influenced by trial set statistics and other measures of efficiency.

5.7.2 Computational considerations of chunking

Computational theories for how tasks or environments should be hierarchically deconstructed are still in their infancy (McNamee et al., 2016; Solway et al., 2014). One recent theory formalised the optimal hierarchy as the one that best facilitates average performance over a set of possible tasks (Solway et al., 2014). This framework casts the selection of a behavioural action hierarchy as Bayesian model selection, whereby the likelihood (model evidence) $P(\text{best behaviour} \,|\, \text{hierarchy})$ is maximised to select the optimal choices of subgoals across a set of required tasks. When tested experimentally, participants were found to select virtual subgoal positions (to which they could move more quickly) that behaviourally approximated the Bayes-optimal locations for efficient action-taking. This approach is closely related to selecting the behaviour with the shortest information-theoretic description length (Grunwald, 2004). More recently, McNamee et al. (2016) determined how to optimally deconstruct environments for efficient planning, without a priori knowledge of target behaviours. Specifically, environments were modularised so as to minimize the average description length of planning within and across modules. As descriptive complexity is related to the ease of learning (Feldman, 2000), these styles of approach that minimise the entropy in planning may also facilitate the learning of new behaviours. Here, we considered a similar theory, whereby we hypothesized that an action hierarchy may be selected so as to encode motor commands with the minimum complexity (description length). However, participant behaviours did not align with our predictions, suggesting instead that either the factors underlying action chunking may be more complex than optimising for encoding efficiency alone, or that the types of efficient chunking we predict may simply require more time to develop (Ramkumar et al., 2016). Therefore, these results suggest that of the many possible efficiency metrics, trial set encoding complexity is not a sufficient predictor of motor chunking after limited trial set exposure.

While our model may capture the intuition of trading off movement efficiency with the efficient allocation of neural resource, a fundamental limitation to our approach is the insensitivity of our control entropy estimations to temporal correlations in motor commands. That is, for computational feasibility we have estimated the total control entropy by collapsing the time-series of motor commands across time, when in reality such temporal correlations and dependencies may have a marked effect on representational cost. An alternative approach would be to calculate the distribution of motor command trajectories (i.e. to estimate $p_\pi(u_{1:T}|u_0,x_0) = \prod_{t=0}^{T-1} p_\pi(u_{t+1}|u_t,x_t)$, under the policy π), and calculate the associated entropy of this trajectory. It is possible that this would yield more accurate predictions of chunking, however, given the heterogeneity of early chunking we observed experimentally, it seems likely that other factors such as energy efficiency and task performance may impact chunking of less familiar tasks more readily than total trial set encoding complexity. Additionally, our model assesses task set entropy independently of the temporal structure of trials, and the volatility of these tasks over time may additionally influence the extent and rate at which participants adapt (Behrens et al., 2007).

In summary, we developed an efficient coding model for motor chunking, based on the hypothesis that motor chunking may reflect the distribution of required movements in a trial set. We estimated the encoding costs of optimal movements simulated under different chunking schemes, to yield distinct predictions for normative chunking for different sets of movements. These predictions were not reflected in the behavioural data. Rather, chunking behaviours were varied across participants and concurrent adaptation depended at least partially on which trials in the set were associated with curl field dynamics. Interestingly however, the way participants chunked movements early in the experiments appeared to remain relatively consistent when task dynamics change, suggesting that early motor chunking may indeed scaffold subsequent motor adaptation.

Chapter 6

Conclusions

It is clear from observation that humans can learn a remarkable diversity of motor skills. However, despite considerable research, the factors that underlie motor memory interference have remained elusive, making it difficult for researchers to predict whether two tasks will develop a single, or two separate, control policies, and how these will be retained when later tasks are performed. Moreover, the issue of whether motor memories for single tasks will develop as cohesive or segmented policies, which are either specialised or composable, has been somewhat neglected in the recent motor learning literature. Despite the prevalence of complex, decomposable motor behaviours in human activity, predicting motor chunking remains an unsolved challenge. The objective of this thesis has been to examine the role of motor planning in these two fundamental problems.

Considerable effort has been expended by the research community to establish the states of the motor system or environment that motor learning is, in a sense, 'attached' to. That is, many studies have investigated what factors need to be different to enable new motor memories to be parcellated and protected from interference from intervening tasks, yet accessed and updated when a similar task is re-experienced (Gandolfo et al., 1996; Hirashima and Nozaki, 2012; Howard et al., 2012, 2013, 2015; Hwang et al., 2003, 2006; Krakauer et al., 1999, 2006; Nozaki et al., 2006; Wainscott et al., 2005; Yeo et al., 2015). However the dominant focus has, with limited exception[1] been on which physical movement parameters, such as movement direction, velocity, workspace position, or joint angles, enable distinct

---

[1] In 2012 Hirashima and Nozaki conducted a cleverly designed experiment which we discussed in Chapter 2. The authors drew a similar basic conclusion from their results as we have in Chapter 2, however, their paradigm did not precisely isolate planning, over the inferred state of the limb, as the important component in concurrent adaptation to opposing fields.

skills to be developed. Taking inspiration from recent electrophysiological data from motor cortex, this thesis demonstrates that these observations of motor state-dependence are simply a reflection of a more fundamental property that allows multiple motor skills to be learned, that is, differences in the neural state (i.e. motor plan), rather than physical state of the body or environment. Interestingly however, the same principle does not appear to underlie contextual motor memory decay, indicating a further separation between the mechanisms underlying adaptation and retention of motor skills. Building on this hypothesis regarding the importance of neural states to motor memory development, this thesis further explores whether theoretical simulations of normative motor plan chunking can predict how new motor skills will develop. We demonstrate that the factors underlying motor chunking are still far from established, and that theoretical predictions for efficient ways to chunk continuous movements are difficult to reconcile with behavioural data. Considering the prevalence of complex, hierarchical behaviours in daily life, this strongly supports the need for further research on chunking to match the wealth of more naturalistic behaviour that is unaccounted for.

6.1 Contributions of this thesis

Chapter 2 concerned the representation of motor skills, specifically how multiple motor memories can be learned concurrently without interference. We took inspiration from both low- and high-level motor research - that is recent advances in electrophysiological perspectives of motor cortex, and recent studies of concurrent motor learning behaviour with follow-throughs - to hypothesize that motor adaptation maps neural, rather than physical, states of the limb to changes in motor command. This challenges a predominant view of motor learning which suggests that multiple perturbations can only be learned when each is associated (closely in time) with a different physical state of the body, or world. Instead, by factorially separating the planning and execution components of follow-through movements, we showed that the key to representing multiple motor memories is to have each associated with a different neural state (i.e. motor plan) and not differences in the physical state of the body (Sheahan et al., 2016).

In Chapter 3, we extended this first result by asking whether motor imagery can change the preparatory neural state, so that skills which normally interfere can be learned. Our question contrasts with many studies of motor learning with imagery in which the role of imagery is to rehearse or mentally practice a movement. We discovered a powerful and complementary role for imagery, in which motor imagery not of the skill itself, but of different movements after physically performing the skill, permitted learning that was not possible without imagery. Our findings relate to recent recordings in monkey motor cortex which show similar neural dynamics during preparation in both BMI control and overt execution (Vyas et al., 2018). Here, we suggested that motor imagery in humans changes motor cortical neural states via a similar mechanism, such that different motor memories can be formed and retrieved for the same motor command (Sheahan et al., 2018). This chapter challenges the traditional way the field thinks about the relation between motor imagery and skill learning.

In Chapter 4 we asked whether context-dependent decay, like context-dependent adaptation, may also result from the planning of different movements, rather than their execution. We concurrently adapted participants to two oppositely directed force field perturbations using distinct lead-in movements, and subsequently assessed how de-adaptation depended on planning, execution and time. Surprisingly, we showed that while executing the adapted physical states of a movement resulted in a strong contextual de-adaptation effect, just planning and initiating the same movements did not. That is, just planning and initiating the different lead-ins resulted in no more decay than occurred passively with time. This highlights a novel disassociation between the plan-specificity of motor memory acquisition and retention.

Finally, having shown that the actions we plan can be instrumental in the representation of skills that develop, in Chapter 5, we extended a recent model (McNamee et al., 2017a) and attempted to predict *how* motor plans should be divided when trial sets become more complex. We approached this problem by considering the brain as a resource-constrained controller, and hypothesized that the optimal chunking scheme is the one that allows behaviours to be represented most efficiently. We simulated normative chunking of an optimal feedback controller for three trial sets and tested these chunking predictions against real human behaviour in both familiar and altered dynamics. While our simulations predicted different optimal chunking schemes for each of the simple trial sets we considered, these predictions were not borne out in the behavioural data. Instead, chunking behaviour varied across participants in all groups, but correlated with changes to chunking when environmental dynamics were altered with curl fields. Together this suggests that, while chunking behaviour in short motor sequences reflects more than simply the encoding efficiency captured in our model, the planning horizon used in familiar environments may scaffold planning when environment dynamics change.

