SENSORIMOTOR MECHANISMS INVOLVED IN
OBJECT ORIENTED BEHAVIOUR

by

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To my exceptional parents, Nina and Harvey, who taught me to work hard and be a mensch while doing so. And to my grandfather, Bernard, who taught me the value of curiosity through his intolerance for boredom.
Abstract

The manipulation of objects is a hallmark skill in the repertoire of human motor behaviour that involves the grasping, lifting and transporting of objects as well as movement decisions about what objects to interact with. These components of manipulation are often the focus of experiments as they offer a window into the sensormotor mechanisms that support complex and adaptable manipulatory skill. This thesis was designed to extend the scope of object manipulation studies by focusing on functional, object oriented tasks. Three of the four studies in this thesis focus on object transport, involving reaching movements while grasping novel objects. In the first study we examined the role of haptic feedback while participants transported a non-rigid object. We showed first, the importance of haptic feedback during learning, and second, that training without haptic feedback lead to persistent deficits when subsequently performing the task after the re-introduction of haptic feedback. In a second learning study we demonstrated that kinetic errors alone are insufficient to drive the adaption of movement trajectory during learning, even in highly contextualized scenarios where the mapping of load force to motion was made apparent. In the third study, we showed that people incorporate the dynamics of the arm and object to generate grip force responses that are tuned to the change in load force during rapid, automatic arm movement responses to visuomotor perturbations. Object-oriented
behaviour may also involve the linking of actions to produce an overall goal, i.e., unloading a bag of groceries is composed of numerous movements linked together. Implicit in this global task are decisions about what objects to move to and in what order. As such, in the final study, we designed a laboratory foraging task and showed that decisions about what targets to reach to were highly driven by motor factors, such as object position and size as well as cognitive factors such as value. Taken together, these studies extend the current understanding of object manipulation and offer insights into how movement factors are incorporated into decisions about what objects to move to.
Co-Authorship

I conducted the research in this thesis under the supervision of Dr. Randy Flanagan. I took the lead on the research presented in chapters 3–5 and I was involved in all aspects of the work, including experimental design, data collection, data analyses, and manuscript preparation. Dr. Frédéric Danion took the lead role on the study presented in chapter 2. Dr. Frédéric Danion also shared the primary authorship in chapter 3. The model in chapter 5 was developed by Dr. Daniel Wolpert. The research in chapters 2 and 3 is presently published and the work in chapters 4 and 5 is being prepared for submission.


**Chapter 4** Diamond, J. S., Nashed, J. Y., Johansson, R. S, Wolpert, D. M., and Flanagan, J. R. Grip-load coordination during rapid arm movement corrections
in response to visuomotor perturbations.

Chapter 5 Diamond, J. S., Dorris, M. C., Wolpert, D. M., and Flanagan, J. R.

Rapid target foraging with reach or gaze: the hand looks further ahead than the eye.
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List of Abbreviations

ANOVA  Analysis of Variance

BIC  Bayesian information criterion

cm  Centimetre

cm/s  Centimetre per second

EMG  Electromyography

F  Force

fMRI  Functional magnetic resonance imaging

GF  Grip force

HV  Haptic-visual condition

Hz  Hertz

kg  Kilogram

LF  Load force

M  Mean

m  Metre
min  Minute

mm  Millimetre

ms  Millisecond

MT  Movement time

N  Newton

N/m  Newton per metre

N/m/s  Newton per metre per second

R  Correlation coefficient

r  Correlation coefficient

s  Seconds

SD  Standard deviation

SE  Standard error

SEM  Standard error of the mean

TSP  Traveling salesman problem

V  Visual condition

VR  Virtual reality

yrs  Years
Chapter 1

General Introduction

1.1 Preamble

Object manipulation is a hallmark skill in the repertoire of human motor behaviour. Indeed, most tasks people perform on a daily basis involve some form of object manipulation, from raising a glass to complex tool use. The importance of studying object manipulation manifests not only in the wide range of motor behaviours it underlies, but also because manipulatory skill may decline with age and/or be disrupted by neurological impairment (Carr and Shepherd, 1998). Therefore, it is of fundamental and practical importance to better understand how object manipulation tasks are performed (Johansson and Flanagan, 2009b).

At least some insight into the mechanisms supporting manipulatory skill can be gleaned from the anatomy and sensory capabilities of the hand; however, many questions remain about how manual tasks are organized and represented within the nervous system (Flanagan et al., 2006; Johansson and Flanagan, 2009a). This thesis builds upon a rich history of research exploring the basic sensorimotor mechanisms
underlying manipulatory skill (Johansson and Flanagan, 2009b). The following review will present some of the overarching theories and empirical findings important for interpreting the results of this thesis.