6.2 Future work

The approach to understanding motor learning that was taken in this thesis was based entirely on a reductionist philosophy: that studying human motor learning can be pragmatically reduced to the short-term adaptation of point-to-point reaching movements in a laboratory setting. Despite the simplistic reaching tasks we have used, we have attempted to draw conclusions about human motor adaptation, retention, and chunking in general. It remains to be seen to what extent our findings generalise to other motor tasks studied in the laboratory, and to naturalistic behaviours in the wild.

In many instances, particularly in Chapters 2 and 3, we have attempted to draw connections between our high level behavioural findings in humans and neural population recordings from PMd and M1 in rhesus macaques. These monkeys display motifs of activity that have only recently begun to be experimentally observed in humans too (Pandarinath et al., 2015), and so our hypotheses about the relevance of neural dynamics to human motor learning is naturally bounded by further human electrophysiological work. In particular, it remains to be seen to what extent the effects observed in this thesis of planning on learning are specific to the motor system, or a more general feature of cognition.

Finally, we acknowledge that all studies we present here examined small numbers of healthy adult human participants (less than 20 per group) performing reaching tasks that yield intentionally constrained behaviours. Our conclusions must therefore be constrained until the robustness of our findings to larger, more general populations and different tasks is evaluated. Here we suggest and discuss further research that is needed to extend our conclusions.

6.2.1 The need for neural support

In Chapters 2 and 3 we used behavioural evidence of concurrent field learning across the same physical states, to suggest that planning different follow-throughs results in different neural states during the execution of the identical kinematic trajectories. While we were able to use controlled behaviours to isolate neural, over physical, states as the critical factor associated with motor adaptation, the suggestion that planning different motor sequences produces distinct neural trajectories needs electrophysiological verification. It is also worth acknowledging that the evidence for dynamical neural trajectories on which our interpretation is built, lie entirely within premotor and primary motor cortices (Churchland et al., 2012;

Pandarinath et al., 2015), while other motor regions such as the supplementary motor area do not appear to show these population-level rotations (Lara et al., 2018). A dynamical systems view of motor cortex ascribes motor preparation to seeding the system with an initial condition that gives rise to the subsequent neural trajectory. While it has been shown that these states are re-established albeit briefly under delayed, self-paced, and pressured reaction time movements (Ames et al., 2014; Lara et al., 2018), it remains to be seen whether this preparatory activity has a causal impact on the movement that follows. Establishing this causal link is necessary for our hypothesized connection between preparatory activity and motor adaptation.

Many studies have suggested that the cerebellum is important for supervised error-based learning such as incremental motor adaptation (Albus, 1971; Criscimagna-Hemminger et al., 2010; Galea et al., 2011; Herzfeld et al., 2015; Ito, 2006; Marr, 1969; Smith and Shadmehr, 2005; Tseng et al., 2007; Wolpert et al., 1998), while in Chapters 2 and 3 we have speculated that the dynamics of motor cortex may facilitate the specificity of such motor adaptation. These views are complementary, as in theory the different motor cortical dynamics resulting from different plans may very well be paralleled by different patterns of activation in the cerebellum (although it is unlikely that they display similar dynamical motifs). Subsequently, in Chapter 4 our results suggested that deadaptation may be plan-independent, appearing to be specific to particular motor memories only upon their execution. It is difficult at this point to reconcile these later behavioural results with the relative contributions of the cerebellum and cortex to the specificity of adaptation and de-adaptation, but it is hoped that further evidence, both behavioural and neural may help to delineate their contributions more clearly.

Related to this, a dynamical systems perspective of motor cortex may still provide a framework for interpreting the temporal de-adaptation observed in Chapter 4. Previously, Churchland et al. (2006a) demonstrated that small variations in motor cortical preparatory activity were predictive of variations in the output of the upcoming reach, suggesting that fluctuations in the motor cortical initial state have a causal effect on motor output. A similar theory might support the gradual deadaptation we observe in time, such that as endogenous neural states drift with the passage of time, the same input to motor cortex may result in either slightly different preparatory activity (input, X), or different dynamics resulting from this input (f(X)), to produce a slightly different subsequent movement. That motor de-adaptation was not specific to the planned action (the input, X) might suggest that such a neural drift was in the dynamics themselves (f(X)). This is speculative, but yields testable neural predictions.

It is also worth clarifying that in Chapter 5, the assumption that chunking would affect adaptation does not imply that movements are chunked in M1. Rather, our theory is based upon the assumption that the different ways of chunking movements will ultimately yield different preparatory activity, and hence different subsequent motor cortical dynamics that may affect the specificity of force-field adaptation. The idea that sequence-related activity is reflected in areas associated with motor preparation, such as supplementary motor, parietal and premotor areas has been supported by imaging studies (Abe et al., 2007; Yokoi et al., 2018) and single-cell recordings in macaques (Tanji and Shima, 1994), but this chunking may have origins elsewhere such as in the basal ganglia (Graybiel, 1998; Jin et al., 2014). Our theory makes no claims about the locus of chunking computation, only that the downstream impact of chunked motor plans may affect the specificity of adaptation. A multi-day pre-post training human fMRI study, which extends the duration of the training protocol we put forward in Chapter 5 may help to provide support for such a hypothesis.

Our hypotheses for neural mechanisms that support motor adaptation have centred on the neural dynamics of motor cortex, however this does not preclude the involvement of more cognitive processes and upstream areas such as the prefrontal cortex. In cognitive planning tasks, functional neuroimaging studies have shown that the prefrontal cortex is highly involved in planning (Balaguer et al., 2016; Schacter and Addis, 2007; Unterrainer and Owen, 2006), and patients with prefrontal lesions exhibit unstructured actions that either fail to achieve the task goal or result in participants taking significantly longer to achieve it (Shallice, 1982; Tim Shallice, 1991). Recently, the involvement of such cognitive or strategic processes in motor adaptation has risen to the fore (McDougle et al., 2016, 2015; Taylor and Ivry, 2014). McDougle et al. (2015) has suggested that the canonical learning curves observed in both force-field and visuomotor adaptation experiments may result from an interaction between explicit (cognitive) and implicit learning processes, paralleling the traditional dual-rate fast (explicit) and slow (implicit) process view of motor adaptation (Smith et al., 2006). By requiring participants to verbally report their reaching direction during adaptation, McDougle et al. (2015) demonstrated significant explicit strategy use in motor adaptation during blocked training. However this same work also suggests that an additional, much slower learning process is present which is unaccounted for by the explicit reports of strategy. Interestingly, when comparing to our own results, the learning we observe in all studies presented in this thesis is considerably slower (around 30-40 times slower) than the single-field learning examined by (McDougle et al., 2015), with participants adapting across 1200 trials to around 40% of the perturbations in our studies, compared to (approximately) 30 trials it took the participants to completely adapt in the study by McDougle and colleagues, and much slower than would typically be associated with a fast-learning process. Interpreted within the explicit/implicit framework, this implicates the role of more implicit over explicit forms learning in our results.

While the extent to which explicit processes are involved in the follow-through or lead-in tasks presented in this thesis was not directly tested, the development and usage of cognitive strategies with adaptation remains possible, but may be coherent with the neural mechanisms of learning we have proposed. Tracing studies have shown that dorsolateral prefrontal cortex projects strongly to premotor areas, suggesting the possibility that changes in cognitive plans or strategy use may result in significant changes in premotor activity, such as leading to different initial preparatory neural states (Lu et al., 1994). Indeed under this hypothesis, the resultant slow learning we observe could still be motor cortical, such that with learning, different physical movements are generated across the course of adaptation for the same cognitive strategy (plan), so long as this plan is different for each context.

In the absence of neural data, one way to dissociate the roles of explicit and implicit processes in the adaptation we observe may be to force participants to initiate their movements at very low preparation times, a technique used recently by (Haith et al., 2015) in a visuomotor adaptation paradigm. When participants were forced to initiate action on these low preparation time trials, responses produced a learning curve which corresponded closely to the slow, or more implicit component of motor adaptation. In theory, if the effects we observe are indeed an implicit form of adaptation, requiring participants to respond at reduced reaction times should result in similar rates of learning to the net learning curves we have demonstrated.

An interesting control for the work on imagery in Chapter 3 would be to establish whether imagery must be motor-related to enable distinct motor memories to form for the same physical states. That is, would associating each direction of force perturbation with a more abstract image, such as a car or house, be sufficient to drive concurrent adaptation. A negative result would support the interpretation that the learning we observe is not the consequence of cognitive associations between the follow-through and perturbation directions, but due to the similarity between motor imagery and overt movement. Previous behavioural work suggesting that passive visual cues are insufficient contextual cues for such tasks would strongly suggest such images would be insufficient (Howard et al., 2013). Neural recordings from motor cortex during the preparation of these images, versus motor imagery would help to verify our claims.

Initial neural support

Initial neural support for our hypothesis that planning is key to the representation of motor adaptation has, however, already begun to emerge. Recently neural recordings from monkeys covertly controlling a BMI-cursor showed that the proximity of motor preparatory states associated with covert and overt movements significantly correlated with the magnitude of subsequent motor adaptation transfer between the two (Vyas et al., 2018). Moreover, trial-by-trial kinematic errors significantly correlated with changes to the preparatory state with adaptation, together suggesting that 1) adaptation may involve finding the optimal set of initial neural conditions for producing the subsequent movement, and 2) the overlap of preparatory states may be a good neural correlate for motor learning transfer or interference in our force-field adaptation tasks. Together these results provide promising indications that our hypotheses on the neural underpinnings of motor memory separation may have milage.

6.2.2 The need for computational models

In all chapters of this thesis we have examined the intentionally constrained and repetitive reaching behaviours of small numbers of healthy adult human participants. In Chapters 2 and 3 we have subsequently quantified the presence or absence of learning behaviour from these data and drawn conclusions about the mechanisms that underlie the ability of motor memories to form. In these chapters we were largely interested in the binary learn or no-learn case. However, more subtle variants in the amount of learning were observed in the results from Chapter 5 in which participants were perturbed on movements that were part of sequences of different lengths. This suggests that the amount of interference between two motor plans is likely a continuous function which may depend on the parameters of the planned movements, such as movement extent, which has been shown to affect preparatory activity (Cisek and Kalaska, 2005; Fu et al., 1993; Kalaska and Crammond, 1992; Messier and Kalaska, 2000; Riehle and Requin, 1989). This thesis makes no claims about the degree to which two movements that have (at least partially) different motor plans will interact, and indeed this is a problem which could benefit greatly from a computational model. Given the many different parameters that can vary in a given movement, making more nuanced predictions of the rates at which concurrent learning occurs will require a model which can predict the representational similarity of different motor plans.

In Chapter 4, we encountered the novel phenomenon that executing a recently adapted motor memory in a virtual channel resulted in significantly less net decay of a competitor motor memory than would occur passively with time. While we refrained from modeling the potential interactions between the two concurrently adapted skills during de-adaptation that could give rise to such phenomena, this avenue is also ripe for further exploration.

6.2.3 The need for more naturalistic tasks

Finally, we note that as a result of convenience of technique, this thesis has focused almost exclusively on dynamic motor adaptation, which is likely to be just one of potentially many forms of motor learning (see Krakauer and Mazzoni (2011) for a discussion). It is unclear to what extent the work here translates to how children come to acquire complex motor skills, or even how an adult learns de novo tasks like juggling. In Chapter 5 we took a small step away from this reductionist approach, and while we again examined motor adaptation and simple reaching tasks, we did so to explore a theory for more complex behaviours that would benefit from hierarchical decomposition.

Chapter 5 took a more normative, model-driven approach to hypothesis testing than previous chapters. We tested a theory for chunking using a simple reaching task consisting of short motor sequences, and subsequently observed that behaviours were qualitatively distinct from our predictions. This does not however, necessarily suggest that larger, more naturalistic task sets with more complex, extended motor sequences would not place a premium on the need for efficient representations of action. Indeed, complex behaviour which approaches that of the real-world may be necessary to elicit clear chunking for testing these predictions more thoroughly. A very small step in this direction would be to simply increase the spatial and temporal complexity of reaching tasks like those in Chapter 5 by increasing the number of targets and length of the reaching sequence. A more ambitious approach might be to expand the examination of chunking past point-to-point reaches in favor of more complex sequential motor actions such as those required when learning a new dance.

The use of more naturalistic tasks and data poses significant challenges. For example, when data is obtained outside of a controlled lab environment, sensory feedback may be more difficult to control, and stereotyped behaviours may be harder to elicit. However, to understand the complexity of behaviour that arises through interaction with real environments, we must at some point expand our methodology away from the canonical robotic manipulandum. Recent advances in motion tracking and pose-estimation may make sourcing more complex, naturalistic movement data sets possible (Wei and Kording, 2018). Such an approach would be well-placed for examining the hierarchies that are induced by the complex motor tasks humans plan and execute in everyday life.

References

Abe, M., Hanakawa, T., Takayama, Y., Kuroki, C., Ogawa, S., and Fukuyama, H. (2007). Functional Coupling of Human Prefrontal and Premotor Areas during Cognitive Manipulation. *Journal of Neuroscience*, 27(13):3429–3438.

Acuna, D. E., Wymbs, N. F., Reynolds, C. a., Picard, N., Turner, R. S., Strick, P. L., Grafton, S. T., and Kording, K. P. (2014). Multi-faceted aspects of chunking enable robust algorithms. *Journal of neurophysiology*, pages 1–17.

Albus, J. S. (1971). A Theory of Cerebellar Function. *Mathematical Biosciences*, 10:25–61.

Ames, K. C., Ryu, S. I., and Shenoy, K. V. (2014). Neural dynamics of reaching following incorrect or absent motor preparation. *Neuron*, 81(2):438–451.

Bakker, M., De Lange, F. P., Stevens, J. A., Toni, I., and Bloem, B. R. (2007). Motor imagery of gait: A quantitative approach. *Experimental Brain Research*, 179(3):497–504.

Balaguer, J., Spiers, H. J., Hassabis, D., and Summerfield, C. (2016). Neural Mechanisms of Hierarchical Planning in a Virtual Subway Network. *Neuron*, 90(4):893–903.

Behrens, T. E. J., Woolrich, M. W., Walton, M. E., and Rushworth, M. F. S. (2007). Learning the value of information in an uncertain world. *Nature Neuroscience*, 10(9):1214–1221.

Bizzi, E., Accornero, N., Chapple, W., and Hogan, N. (1984). Posture control and trajectory formation during arm movement. *Journal of Neuroscience*, 4(11):2738–2744.

Blakemore, S., Wolpert, D., and Frith, C. D. (1998). Central cancellation of self produced tickle sensation. *Nature Neuroscience*, 1(7):635–640.

Botvinick, M. M., Niv, Y., and Barto, A. C. (2009). Hierarchically organized behavior and its neural foundations: A reinforcement learning perspective. *Cognition*, 113(3):262–280.

Brashers-Krug, T., Shadmehr, R., and Bizzi, E. (1996). Consolidation in human motor memory. *Nature*, 382(6588):252–255.

Butler, A. J., Cazeaux, J., Fidler, A., Jansen, J., Lefkove, N., Gregg, M., Hall, C., Easley, K. A., Shenvi, N., and Wolf, S. L. (2012). The movement imagery questionnaire-revised, second edition (MIQ-RS) is a reliable and valid tool for evaluating motor imagery in stroke populations. *Evidence-based Complementary and Alternative Medicine*.

Caithness, G., Osu, R., Bays, P. M., Chase, H., Klassen, J., Kawato, M., Wolpert, D., and Flanagan, J. R. (2004). Failure to consolidate the consolidation theory of learning for sensorimotor adaptation tasks. *The Journal of Neuroscience*, 24(40):8662–8671.

Cerritelli, B., Maruff, P., Wilson, P., and Currie, J. (2000). The effect of an external load on the force and timing components of mentally represented actions. *Behavioural Brain Research*, 108(1):91–96.

Cheney, P. D. and Fetz, E. E. (1980). Functional classes of primate corticomotoneuronal cells and their relation to active force. *Journal of Neurophysiology*, 44(4):773–791.

Churchland, M. M., Afshar, A., and Shenoy, K. V. (2006a). A Central Source of Movement Variability. *Neuron*, 52(6):1085–1096.

Churchland, M. M. and Cunningham, J. P. (2014). A Dynamical Basis Set for Generating Reaches. *Cold Spring Harbor Symposia on Quantitative Biology*, 79:67–80.