1.2 Object manipulation

Object manipulation typically involves grasping, lifting, moving, and replacing of an object on a surface. Such tasks may include a simple lift of an object or the manipulation of dynamically complex tools. Yet regardless of the specific form, most natural object manipulation tasks involve a series of discernible action phases, or subgoals, demarcated by mechanical events (Flanagan et al., 2006; Johansson and Flanagan, 2009a,b). For example, simply lifting an object off a surface and replacing it involve the initial reach phase, demarcated by the digits contacting the surface of the object, the load phase during which vertical forces are applied, demarcated by the object breaking contact with the supporting surface, the hold phase, the replacement phase, demarcated by contact between the object and surface, and finally the release phase, demarcated by release of contact between the object and digits. These mechanical events often generate discrete sensory signals from one or more sensory modalities (Johansson and Flanagan, 2009b), including tactile, visual, and/or auditory signals. Thus, the detection of these sensory signals provides information about the completion of task subgoals, e.g., object liftoff. In this way, the nervous system can exploit these discrete signals to optimize complex manipulatory behaviour.

Object manipulation tasks therefore possess a sensory signature that reflects the nature of the action phases, and their subgoals, comprising the manipulatory task.
This framework led to the hypothesis that manipulatory tasks are mediated by action-phase specific controllers that guide the completion of each action phase (Johansson and Flanagan, 2009a). In this way, the nervous system may monitor the completion of each action phase by comparing predicted and actual sensory feedback, particularly with respect to the timing and characteristics of the discrete sensory signals separating each action phase (Bowman et al., 2009). This control framework provides a mechanism for the nervous system to monitor task progression and launch task-protective corrective actions when predictions are erroneous, such as when an object is heavier than predicted.

1.3 Lifting objects

Object lifting lies at the core of many manipulation tasks. For this reason, it is important to summarize the basic sensorimotor mechanisms mediating this behaviour. To create a context for discussion, we will use the simple scenario of lifting an object off a surface using a precision grip with the tips of the thumb and index finger on either (vertical) side of the object. Johansson and colleagues subdivided a basic lift into several measurable phases (Johansson and Westling, 1984; Westling and Johansson, 1984). The first phase is the preload phase, which begins when the digits contact the surface of the object. Grip force, applied normal to the object surface, is increased over approximately 100 ms to achieve a stable interface with the object, occurring without any appreciable change in load force (i.e., lifting force applied tangential to the surface of the object). Next occurs the loading phase whereby grip and load force are smoothly increased in parallel. Thus, object lifting will occur once vertical load force exceeds the weight of the object. When lifting the object just a little above
1.3. LIFTING OBJECTS

the surface, peak forces will typically be achieved shortly after liftoff and will then decrease with the load force matching the weight of the object, characterizing the static hold phase.

Numerous studies have examined lifting behaviour within this framework (e.g., Flanagan and Beltzner (2000); Forssberg et al. (1991); Johansson and Westling (1984); Westling and Johansson (1984, 1987)). These studies have consistently supported the notion that motor output during lifting is well adapted to the expected physical properties of the object, most critically object weight and the frictional conditions between the object and digits. The aim is to generate the load forces needed to achieve the task goals and generate grip forces that will achieve grasp stability. Even when predictions about weight and friction are incorrect, reflex-mediate responses will adapt grip and load force appropriately. The result is a relatively consistent ratio between grip and load force, which slightly exceeds the ratio necessary to maintain grasp stability. Effectively the nervous system optimizes lifting behaviour to prevent excessive grip forces that may damage the hand or object, or waste energy, and also prevent insufficient grip forces that will cause the object to slip from grasp.

Skilled manipulation is dependent on incorporating knowledge of the object properties into predictive grip and load force control. People typically lift objects of different known weights in about the same amount of time. To achieve this they scale the rates of change of grip and load forces, during the loading phase, to the predicted object weight; i.e., the greater the expected weight, the greater the rates of force increase. This adaptation is consistent during the static phase too, whereby grip force is proportional to object weight (Forssberg et al., 1992; Westling and Johansson, 1984) and even to torque (Salimi et al., 2000). Furthermore, changes in grip
1.3. LIFTING OBJECTS

force are tuned to variation in surface structure, such that objects with less slippery surfaces are grasped with lower grip forces than objects with more slippery material (Johansson and Westling, 1984; Westling and Johansson, 1984). Impressively, even the small changes in frictional conditions attributed to hand washing influence the amount of grip force applied to the object (Johansson and Westling, 1984). Without information about the physical properties of manipulated objects, predictive and hence dexterous control of grip and load forces is not possible.

The robust patterns of grip-load coordination during object lifting is made possible through sensory predictions based on an internal representation of the properties of the object. Unlike the shape of an object, which can be directly appreciated via vision, object weight can only be directly appreciated once the object is lifted. It is for this reason that prediction of weight is of essential importance to lifting behaviour, allowing people to often accurately scale lifting and grip forces when lifting an object for the first time. Evidence for prediction in object lifting comes from experiments that unexpectedly alter the weight of the lifted object. For example, Johansson and Westling (1988a) showed that when an object is heavier than expected, the duration of the loading phase will be increased, and the object will liftoff later than expected. Conversely, when an object is lighter than expected, the object will liftoff earlier than expected. In both cases the initial loading phase for the test object will resemble the loading phase for the expected object. These findings show that lifting behaviour is driven, at least partly, by feedforward commands tuned to sensory expectations.

When sensory predictions are erroneous, the nervous system will quickly launch task protective corrective responses. These responses are largely automatic and are
driven by online sensory feedback about the evolving lift. For example, rapid adjustments in grip force may be triggered when lifting an object of unexpected frictional conditions (Johansson and Westling, 1984). This updating is observed approximately 100 ms following initial contact with the surface of the object. A similar updating occurs when lifting an unexpected weight. Here, either the premature liftoff of the object, i.e., when it is lighter than expected, or the absence of liftoff at the expected time, i.e., when it is heavier than expected, will trigger a rapid adjustment in grip and load force. In the former case, load force (and grip force) will rapidly decrease to mitigate the upwards acceleration of the object, and in the latter case, load force (and grip force) will continue to increase until liftoff is detected. Thus liftoff represents a discrete, and task relevant, event for the evaluation of task progression and success.

Rapid and automatic grip force adjustments also occur in response to small, imperceptible slips between the skin and object surface. Such slips may occur during typical object lifting and are at least partly counteracted by the grip force safety margin. Notwithstanding, these slips will trigger automatic grip force increases approximately 60–80 ms following the slip event (Johansson and Westling, 1984, 1987a), which is similar to the latency of responses to larger, unexpected mechanical perturbations, such as when a handheld object is physically perturbed (Johansson and Westling, 1988b). These grip force increases function to not only compensate for the discrete slip event but also to raise the overall safety margin to guard against future slips. Indeed, the tips of the digits are exceptionally tuned to sensing these events, particularly by way of the large density of mechanoreceptors within the glabrous tissue. Moreover, their dynamic sensitivity to small mechanical perturbations renders
them ideal transducers of slip events and information about surface textures. Empir-
ical studies have confirmed this hypothesis by showing the disruption of these task protective grip force responses during anaesthetization of the digits (Jenmalm and Johansson, 1997; Johansson and Westling, 1984; Westling and Johansson, 1984) and through microneurography (Johansson and Westling, 1987a).

1.4 Transporting familiar objects

During natural behaviour, object manipulation tasks may consist of various actions superimposed on basic lifting. For instance, an object may be moved through the air from one location to another, waved about, or contacted with another object such as during tool use. These actions categorize the movement phase during manipulatory tasks. Indeed, these seemingly simple actions pose new dynamical challenges for the nervous system to overcome related to the load forces of the object evoked by the movement. For instance, when a grasped object with a standard mass load is ac-
celerated (or decelerated) during reaching movements, there will be an inertial load, proportional to the mass and acceleration (or deceleration) of the object experienced at the fingertips. In order to move the object as desired it is necessary to adapt the applied load force to the mass. In addition, without generating the appropriate grip force for the load, the object may slip from grasp. Yet our ability to effortlessly trans-
port handheld objects demonstrates our capacity to adapt to such motion induced loads.

Studies examining grip force modulation during rapid arm movements with fa-
miliar hand-held objects, have shown that grip and load force modulate in parallel (Flanagan et al., 1993; Flanagan and Tresilian, 1994; Flanagan et al., 1995; Flanagan
and Wing, 1993, 1995). This finding compliments previous work by Johansson and colleagues who have shown that when lifting objects, or pulling on fixed loads, there is a tight coupling between grip and load force, such that grip force is modulated in phase with load force and slightly exceeds the minimum grip force (required to prevent slip) so to produce a margin of safety (Johansson and Westling, 1984, 1987a,b, 1988b; Westling and Johansson, 1984). The close coupling of grip and load force observed during the transport of a handheld object provides insight into how such tasks are accomplished through the notion that the central nervous system predicts the load consequences of arm-movement. Such prediction is posited to derive from an internal representation of the body and its interactions with the environment within the central nervous system, also described as an internal model (Flanagan and Wing, 1997; Kawato, 1999; Wolpert and Flanagan, 2001; Wolpert et al., 1995).