Churchland, M. M., Cunningham, J. P., Kaufman, M. T., Foster, J. D., Nuyujukian, P., Ryu, S. I., and Shenoy, K. V. (2012). Neural population dynamics during reaching. *Nature*, 487(7405):51–56.

Churchland, M. M., Cunningham, J. P., Kaufman, M. T., Ryu, S. I., and Shenoy, K. V. (2010). Cortical preparatory activity: representation of movement or first cog in a dynamical machine? *Neuron*, 68(3):387–400.

Churchland, M. M., Santhanam, G., and Shenoy, K. V. (2006b). Preparatory activity in premotor and motor cortex reflects the speed of the upcoming reach. *Journal of Neurophysiology*, 96(6):3130–3146.

Churchland, M. M. and Shenoy, K. V. (2007). Temporal Complexity and Heterogeneity of Single-Neuron Activity in Premotor and Motor Cortex. *Journal of Neurophysiology*, 97(6):4235–4257.

Churchland, M. M., Yu, B. M., Ryu, S. I., Santhanam, G., and Shenoy, K. V. (2006c). Neural Variability in Premotor Cortex Provides a Signature of Motor Preparation. *Journal of Neuroscience*, 26(14):3697–3712.

Cisek, P. and Kalaska, J. F. (2005). Neural correlates of reaching decisions in dorsal premotor cortex: Specification of multiple direction choices and final selection of action. *Neuron*, 45(5):801–814.

Cohen, M. R., Meissner, G. W., Schafer, R. J., and Raymond, J. L. (2004). Reversal of motor learning in the vestibulo-ocular reflex in the absence of visual input. *Learning & memory (Cold Spring Harbor, N.Y.)*, 11(5):559–565.

Cothros, N., Wong, J., and Gribble, P. L. (2009). Visual cues signaling object grasp reduce interference in motor learning. *Journal of neurophysiology*, 102(4):2112–2120.

Crammond, D. J. and Kalaska, J. F. (2000). Prior information in motor and premotor cortex: activity during the delay period and effect on pre-movement activity. *Journal of neurophysiology*, 84(2):986–1005.

Criscimagna-Hemminger, S. E., Bastian, A. J., and Shadmehr, R. (2010). Size of error affects cerebellar contributions to motor learning. *Journal of neurophysiology*, 103(4):2275–2284.

Criscimagna-Hemminger, S. E. and Shadmehr, R. (2008). Consolidation patterns of human motor memory. *Journal of Neuroscience*, 28(39):9610–9618.

D'Avella, A., Saltiel, P., and Bizzi, E. (2003). Combinations of muscle synergies in the construction of a natural motor behavior. *Nature Neuroscience*, 6(3):300–308.

Day, K. A., Roemmich, R. T., Taylor, J. A., and Bastian, A. J. (2016). Visuomotor learning generalizes around the intended movement. *eNeuro*, 3(April):1–12.

Decety, J. (1996). Do imagined and executed actions share the same neural substrate? *Cognitive Brain Research*, 3(2):87–93.

Decety, J. and Jeannerod, M. (1995). Mentally simulated movements in virtual reality: does Fitt's law hold in motor imagery? *Behavioural Brain Research*, 72(1-2):127–134.

Decety, J., Jeannerod, M., and Prablanc, C. (1989). The timing of mentally represented actions. *Behavioural Brain Research*, 34(1-2):35–42.

Dechent, P., Merboldt, K.-D., and Frahm, J. (2004). Is the human primary motor cortex involved in motor imagery? *Cognitive Brain Research*, 19(2):138–144.

Diedrichsen, J. (2007). Optimal Task-Dependent Changes of Bimanual Feedback Control and Adaptation. *Current Biology*, 17(19):1675–1679.

Diedrichsen, J., Hashambhoy, Y., Rane, T., and Shadmehr, R. (2005). Neural Correlates of Reach Errors. *Journal of Neuroscience*, 25(43):9919–9931.

Doya, K. (2000). Complementary roles of basal ganglia and cerebellum in learning and motor control. *Current Opinion in Neurobiology*, 10:732–739.

Doyon, J. and Benali, H. (2005). Reorganization and plasticity in the adult brain during learning of motor skills. *Current Opinion in Neurobiology*, 15:161–167.

Driskell, J. E., Copper, C., and Moran, A. (1994). Does mental practice enhance performance? *Journal of Applied Psychology*, 79(4):481–492.

Evarts, E. V. (1968). Relation of pyramidal tract activity to force exerted during voluntary movement. *Journal of Neurophysiology*, 31(1):14–27.

Faisal, A. A., Selen, L. P. J., and Wolpert, D. (2008). Noise in the nervous system. *Nature Reviews Neuroscience*, 9(4):292–303.

Feldman, A. (1966). Functional tuning of the nervous system with control of movement or maintenance of a steady posture. *Biophysics*, 11.

Feldman, A. G. and Levin, M. F. (1995). The origin and use of positional frames of reference in motor control. *Behavioral and Brain Sciences*, 18(4):723–744.

Feldman, J. (2000). Minimization of Boolean complexity in human concept learning. *Nature*, 407(6804):630–633.

Fernandez-Ruiz, J., Wong, W., Armstrong, I. T., and Flanagan, J. R. (2011). Relation between reaction time and reach errors during visuomotor adaptation. *Behavioural Brain Research*, 219(1):8–14.

Flanagan, J. R., Vetter, P., Johansson, R. S., and Wolpert, D. (2003). Prediction precedes control in motor learning. *Current Biology*, 13(2):146–150.

Flanagan, J. R. and Wing, a. M. (1997). The role of internal models in motion planning and control: evidence from grip force adjustments during movements of hand-held loads. *Journal of Neuroscience*, 17(4):1519–1528.

Flash, T. (1987). The control of hand equilibrium trajectories in multi-joint arm movements. *Biological cybernetics*, 425:257–274.

Flash, T. and Hogan, N. (1985). The coordination of arm movements: an experimentally confirmed mathematical model. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, 5(7):1688–1703.

Flesch, T., Balaguer, J., Dekker, R., Nili, H., and Summerfield, C. (2018). Focused learning promotes continual task performance in humans. *bioRxiv*, page 247460.

Franklin, D. W. and Wolpert, D. (2011). Computational mechanisms of sensorimotor control. *Neuron*, 72(3):425–442.

Fu, Q. J., Suarez, J. I., and Ebner, T. J. (1993). Neuronal specification of direction and distance during reaching movements in the superior precentral premotor area and primary motor cortex of monkeys. *Neurosurgery*, 70(5):2097 – 2166.

Galea, J. M., Vazquez, A., Pasricha, N., Xivry, J.-j. O. D., and Celnik, P. (2011). Dissociating the Roles of the Cerebellum and Motor Cortex during Adaptive Learning : The Motor Cortex Retains What the Cerebellum Learns. *Cerebral Cortex*, 21(August):1761–1770.

Gandolfo, F., Mussa-Ivaldi, F. A., and Bizzi, E. (1996). Motor learning by field approximation. *Proceedings of the National Academy of Sciences*, 93(April):3843–3846.

Gentili, R., Han, C. E., Schweighofer, N., and Papaxanthis, C. (2010). Motor Learning Without Doing: Trial-by-Trial Improvement in Motor Performance During Mental Training. *Journal of Neurophysiology*, 104(2):774–783.

Gentili, R. and Papaxanthis, C. (2015). Laterality effects in motor learning by mental practice in right-handers. *Neuroscience*, 297:231–242.

Gentili, R., Papaxanthis, C., and Pozzo, T. (2006). Improvement and generalization of arm motor performance through motor imagery practice. *Neuroscience*, 137(3):761–772.

Georgopoulos, A. P., Kalaska, J. F., Caminiti, R., and Massey, J. T. (1982). On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. *Journal of Neuroscience*, 2(11)(11):1527–1537.

Georgopoulos, A. P., Schwartz, A. B., and Kettner, R. E. (1986). Neuronal Population Coding of Movement Direction. *Science*, 233(March):1416–1419.

Gershman, S. J., Pesaran, B., and Daw, N. D. (2009). Human Reinforcement Learning Subdivides Structured Action Spaces by Learning Effector-Specific Values. *Journal of Neuroscience*, 29(43):13524–13531.

Gomi, H. and Kawato, M. (1996). Equilibrium-point control hypothesis examined by measured arm stiffness during multijoint movement. *Science (New York, N.Y.)*, 272(5258):117–120.

Graybiel, A. M. (1998). The Basal Ganglia and Chunking of Action Repertoires. 136(70):119–136.