1.5 Transporting unfamiliar objects

Not only can people skillfully manipulate familiar objects, where the mapping between applied force and motion is known through experience, they can also learn to manipulate unfamiliar objects where the mapping between applied force and motion is initially unknown. Numerous studies have shown that people can learn a variety of novel object loads, such as position-dependent (i.e., elastic), velocity-dependent (i.e., viscous), and acceleration-dependent loads (i.e., inertial) (Flanagan et al., 2003; Flanagan and Wing, 1997). In these studies, people initially show poor modulation between grip force and load force; however, with experience, people adapt their movement trajectory to produce relatively straight movements and adapt grip force to load force to produce synchronous grip-load coordination (Flanagan et al., 1993; Flanagan
and Tresilian, 1994; Flanagan et al., 1995; Flanagan and Wing, 1993, 1995; Wing and Flanagan, 1998). This learning is explained through the adaptation of the internal model to the dynamical properties of the object.

The previous examples illustrate that people can learn to manipulate objects with novel dynamics. However, even these examples involve simple objects where there is a direct mapping between applied force and motion. On the other hand, the control strategies involved in manipulating non-rigid objects, such as a slinky, rope, or water in a glass present a more complex control problem because the mapping of applied force to motion is complicated by the internal degrees of freedom of the object itself. In such cases, the desired motion of the object is achieved indirectly through the interaction of the hand with the internal dynamics of the object. Studies examining the manipulation of non-rigid objects, such as a mass-spring system, show that people develop an internal model of the arm-object system that specifies the forces required to induce the desired object motion (Dingwell et al., 2002, 2004). For instance, Dingwell et al. (2002) noted that after participants learned to control a mass-spring object, movement trajectory did not return to a straight-line, which would be expected if the object were interpreted as a perturbation to free reaching. Furthermore, the authors showed that participants learned an internal model of the object by showing that altering the mass and spring constant, but not the ratio of the two, influenced movement trajectory despite the kinematic requirements of the two objects being the same.
1.6 Internal representations of limbs and objects

One of the most influential concepts in motor control is that of the internal model. An internal model functions to mimic the input-output transformations of the sensorimotor system and the environment with which it interacts, thereby capturing the relationship between motor output and sensory feedback (Flanagan and Wing, 1997; Kawato, 1999; Wolpert and Flanagan, 2001; Wolpert et al., 1995). In the context of object manipulation, the internal model incorporates implicit knowledge of the dynamics of the limb and that object; i.e., the mapping between applied force and motion. Support for the existence of internal models comes from a variety of behavioural (Flanagan and Wing, 1997; Kurtzer et al., 2008; Scarchilli and Vercher, 1999; Wolpert et al., 1995), theoretical (Jordan and Rumelhart, 1992; Kawato et al., 1987; Wolpert and Kawato, 1998), neurophysiological (Shidara et al., 1993; Yamamoto et al., 2002), and imaging studies (Kawato et al., 2003). Internal models have also been used extensively to explain a variety of volitional motor behaviours including object transport (Flanagan and Wing, 1997), the manipulation of non-rigid objects (e.g., mass-spring system) (Dingwell et al., 2002, 2004), and force-field adaptation (Shadmehr and Mussa-Ivaldi, 1994).

One important class of internal models is the forward model, which functions to predict the sensory consequences of motor output via an efference copy of motor commands. This transformation, from motor commands to simulated sensory consequences, has fundamental implications for a variety of behavioural phenomenon involved in manipulatory tasks. First, a forward model provides a solution for how people move despite delays in sensorimotor feedback (Miall et al., 1993). For example, rapid arm movements would induce load forces that could not be countered
if grip force was adjusted solely through reactive means. Second, a forward model provides a mechanism to distinguish self-produced from externally produced stimuli (Blakemore et al., 2000, 1998). Third, a forward model can contribute to state estimation (i.e., position and velocity) by providing predictions about the current state (Goodwin and Sin, 1984). Lastly, the output of a forward model (i.e., expected sensory consequences) provides a signal to compare against actual sensory feedback, which is important for error-based learning (Wolpert and Flanagan, 2010; Wolpert and Ghahramani, 2000). Thus, a forward model of the object’s dynamics could drive predictive grip force modulation in the context of object manipulation.

Until recently, much of the support for internal models comes from studies of voluntary movement. However, it has also been shown that rapid motor responses (i.e., non-volitional) of the upper limb also incorporate internal models (Kurtzer et al., 2008). Because of the interaction torques between limb segments, a perturbation applied to one joint of the arm affects other joints (Kurtzer et al., 2008; Lacquaniti and Soechting, 1984, 1986a,b; Scott, 2004). Kurtzer et al. (2008) showed that an unexpected perturbation of the upper limb elicited a rapid corrective response that reflected the multi-joint interactions of the limb segments (Kurtzer et al., 2008). Specifically, a corrective response was launched in muscles indirectly tied to the perturbation by way of intersegmental joints and this response occurred before feedback was available. This finding implies that the sensorimotor system effectively incorporates an internal model of multijoint dynamics that can be employed rapidly in response to unexpected perturbations. Furthermore, Cluff and Scott (2013) demonstrated that long-latency feedback responses adapt to altered sensorimotor contexts. Specifically, the authors show that as people adapt their feedforward motor output to
the altered sensorimotor environment, their feedback gains adapt as well. The latter finding highlights the important relationship between feedforward and feedback control and suggests both are mediated by a common representation of the dynamics of the limb.

1.7 Learning object dynamics

When interacting with an unfamiliar object for the first time, there will often be mismatches between the actual and intended outcomes. For instance, reaches with a novel object may induce both kinetic errors, involving poor modulation of grip to load force, and kinematic errors, involving errors in movement trajectory. In the context of an internal model, this scenario implies that the prediction about the mapping between applied force and motion is erroneous. Thus, predictions will only facilitate motor control when accurate predictions can be generated, involving knowledge of the dynamics of the body and a hand-held object. Indeed, during development, when the body is growing (i.e., changing size, weight), the mapping between motor commands and motion will change. This may also occur during disease or injury. In the context of object manipulation, this scenario arises when an object is grasped, thereby altering the dynamics that the motor system must deal with in order to generate skilled hand (and object) movements. Therefore, in order for the nervous system to maintain a functional level of motor performance, it must be able to deal with dynamical changes in the body and environment, both short and long term. This is proposed to be due to the updating of an internal model through the process of motor adaption, or motor learning (Krakauer, 2006; Wolpert and Flanagan, 2010).
One common method used to study motor learning is through force field adaptation paradigms. Such paradigms typically involve the use of a robotic manipulandum, which the participant grasps, that can be programmed to apply force mapped, in novel ways, to position, velocity, or acceleration (Cothros et al., 2006; Davidson, 2005; Kluzik et al., 2008; Shadmehr and Moussavi, 2000; Shadmehr and Mussa-Ivaldi, 1994; Shadmehr et al., 2010). The general finding from these studies is that people’s initial movements are perturbed in the direction of the force, described as movement errors. Over subsequent movements, however, these errors are gradually reduced to near zero and movement trajectories resemble those movements made in free space. Furthermore, upon the subsequent removal of the force field, people show an aftereffect in which movement trajectories are perturbed in the opposite direction of that initially experienced. This finding supports the notion of an internal model because it suggests that people counter the dynamics of the experienced force field by applying the opposite force rather than simply co-contracting and stiffening the limb (Flanagan et al., 1999; Kawato, 1999; Kawato et al., 2003). This intelligent strategy thus involves knowledge of dynamics.

Motor learning studies involving force fields highlight the role of internal models for predicting object dynamics. In this way, motor output can be tailored to the specific dynamical context of the movement. However, in the real world there are often unexpected perturbations that occur. For instance, reaching movements may be disrupted midflight by an obstacle that may physically perturb the limb. Additionally, the position of targets may suddenly change, for example during sports. In order to compensate for this type of online variation, reaching behaviour also incorporates rapid online feedback corrections (Kurtzer et al., 2014; Pruszynski and Scott,
2012; Scott, 2004), which function to compensate for natural variation in movement or unexpected perturbations (Franklin and Wolpert, 2008; Oostwoud Wijdenes et al., 2011; Prablanc and Martin, 1992; Saunders and Knill, 2004). Thus, feedback control reflects an aspect of intelligent motor behaviour that accommodates unexpected variation that cannot be predicted through a feedforward policy.