Gregg, M., Hall, C., and Butler, A. J. (2010). The MIQ-RS: A suitable option for examining movement imagery ability. *Evidence-based Complementary and Alternative Medicine*, 7(2):249–257.

Gribble, P. L., Ostry, D. J., Sanguineti, V., and Laboissiere, R. (1998). Are complex control signals required for human arm movement? *J Neurophysiol*, 79(3):1409–1424.

Grunwald, P. (2004). *A Tutorial Introduction to the Minimum Description Length Principle*.

Grush, R. (2004). The emulation theory of representation: Motor control, imagery, and perception. *Behavioral and Brain Sciences*, 27(3):377–396.

Hadipour-Niktarash, A., Lee, C. K., Desmond, J. E., and Shadmehr, R. (2007). Impairment of Retention But Not Acquisition of a Visuomotor Skill Through Time-Dependent Disruption of Primary Motor Cortex. *Journal of Neuroscience*, 27(49):13413–13419.

Haith, A. M., Huberdeau, D. M., and Krakauer, J. W. (2015). The Influence of Movement Preparation Time on the Expression of Visuomotor Learning and Savings. *The Journal of Neuroscience*, 35(13):5109–5117.

Haith, A. M. and Krakauer, J. W. (2018). The multiple effects of practice: skill, habit and reduced cognitive load. *Current Opinion in Behavioral Sciences*, 20:196–201.

Hardwick, R. M., Caspers, S., Eickhoff, S. B., and Swinnen, S. P. (2017a). Neural Correlates of Motor Imagery, Action Observation, and Movement Execution: A Comparison Across Quantitative Meta-Analyses. *bioRxiv*.

Hardwick, R. M., Forrence, A. D., Krakauer, J. W., and Haith, A. M. (2017b). Skill Acquisition and Habit Formation as Distinct Effects of Practice. *bioRxiv*, pages 1–35.

Harris, C. M. and Wolpert, D. (1998). Signal-dependent noise determines motor planning. *Nature*, 394(August).

Heald, J. B., Ingram, J. N., Flanagan, J. R., and Wolpert, D. (2018). Multiple motor memories are learned to control different points on a tool. *Nature Human Behaviour*, 2(4):300–311.

Hennequin, G., Vogels, T. P., and Gerstner, W. (2014). Optimal control of transient dynamics in balanced networks supports generation of complex movements. *Neuron*, 82(6):1394–1406.

Herzfeld, D., Kojima, Y., Soetedjo, R., and Shadmehr, R. (2015). Encoding of action by the Purkinje cells of the cerebellum. *Nature*, 526(7573):439–42.

Herzfeld, D., Vaswani, P. A., Marko, M., and Shadmehr, R. (2014a). A memory of errors in sensorimotor learning. *Science*, 345(6202).

Herzfeld, D. J., Kojima, Y., Soetedjo, R., and Shadmehr, R. (2018). Encoding of error and learning to correct that error by the Purkinje cells of the cerebellum. *Nature Neuroscience*, 21(5):736–743.

Herzfeld, D. J., Pastor, D., Haith, A. M., Rossetti, Y., Shadmehr, R., and O'Shea, J. (2014b). Contributions of the cerebellum and the motor cortex to acquisition and retention of motor memories. *NeuroImage*, 98:147–158.

Hétu, S., Grégoire, M., Saimpont, A., Coll, M. P., Eugène, F., Michon, P. E., and Jackson, P. L. (2013). The neural network of motor imagery: An ALE meta-analysis. *Neuroscience and Biobehavioral Reviews*, 37(5):930–949.

Hirashima, M. and Nozaki, D. (2012). Distinct motor plans form and retrieve distinct motor memories for physically identical movements. *Current Biology*, 22(5):432–436.

Hocherman, S. and Wise, S. P. (1991). Effects of hand movement path on motor cortical activity. *Experimental Brain Research*, 83:285–302.

Hogan, N. (1984). An organizing principle for a class of voluntary movements. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, 4(11):2745–2754.

Hosseini, E. A., Nguyen, K. P., and Joiner, W. M. (2017). The decay of motor adaptation to novel movement dynamics reveals an asymmetry in the stability of motion state-dependent learning. *PLoS Computational Biology*, 13(5):1–29.

Howard, I. S., Ford, C., Cangelosi, A., and Franklin, D. W. (2017). Active lead-in variability affects motor memory formation and slows motor learning. *Scientific Reports*, 7(1):7806.

Howard, I. S. and Franklin, D. W. (2015). Neural Tuning Functions Underlie Both Generalization and Interference. *PLoS ONE*, 10(6):1–21.

Howard, I. S., Ingram, J. N., Franklin, D. W., and Wolpert, D. (2012). Gone in 0.6 Seconds: The Encoding of Motor Memories Depends on Recent Sensorimotor States. *Journal of Neuroscience*, 32(37):12756–12768.

Howard, I. S., Ingram, J. N., and Wolpert, D. (2009). A modular planar robotic manipulandum with end-point torque control. *Journal of Neuroscience Methods*, 181(2):199–211.

Howard, I. S., Ingram, J. N., and Wolpert, D. (2010). Context-Dependent Partitioning of Motor Learning in Bimanual Movements. *Journal of Neurophysiology*, 104(4):2082–2091.

Howard, I. S., Wolpert, D., and Franklin, D. W. (2013). The effect of contextual cues on the encoding of motor memories. *Journal of Neurophysiology*, 109(10):2632–2644.

Howard, I. S., Wolpert, D., and Franklin, D. W. (2015). The value of the follow-through derives from motor learning depending on future actions. *Current Biology*, 25(3):397–401.

Hwang, E. J., Donchin, O., Smith, M. A., and Shadmehr, R. (2003). A gain-field encoding of limb position and velocity in the internal model of arm dynamics. *PLoS Biology*, 1(2).

Hwang, E. J., Smith, M. A., and Shadmehr, R. (2006). Adaptation and generalization in acceleration-dependent force fields. *Experimental Brain Research*, 169(4):496–506.

Ingram, J. N., Flanagan, J. R., and Wolpert, D. (2013). Context-dependent decay of motor memories during skill acquisition. *Current Biology*, 23(12):1107–1112.

Ito, M. (2006). Cerebellar circuitry as a neuronal machine. *Progress in Neurobiology*, 78:272–303.

Ivanenko, Y. P. (2003). Temporal Components of the Motor Patterns Expressed by the Human Spinal Cord Reflect Foot Kinematics. *Journal of Neurophysiology*, 90(5):3555–3565.

Izawa, J., Rane, T., Donchin, O., and Shadmehr, R. (2008). Motor Adaptation as a Process of Reoptimization. *Journal of Neuroscience*, 28(11):2883–2891.

Javadi, A.-H., Emo, B., Howard, L. R., Zisch, F. E., Yu, Y., Knight, R., Pinelo Silva, J., and Spiers, H. J. (2017). Hippocampal and prefrontal processing of network topology to simulate the future. *Nature Communications*, 8:1–11.

Jeannerod, M. (2001). Neural simulation of action: A unifying mechanism for motor cognition. *NeuroImage*, 14:103–109.

Jin, X., Tecuapetla, F., and Costa, R. M. (2014). Basal ganglia subcircuits distinctively encode the parsing and concatenation of action sequences. *Nature Neuroscience*, 17(3):423–430.

Johansson, R. S. and Westling, G. (1984). Roles of glabrous skin receptors and sensorimotor memory in automatic control of precision grip when lifting rougher or more slippery objects. *Experimental Brain Research*, 56:550–564.

Joiner, W. M. and Smith, M. A. (2008). Long-Term Retention Explained by a Model of Short-Term Learning in the Adaptive Control of Reaching. *Journal of Neurophysiology*, 100(5):2948–2955.

Jones, K. E., Hamilton, A. F., and Wolpert, D. (2002). Sources of signal-dependent noise during isometric force production. *Journal of Neurophysiology*, 88(3):1533–1544.

Jordan, M. I. and Rumelhart, D. E. (1992). Forward models: Supervised learning with a distal teacher. *Cognitive Science*, 16:307–354.

Kalaska, J. F. (2009). From Intention to Action: Motor Cortex and the Control of Reaching Movements. In Sternad, D., editor, *Progress in Motor Control*, pages 139–178.

Kalaska, J. F. and Crammond, D. J. (1992). Cerebral cortical mechanisms of reaching movements. *Science (New York, N.Y.)*, 255(5051):1517–23.

Kasai, T., Kawai, S., Kawanishi, M., and Yahagi, S. (1997). Evidence for facilitation of motor evoked potentials (MEPs) induced by motor imagery. *Brain Research*, 744(1):147–150.

Kassardjian, C. D. (2005). The Site of a Motor Memory Shifts with Consolidation. *Journal of Neuroscience*, 25(35):7979–7985.

Kaufman, M. T., Churchland, M. M., Ryu, S. I., and Shenoy, K. V. (2014). Cortical activity in the null space: permitting preparation without movement. *Nature neuroscience*, 17(3):440–8.

Kawato, M. (1999). Internal models for motor control and trajectory planning. *Current opinion in neurobiology*, 9(6):718–727.

Kawato, M., Kuroda, T., Imamizu, H., Nakano, E., Miyauchi, S., and Yoshioka, T. (2003). Internal forward models in the cerebellum: fMRI study on grip force and load force coupling. *Progress in Brain Research*, 142:171–188.

Keramati, M., Smittenaar, P., Dolan, R. J., and Dayan, P. (2016). Adaptive integration of habits into depth-limited planning defines a habitual-goal–directed spectrum. *Proceedings of the National Academy of Sciences*, 113(45):12868–12873.

Kirkpatrick, J., Pascanu, R., Rabinowitz, N., Veness, J., Desjardins, G., Rusu, A. A., Milan, K., Quan, J., Ramalho, T., Grabska-Barwinska, A., Hassabis, D., Clopath, C., Kumaran, D., and Hadsell, R. (2016). Overcoming catastrophic forgetting in neural networks. *ArXiv*.

Kitago, T., Ryan, S. L., Mazzoni, P., Krakauer, J. W., and Haith, A. M. (2013). Unlearning versus savings in visuomotor adaptation: comparing effects of washout, passage of time, and removal of errors on motor memory. *Frontiers in human neuroscience*, 7(June):307.

Krakauer, J. W., Ghazanfar, A. A., Gomez-Marin, A., Maciver, M. A., and Poeppel, D. (2017). Neuroscience Needs Behavior: Correcting a Reductionist Bias. *Neuron*, 93(3):480–490.

Krakauer, J. W., Ghez, C., and Ghilardi, M. F. (2005). Adaptation to Visuomotor Transformations: Consolidation, Interference, and Forgetting. *Journal of Neuroscience*, 25(2):473–478.

Krakauer, J. W., Ghilardi, M. F., and Ghez, C. (1999). Independent learning of internal models for kinematic and dynamic control of reaching. *Nature neuroscience*, 2(11):1026–31.

Krakauer, J. W. and Mazzoni, P. (2011). Human sensorimotor learning: Adaptation, skill, and beyond. *Current Opinion in Neurobiology*, 21(4):636–644.

Krakauer, J. W., Mazzoni, P., Ghazizadeh, A., Ravindran, R., and Shadmehr, R. (2006). Generalization of motor learning depends on the history of prior action. *PLoS Biology*, 4(10):1798–1808.

Krakauer, J. W., Pine, Z. M., Ghilardi, M. F., and Ghez, C. (2000). Learning of visuomotor transformations for vectorial planning of reaching trajectories. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, 20(23):8916–8924.

Kriegeskorte, N. and Douglas, P. K. (2018). Cognitive computational neuroscience. *Nature Neuroscience*, 21:1148–1160.

Lago-Rodriguez, A. and Miall, R. C. (2016). Online Visual Feedback during Error-Free Channel Trials Leads to Active Unlearning of Movement Dynamics: Evidence for Adaptation to Trajectory Prediction Errors. *Frontiers in Human Neuroscience*, 10(September):472.

Lara, A. H., Elsayed, G. F., Zimnik, A. J., Cunningham, J. P., and Churchland, M. M. (2018). Conservation of preparatory neural events regardless of how movement is initiated. *eLife*, 7(31826):1–34.

Lashley, K. (1951). The problem of serial order in behavior. *Cerebral mechanisms in behavior*, pages 112–136.

Lebon, F., Ruffino, C., Greenhouse, I., Labruna, L., Ivry, R. B., and Papaxanthis, C. (2018). The Neural Specificity of Movement Preparation During Actual and Imagined Movements. *Cerebral Cortex*, pages 1–12.

Lee, J.-Y. and Schweighofer, N. (2009). Dual adaptation supports a parallel architecture of motor memory. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, 29(33):10396–10404.

Liu, D. (2008). *Computational and Psychophysical Studies of Goal-Directed Arm Movements*. PhD thesis, University of California, San Diego.

Liu, D. and Todorov, E. (2007). Evidence for the Flexible Sensorimotor Strategies Predicted by Optimal Feedback Control. *Journal of Neuroscience*, 27(35):9354–9368.

Lu, M.-t., Preston, J. B., and Strick, P. L. (1994). Interconnections Between the Prefrontal Cortex and the Premotor Areas in the Frontal Lobe. *The Journal of Comparative Neurology*, 341:375–392.

MacKay, D. J. C. (2003). *Information Theory, Inference and Learning Algorithms*. Cambridge University Press, 7.2 edition.

Marr, D. (1969). A theory of cerebellar cortex. *Journal of Physiology*, 202:437–470.

Mazzoni, P. and Krakauer, J. W. (2006). An Implicit Plan Overrides an Explicit Strategy during Visuomotor Adaptation. *Journal of Neuroscience*, 26(14):3642–3645.

McCloskey, M. and Cohen, N. J. (1989). Catastrophic Interference in Connectionist Networks: The Sequential Learning Problem. *Psychology of Learning and Motivation - Advances in Research and Theory*, 24(C):109–165.

McDougle, S. D., Boggess, M. J., Crossley, M. J., Parvin, D., Ivry, R. B., and Taylor, J. A. (2016). Credit assignment in movement-dependent reinforcement learning. *Proceedings of the National Academy of Sciences*, 113(24):6797–6802.

McDougle, S. D., Bond, K. M., and Taylor, J. A. (2015). Explicit and Implicit Processes Constitute the Fast and Slow Processes of Sensorimotor Learning. *Journal of Neuroscience*, 35(26):9568–9579.

McDougle, S. D., Bond, K. M., and Taylor, J. A. (2017). Implications of plan-based generalization in sensorimotor adaptation. *Journal of Neurophysiology*, 118:383–393.

McNamee, D., Lengyel, M., and Wolpert, D. (2017a). Neural coding constraints on motor chunking. In *27th Annual Society for the Neural Control of Movement Meeting*.

McNamee, D., Wolpert, D., and Lengyel, M. (2016). Efficient state-space modularization for planning: theory, behavioral and neural signatures. *NIPS*.

McNamee, D., Wolpert, D., and Lengyel, M. (2017b). Efficient multi-dimensional neural coding via conformal diffusion flow. In *Computational and Systems Neuroscience*, pages 159–160.

Messier, J. and Kalaska, J. F. (2000). Covariation of primate dorsal premotor cell activity with direction and amplitude during a memorized-delay reaching task. *Journal of Neurophysiology*, 84(1):152–165.

Miall, R. C., Weir, D. J., Wolpert, D., and Stein, J. F. (1993). Is the cerebellum a smith predictor? *Journal of motor behavior*, 25(3):203–216.

Michaels, J. A., Dann, B., and Scherberger, H. (2016). Neural Population Dynamics during Reaching Are Better Explained by a Dynamical System than Representational Tuning. *PLOS Computational Biology*, 12(11):e1005175.

Miller, G. A., Galanter, E., and Pribram, K. H. (1960). *Plans and the Structure of Behavior*. Holt, Rinehart and Winston, Inc.

Miller, K., Schalk, G., Fetz, E., den Nijs, M., Ojemann, J., and Rao, R. (2010). Cortical activity during motor execution, motor imagery, and imagery-based online feedback. *Proceedings of the National Academy of Sciences*, 107(15):7113–7113.

Milner, T. E. and Franklin, D. W. (2005). Impedance control and internal model use during the initial stage of adaptation to novel dynamics in humans. *The Journal of Physiology*, 567(Pt 2):651–664.

Mokienko, O. A., Chervyakov, A. V., Kulikova, S. N., Bobrov, P. D., Chernikova, L. A., Frolov, A. A., and Piradov, M. A. (2013). Increased motor cortex excitability during motor imagery in brain-computer interface trained subjects. *Frontiers in computational neuroscience*, 7.

Monsell, S. (2003). Task switching. *Trends in Cognitive Sciences*, 7(3):134–140.

Morasso, P. G. (1981). Spatial control of arm movements. *Experimental Brain Research*, 42:223–227.

Morasso, P. G. and Schieppati, M. (1999). Can Muscle Stiffness Alone Stabilize Upright Standing? *Journal of Neurophysiology*, 82(1994):1622–1626.