Rapid feedback responses have been studied using reaching tasks involving both visuomotor and mechanical perturbations. In the case of visuomotor perturbations either the target or the viewed hand, or cursor representing the hand, unexpectedly changes position while participants reach to a target. These online perturbations trigger rapid feedback responses within approximately 150 ms in the reaching limb to bring the hand, or cursor representing hand position to the target (Elliott et al., 2001; Franklin and Wolpert, 2008; Oostwoud Wijdenes et al., 2011; Prablanc and Martin, 1992; Saunders and Knill, 2004). In the case of mechanical perturbations, participants grasp and reach to a target using a robotic device that can physically perturb the limb unexpectedly (Nashed et al., 2012, 2014). Such physical perturbations evoke a long-latency feedback response, which counters the perturbation to bring the limb towards the target within approximately 45–105 ms as measured through EMG (Pruszynski and Scott, 2012). Similar to the adaption of voluntary movements during visuomotor and force field learning, rapid feedback responses also show certain adaptations during learning (Cluff and Scott, 2013; Dimitriou et al., 2013; Kurtzer et al., 2008).
1.8 Linking action phases

As previously discussed, object manipulation is composed of a series of action phases (i.e., reaching to, lifting, and moving objects) demarcated by mechanical events (Johansson and Flanagan, 2009b). For example, the reaching phase ends with discrete contact between the digits and object surface. Furthermore, these mechanical events function as sensorimotor control points around which predicted and actual sensory feedback can be compared. To date, most studies of object manipulation have traditionally focused on individual action phases i.e., lifting phase, or movement phase (including robotic handles) (Flanagan and Wing, 1993; Shadmehr and Mussa-Ivaldi, 1994; Westling and Johansson, 1984). However, a few studies have examined how these action phases are linked together (Bowman et al., 2009).

In general, skilled motor behaviour often requires predictively linking action phases such that each phase is launched in anticipation of successful completion of the previous phase, rather than being reactively triggered by sensory signals registering completion of the previous phase. In a recent study, Bowman et al. (2009) measured the timing of gaze shifts relative to hand movements during a task in which participants sequentially contacted a series of objects in a prescribed order. They found that gaze typically stayed on the current target until shortly after it was contacted, before shifting to the next target. To determine whether eye movements were made predictively of hand contact or in response to haptic feedback about hand contact, the authors included catch trials where haptic feedback was eliminated unexpectedly. The authors found that in the majority of contacts, anticipatory saccades to the next target were observed, indicating that, in general, gaze shifts were not triggered by haptic feedback of target contact. Instead the authors concluded that gaze shifts
were predictive of contact, supporting the notion that action phases in this task were predictively linked.

When action phases are linked in a predictive manner the motor commands specifying the forthcoming action phase are initiated prior to feedback about the completion of the current phase (Johansson et al., 2001). In contrast, a strategy based on the verification of completed action phases may certainly add to the overall completion time, especially given the marked delays in the sensorimotor system (Miall et al., 1993; Wolpert and Flanagan, 2001). Recent studies by Safstrom et al. (2013) and Safstrom et al. (2014) have shown that when learning a novel sequential action task involving moving a cursor between successive targets and maintaining the cursor at each target for a required (fixed) duration in order to attain it, participants shifted from a reactive strategy to a predictive strategy with practice. Moreover, participants became very good at predicting the time required to attain the targets such that near-optimally traded off initiating the movement to the next target too early—in which case they would have to return to the previous target—and too late—which would increase overall task completion time. In general, learning to optimize performance in the face of spatial and temporal uncertainty in motor planning and control is an important component of skill learning (Franklin and Wolpert, 2011; Harris and Wolpert, 1998; Hayden et al., 2011; Hudson et al., 2008).

1.9 Movement decision-making

The influence of how movement costs shape the kinematics of single movements has been widely studied (Elliott et al., 2001; Harris and Wolpert, 1998; Scott, 2004; Shadmehr et al., 2010; Todorov, 2004; Wolpert et al., 2011). However, the influence of
how such costs may influence the selection of movement, i.e., choosing between one or several movement options, remains largely unexplored, particularly with respect to the choices involved in sequential actions. Some notable studies on this topic include those of Cos and colleagues who evaluated the influence of biomechanical factors in shaping decisions about what movements to make (Marcos et al., 2011; Cos et al., 2014, 2012). Marcos et al. (2011) showed that when participants were presented with two free-choice movement options that varied in terms of required effort, participants tended to select the movement that was perceived to require the least effort, suggesting that biomechanical costs are incorporated into the decision itself. Another example, is presented by Trommershäuser et al. (2006) who showed that participants incorporated knowledge of their own motor variability to select a target from two choice options, that varied in terms of how a reward and penalty region was configured, to maximize expected gain. These examples show that participants are able to incorporate movement factors into the decision, which is important because decisions must not only be made cognitively, but also executed motorically.