Nashed, J. Y., Crevecoeur, F., and Scott, S. H. (2012). Influence of the behavioral goal and environmental obstacles on rapid feedback responses. *Journal of Neurophysiology*, 108(4):999–1009.

Nashed, J. Y., Crevecoeur, F., and Scott, S. H. (2014). Rapid Online Selection between Multiple Motor Plans. *The Journal of Neuroscience*, 34(5):1769–1780.

Newell, A. (1973). You can't play 20 questions with nature and win: Projective comments on the papers of this symposium. *Visual Information Processing*, pages 283–308.

Nowak, D. A., Timmann, D., and Hermsdörfer, J. (2007). Dexterity in cerebellar agenesis. *Neuropsychologia*, 45(4):696–703.

Nozaki, D., Kurtzer, I. L., and Scott, S. H. (2006). Limited transfer of learning between unimanual and bimanual skills within the same limb. *Nature neuroscience*, 9(11):1364–1366.

Nozaki, D. and Scott, S. H. (2009). Multi-compartment model can explain partial transfer of learning within the same limb between unimanual and bimanual reaching. *Experimental Brain Research*, 194(3):451–463.

Oldfield, R. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, 9(1):97–113.

Omrani, M., Kaufman, M. T., Hatsopoulos, N. G., and Cheney, P. D. (2017). Perspectives on classical controversies about the motor cortex. *Journal of Neurophysiology*, 118:1828–1848.

O'Shea, D. J. and Shenoy, K. V. (2016). The Importance of Planning in Motor Learning. *Neuron*, pages 1–4.

Pandarinath, C., Gilja, V., Blabe, C. H., Nuyujukian, P., Sarma, A. A., Sorice, B. L., Eskandar, E. N., Hochberg, L. R., Henderson, J. M., and Shenoy, K. V. (2015). Neural population dynamics in human motor cortex during movements in people with ALS. *eLife*, 4:e07436.

Papaxanthis, C., Schieppati, M., Gentili, R., and Pozzo, T. (2002). Imagined and actual arm movements have similar durations when performed under different conditions of direction and mass. *Experimental Brain Research*, 143(4):447–452.

Pruszynski, J. A. and Scott, S. H. (2012). Optimal feedback control and the long-latency stretch response. *Experimental Brain Research*, 218(3):341–359.

Ramkumar, P., Acuna, D. E., Berniker, M., Grafton, S. T., Turner, R. S., and Kording, K. P. (2016). Chunking as the result of an efficiency computation trade-off. *Nature Communications*, 7:12176.

Ratcliff, R. (1990). Connectionist models of recognition memory: constraints\nimposed by learning and forgetting functions. *Psychological review*, 97(2):285–308.

Rhodes, B. J., Bullock, D., Verwey, W. B., Averbeck, B. B., and Page, M. P. a. (2004). Learning and production of movement sequences: Behavioral, neurophysiological, and modeling perspectives. *Human Movement Science*, 23(5):699–746.

Riehle, A. and Requin, J. (1989). Monkey primary motor and premotor cortex: single-cell activity related to prior information about direction and extent of an intended movement. *Journal of Neurophysiology*, 61(3):534–49.

Riehle, A. and Requin, J. (1993). The predictive value for performance speed of preparatory changes in neuronal activity of the monkey motor and premotor cortex. *Behavioural Brain Research*, 53(1-2):35–49.

Rosenbaum, D. A., Kenny, S. B., and Derr, M. a. (1983). Hierarchical control of rapid movement sequences. *Journal of experimental psychology. Human perception and performance*, 9(1):86–102.

Ruffino, C., Papaxanthis, C., and Lebon, F. (2017). Neural plasticity during motor learning with motor imagery practice: Review and perspectives. *Neuroscience*, 341:61–78.

Sadeghi, M. (2018). *Representation and Interaction of Sensorimotor Learning Processes*. PhD thesis, University of Cambridge.

Sakai, K., Kitaguchi, K., and Hikosaka, O. (2003). Chunking during human visuomotor sequence learning. *Experimental Brain Research*, 152(2):229–242.

Sarwary, A. M. E., Stegeman, D. F., Selen, L. P. J., and Medendorp, W. P. (2015). Generalization and transfer of contextual cues in motor learning. *Journal of neurophysiology*, 114(3):1565–76.

Schacter, D. L. and Addis, D. R. (2007). The cognitive neuroscience of constructive memory: remembering the past and imagining the future. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1481):773–786.

Scheidt, R. A., Reinkensmeyer, D. J., Conditt, M. A., Rymer, W. Z., and Mussa-Ivaldi, F. A. (2000). Persistence of motor adaptation during constrained, multi-joint, arm movements. *Journal of Neurophysiology*, 84(2):853–862.

Schmidt, R. A., Zelaznik, H., Hawkins, B., Frank, J. S., and Quinn, J. T. (1979). Motor-Output Variability: A Theory for the Accuracy of Rapid Motor Acts. *Psychological Review*, 86(5).

Scholz, J. P. and Schöner, G. (1999). The uncontrolled manifold concept: Identifying control variables for a functional task. *Experimental Brain Research*, 126(3):289–306.

Schween, R., Taylor, J. A., and Hegele, M. (2018). Plan-based generalization shapes local implicit adaptation to opposing visuomotor transformations. *bioRxiv*, pages 1–29.

Scott, S. H. (2008). Inconvenient Truths about neural processing in primary motor cortex. *Journal of Physiology*, 586(5):1217–1224.

Seidler, R. D. (2010). Neural Correlates of Motor Learning, Transfer of Learning, and Learning to Learn. *Exercise and sport sciences reviews*, 38(1):3–9.

Shadmehr, R. and Brashers-Krug, T. (1997). Functional stages in the formation of human long-term motor memory. *The Journal of neuroscience*, 17(1):409–419.

Shadmehr, R. and Holcomb, H. H. (1997). Neural Correlates of Motor Memory Consolidation. *Science*, 277(5327):821–825.

Shadmehr, R. and Moussavi, Z. M. (2000). Spatial generalization from learning dynamics of reaching movements. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, 20(20):7807–15.

Shadmehr, R. and Mussa-Ivaldi, F. A. (1994). Adaptive representation of dynamics during learning of a motor task. *The Journal of Neuroscience*, 74(May):17.

Shallice, T. (1982). Specific Impairments of Planning. 209:199–209.

Sheahan, H. R., Franklin, D. W., and Wolpert, D. (2016). Motor Planning, Not Execution, Separates Motor Memories. *Neuron*, 92(4):773–779.

Sheahan, H. R., James, N. I., Goda, M. Ž., and Wolpert, D. (2018). Imagery of movements immediately following performance allows learning of motor skills that interfere. *bioRXiv*.

Shenoy, K. V., Sahani, M., and Churchland, M. M. (2013). Cortical control of arm movements: a dynamical systems perspective. *Annual review of neuroscience*, 36:337–59.

Shmuelof, L., Huang, V. S., Haith, A. M., Delnicki, R. J., Mazzoni, P., and Krakauer, J. W. (2012). Overcoming Motor "Forgetting" Through Reinforcement Of Learned Actions. *Journal of Neuroscience*, 32(42):14617–14621.

Sirigu, A., Duhamel, J.-R., Cohen, L., Pillon, B., Dubois, B., and Agid, Y. (1996). The Mental Representation of Hand Movements After Parietal Cortex Damage. *Science*, 273(5281):1564–1568.

Smith, M. A., Ghazizadeh, A., and Shadmehr, R. (2006). Interacting adaptive processes with different timescales underlie short-term motor learning. *PLoS Biology*, 4(6):1035–1043.

Smith, M. A. and Shadmehr, R. (2005). Intact Ability to Learn Internal Models of Arm Dynamics in Huntington's Disease But Not Cerebellar Degeneration. *Journal of Neurophysiology*, 93(5):2809–2821.

Solway, A., Diuk, C., Córdova, N., Yee, D., Barto, A. G., Niv, Y., and Botvinick, M. M. (2014). Optimal Behavioral Hierarchy. *PLoS Computational Biology*, 10(8).

Sosnik, R., Hauptmann, B., Karni, A., and Flash, T. (2004). When practice leads to co-articulation : the evolution of geometrically defined movement primitives. *Experimental Brain Research*, 156:422–438.

Stavisky, S. D., Kao, J. C., Ryu, S. I., and Shenoy, K. V. (2017). Motor Cortical Visuomotor Feedback Activity Is Initially Isolated from Downstream Targets in Output-Null Neural State Space Dimensions. *Neuron*, 95(1):195–208.e9.