On the decision-making side, numerous studies have examined cognitive decision-making (for reviews see Glimcher (2002, 2004); Kahneman and Tversky (2000); Shadlen and Kiani (2013)) where the main concern is the value of two competing options. For example, previous studies have examined decision-making under risk (Kahneman and Tversky, 1979, 1984; Tversky and Kahneman, 1974, 1981), where participants make perceptual decisions about which of two probabilistic outcomes they prefer. A number of studies have examined perceptual and cognitive decision making in the context of saccadic eye movement and pointing tasks (Dorris and Glimcher, 2004; Glimcher, 2001, 2003; Hayden et al., 2011; Platt and Glimcher, 1999;
Resulaj et al., 2009; Trommershäuser et al., 2006). However, these studies have focused on single movements, and have not placed much emphasis on movement related costs.

Given the independent influences of movement costs and value on motor control and decision-making, respectively, it is likely that both factors interact to bias movement decisions. Some have argued that movement is, in essence, a decision making problem (Wolpert and Landy, 2012) and others that reductionist approaches to the study of decision making should be interpreted within an ecological framework that defines decision making in the broader context of adaptive behaviour (Cisek and Kalaska, 2010). One framework for studying decision-making that holds promise is optimal foraging theory (Carr and Shepherd, 1998; Stephens and Krebs, 1987). Optimal foraging theory captures the dynamic nature of real-world decision-making, which is often lost in reductionist laboratory approaches. In the real world, decision-making is not isolated to discrete time intervals (as they often are in experimental trials, the most common structure of controlled experimental designs) and discrete stimuli, but instead operates continuously to shape sequential actions in response to a constantly changing environment. In this context, an organism is often presented with a number of possible action choices at any given moment (Cisek and Kalaska, 2010). The free-choice nature of the decision process makes foraging theory an ecologically valid framework for examining decisions, even in laboratory settings where scientific control generally imposes greater constraints (Hayden et al., 2011; Kolling et al., 2012; Rushworth et al., 2012; Walton et al., 2007).

The overarching principle guiding optimal foraging decisions is the rate of the net
energy intake, which is proportional to the net energy yield of the food option and inversely proportional to the amount of energy expended by the organism in harvesting the food option. The optimization of this fundamental tradeoff drives the selection of a given option over its alternatives. It is the cost of the action together with the expected payoff that ultimately governs selection probabilities. Optimal foraging theory states that decisions are made to maximize rate of reward over time, which in the context of foraging theory is the energy derived from a food option (Charnov, 1976; Stephens and Krebs, 1987). However, reward can take other forms too, especially when discussing human decision-making. For example, good investment decisions are rewarded by safety of principle and good route selections are rewarded by reduced travel times. In general, the goal of a decision is to achieve some desired outcome, which can be considered the expected reward. The advantage of foraging theory is that it reconciles value-based decisions with the costs associated with the execution of the movement. This fundamental characteristic of foraging theory makes it an attractive framework for studying human decision-making. In addition, foraging theory offers clear predictions about the outcome of experiments because of its mathematical formalism. This is advantageous because mathematical models offer a powerful tool through which to generate and test hypotheses. They offer a framework to make specific predictions about choice behaviour.

Although foraging theory is typically applied in behavioural ecology, some recent studies have demonstrated its usefulness in evaluating movement decisions in the laboratory (Hayden et al., 2011; Kolling et al., 2012; Rushworth et al., 2012; Walton et al., 2007). Hayden et al. (2011) developed a virtual patch foraging task. In this experiment, primate subjects were required to choose between one of two targets by
fixating their gaze. The fixation on one target yielded a juice reward that decreased with successive target fixations. This structure is equivalent to foraging within a patch that yields diminishing returns. Fixating on the second target would replenish the patch, however this occurred after a delay. This characteristic is analogous to the transportation time from one patch to another. According to foraging theory, the optimization that governs behaviour is that which determines the time at which the monkey “moves to a new patch”. Indeed, Hayden and colleagues found that subjects did produce behaviour that was predicted by foraging theory. Additionally, these researchers found that cells in the anterior cingulate cortex encoded the decision variable signaling the relative value of staying or transporting to a new patch. Kan and colleagues designed a visuosaccadic laboratory foraging task where monkey’s harvested reward by making unconstrained saccades to distributed visual targets (Kan, 2011). The presented targets could yield a given amount of reward and require a pre-specified handling time to harvest. Not only did the task afford foraging type behaviour, but also neural recordings to determine what brain areas are involved. Indeed, the authors found that subjects approached near optimal foraging behaviour, which gradually improved over the duration of the study. These studies demonstrate the utility of reductionist foraging-inspired tasks to better understand decision-making and motor control as well as a basis for exploring the neural mechanisms involved in foraging behaviour (see also Kolling et al. (2012)).