Stinear, C. M., Byblow, W. D., Steyvers, M., Levin, O., and Swinnen, S. P. (2006). Kinesthetic, but not visual, motor imagery modulates corticomotor excitability. *Experimental Brain Research*, 168(1-2):157–164.

Sussillo, D., Churchland, M. M., Kaufman, M. T., and Shenoy, K. V. (2015). A neural network that finds a naturalistic solution for the production of muscle activity. *Nature neuroscience*, 18(7):1025–33.

Sutton, R. S., Precup, D., and Singh, S. (1999). Between MDPs and Semi-MDPs: A Framework for Temporal Abstraction in Reinforcement Learning. *Artificial Intelligence*, 112:181–211.

Takiyama, K. (2015). Context-dependent memory decay is evidence of effort minimization in motor learning: a computational study. *Frontiers in Computational Neuroscience*, 9(February):4.

Tanji, J. and Evarts, E. V. (1976). Anticipatory Activity of Motor Cortex Neurons in Relation to Direction of an Intended Movement. *Journal of Neurophysiology*, 39(5):1062–1068.

Tanji, J. and Shima, K. (1994). Role for supplementary motor area cells in planning several movements ahead.

Taylor, J. A. and Ivry, R. B. (2014). *Cerebellar and Prefrontal Cortex Contributions to Adaptation, Strategies, and Reinforcement Learning*, volume 210. Elsevier B.V., 1 edition.

Thoroughman, K. A. and Shadmehr, R. (2000). Learning of action through adaptive combination of motor primitives. *Nature*, 407(6805):742–747.

Tim Shallice, P. W. B. (1991). Deficits in Strategy Application Following Frontal Lobe Damage in Man. *Brain*, (114):727–741.

Todorov, E. (1998). Studies of goal directed movements. *PhD Thesis*, page 146.

Todorov, E. (2002). Interpreting motor adaptation results within the framework of optimal feedback control. *Advances in Computational Motor Control*, 747:3228.

Todorov, E. (2004). Optimality principles in sensorimotor control. *Nature Neuroscience*, 7(9):907–915.

Todorov, E. (2005). Stochastic optimal control and estimation methods adapted to the noise characteristics of the sensorimotor system. *Neural computation*, 17(5):1084–1108.

Todorov, E. and Jordan, M. I. (2002). Optimal feedback control as a theory of motor coordination. *Nature Neuroscience*, 5(11):1226–1235.

Tseng, Y.-w., Diedrichsen, J., Krakauer, J. W., Shadmehr, R., and Bastian, A. J. (2007). Sensory Prediction Errors Drive Cerebellum-Dependent Adaptation of Reaching. *Journal of Neurophysiology*, 98(1):54–62.

Uno, Y., Kawato, M., and Suzuki, R. (1989). Formation and control of optimal trajectory in human multijoint arm movement. *Biological cybernetics*, 61:89–101.

Unterrainer, J. M. and Owen, A. M. (2006). Planning and problem solving : From neuropsychology to functional neuroimaging. *Journal of Physiology - Paris*, 99:308–317.

Van Der Kooij, K., Brenner, E., Van Beers, R. J., and Smeets, J. B. J. (2015). Visuomotor adaptation: How forgetting keeps us conservative. *PLoS ONE*, 10(2):1–13.

Vaswani, P. A. and Shadmehr, R. (2013). Decay of motor memories in the absence of error. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, 33(18):7700–9.

Vaswani, P. A., Shmuelof, L., Haith, A. M., Delnicki, R. J., Huang, V. S., Mazzoni, P., Shadmehr, R., and Krakauer, J. W. (2015). Persistent Residual Errors in Motor Adaptation Tasks: Reversion to Baseline and Exploratory Escape. *Journal of Neuroscience*, 35(17):6969–6977.

Verbruggen, F. and Logan, G. (2008). Response inhibition in the stop-signal pardigm. *Trends in cognitive sciences*, 12(11):418–424.

Verwey, W. B. (1996). Buffer Loading and Chunking in Sequential Keypressing. *Journal of Experimental Psychology: Human Perception and Performance*, 22(3):544–562.

Verwey, W. B. and Dronkert, Y. (1996). Practicing a Structured Continuous Key-Pressing Task: Motor Chunking or Rhythm Consolidation? *Journal of Motor Behavior*, 28(1):71–79.

Verwey, W. B. and Eikelboom, T. (2003). Evidence for Lasting Sequence Segmentation in the Discrete Sequence-Production Task. *Journal of Motor Behavior*, 35(2):171–181.

Vyas, S., Even-Chen, N., Stavisky, S. D., Ryu, S. I., Nuyujukian, P., and Shenoy, K. V. (2018). Neural Population Dynamics Underlying Motor Learning Transfer. *Neuron*, 97(5):1177–1186.

W. L. Nelson (1983). Physical Principles for Economies of Skilled Movements. *Biological Cybernetics*, 46:135–147.

Wainscott, S. K., Donchin, O., and Shadmehr, R. (2005). Internal models and contextual cues: encoding serial order and direction of movement. *Journal of neurophysiology*, 93(2):786–800.

Wei, K. and Kording, K. P. (2018). Behavioral tracking gets real. *Nature Neuroscience*.

Weiler, J., Gribble, P., and Pruszynski, J. (2015). Goal-dependent modulation of the long-latency stretch response at the shoulder , elbow and wrist. *Journal of Neurophysiology*, 114:3242–3254.

Weinrich, M. and Wise, S. P. (1982). The premotor cortex of the monkey. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, 2(9):1329–45.

Wise, S. P. (1985). The primate premotor cortex: past, present and preparatory. *Annual review of neuroscience*, 8:1–19.

Wolpert, D. and Flanagan, J. R. (2001). Motor prediction. *Current Biology*, 11(18):R729–R732.

Wolpert, D., Ghahramani, Z., and Jordan, M. I. (1995). An internal model for sensorimotor integration. *Science (New York, N.Y.)*, 269(5232):1880–1882.

Wolpert, D. and Kawato, M. (1998). Multiple Paried Forward and Inverse Models for Motor Control. *Neural Networks*, 11:1317–1329.

Wolpert, D., Miall, R. C., and Kawato, M. (1998). Internal models in the cerebellum. *Trends in Cognitive Sciences*, 2(9):338–347.

Wymbs, N. F., Bassett, D. S., Mucha, P. J., Porter, M. A., and Grafton, S. T. (2012). Differential Recruitment of the Sensorimotor Putamen and Frontoparietal Cortex during Motor Chunking in Humans. *Neuron*, 74(5):936–946.

Yeo, S.-H., Franklin, D. W., and Wolpert, D. (2016). When Optimal Feedback Control Is Not Enough: Feedforward Strategies Are Required for Optimal Control with Active Sensing. *PLOS Computational Biology*, 12(12):e1005190.

Yeo, S.-H., Wolpert, D., and Franklin, D. W. (2015). Coordinate representations for interference reduction in motor learning. *PLoS ONE*, 10(6):1–14.

Yokoi, A., Arbuckle, S. A., and Diedrichsen, J. (2018). The role of human primary motor cortex in the production of skilled finger sequences. *The Journal of Neuroscience*, 38(6):2798–17.

Yokoi, A., Hirashima, M., and Nozaki, D. (2011). Gain Field Encoding of the Kinematics of Both Arms in the Internal Model Enables Flexible Bimanual Action. *Journal of Neuroscience*, 31(47):17058–17068.

Appendix A

Parameters used in optimal feedback control simulations

Table A.1 Parameters used in optimal feedback control simulations in Chapter 5.

Parameter	Symbol	Value
Mass (kg)	m	1
Time step (s)	Δt	0.01
Sensorimotor delay (s)		0.05
Time constant of linear muscle filter (s)	τ	0.04
Control-dependent noise constant (parallel to u)	c_1	0.15
Control-dependent noise constant (perpendicular to u)	c_2	0.05
Overall sensory noise scaling factor	σ_s	0.5
Sensory noise covariance, position (cm)	σ_ω	0.5
Sensory noise covariance, velocity (cm/s)	σ_ω	5
Sensory noise covariance, force (N)	σ_ω	5
Goal time for reaching via-point (s)	T_1	0.40
Goal time for reaching secondary target (s)	T_2	0.80
Effort weighting in cost function	r	0.00005
Error weight on position (hitting the targets) in cost function	w_p	100
Error weight on stopping (zero velocity at target) in cost function	w_v	1
Error weight on stopping (zero force at target) in cost function	w_f	0.1