1.10 Outline of experiments

This thesis is composed of four studies. All four studies were performed in a virtual environment in which participants produced hand movements while grasping a
hand-held object attached to a robotic device which could measure the position of the hand and, in some cases, applied forces to the object. Within this environment, we designed a series of experiments to probe key aspects of object-oriented behaviour. The goal of the first two studies was to investigate the use of feedback during motor learning of dynamically novel objects. The first study examined the importance of haptic feedback when controlling objects with complex dynamics associated with internal degrees of freedom. The second study assessed the contributions of kinetic and kinematic errors for learning novel loads. The third study tested the hypothesis that knowledge of object dynamics can be incorporated into fast visuomotor corrections made during reaching movements. Finally, the aim of the fourth study was to assess how movement factors, such as object distance and size, traded off with object value to drive decisions about what objects to reach to.

1.11 Thesis objective

The objective of this thesis was to build upon what is currently known about how the brain organizes and represents object manipulation tasks. This objective was accomplished using novel experimental protocols that capture more naturalistic behaviours that have not traditionally been employed in the field. It was hypothesized that grip-load force coupling is highly integrated with complex movements of the upper limb and that decisions about what objects to reach to are driven by movement factors, such as object distance, in addition to cognitive factors such as value.
1.12 References


Safstrom, D., Johansson, R. S., and Flanagan, J. R. (2014). Gaze behavior when


Chapter 2

The role of haptic feedback when manipulating non-rigid objects

2.1 Abstract

Humans can learn to manipulate objects with complex dynamics, including nonrigid objects with internal degrees of freedom. The first aim of this study was to assess the contribution of haptic feedback when learning to manipulate a nonrigid object. The second aim was to evaluate how learning without haptic feedback influences subsequent learning with haptic feedback and vice versa. The task involved moving a simulated mass—attached to a grasped handle via a simulated, damped spring—to a target as quickly as possible. In the haptic plus vision (HV) condition, appropriate forces were applied to the handle, which was attached to a robot. In the vision only (V) condition, these forces were turned off. Participants completed 80 trials in each condition, with one-half starting with the HV condition. Both groups exhibited significant learning, as measured by movement time, in both conditions. For the condition performed first, initial performance, learning rate, and final performance were better with haptic feedback. Prior experience in the HV condition led to faster
learning and better final performance in the V condition. However, prior experience in the V condition led to slower learning and worse final performance in the HV condition. In the V condition, all participants tended to keep the mass close to the hand. In the HV condition, participants who started with the HV condition allowed the mass to move away from the hand, whereas participants who started with the V condition continued to keep the mass close to the hand. We conclude that haptic feedback as well as prior experience with haptic feedback enhance the ability to control nonrigid objects and that training without haptic feedback can lead to persisting detrimental effects when subsequently dealing with haptic feedback.

2.2 Introduction

Skillful object manipulation, including tool use, requires knowledge of the dynamics of the object relating applied force to motion (Flanagan et al., 2006; Johansson and Flanagan, 2009). People are highly skilled at predicting and controlling the motion of grasped objects with familiar dynamics, including rigid objects with inertial and elastic loads, where the force applied to the hand is proportional to the acceleration and position of the object, respectively (Flanagan and Wing, 1993, 1995, 1997; Johansson and Westling, 1984). People are also capable of effectively manipulating many nonrigid objects with internal degrees of freedom, such as a yoyo or a paddleball consisting of a ball attached to a paddle by a spring. It has been postulated that to formulate an appropriate strategy for controlling such an object, the operator must learn an internal model of the object’s dynamics, specifying the mapping between forces applied to the object and its motion (Dingwell et al., 2004). Such learning can be challenging, because the motion of the controlled object (e.g., the ball of a
paddleball) is governed indirectly through the interaction of the motion of the hand with the internal dynamics of the object and is not yoked to hand motion.

Moving nonrigid objects normally involves interaction forces at the hand. However, in virtual environments, ranging from video games to surgical simulators, such forces are often absent, and therefore, appropriate haptic feedback is unavailable. Previous studies have shown that people can learn to control nonrigid objects both when appropriate haptic feedback is provided (Dingwell et al., 2002, 2004; Nagengast et al., 2009) and when it is not (Mah and Mussa-Ivaldi, 2003; Mehta and Schaal, 2002). However, it remains unclear whether appropriate haptic feedback improves learning and control. The primary objective of the current study was to assess the influence of haptic feedback in learning to control a nonrigid object. On the one hand, we might expect the provision of appropriate haptic feedback to improve learning and control, because such feedback should improve sensory estimates of the state of the object through multisensory integration (Ernst and Banks, 2002; Ernst and Bülthoff, 2004; van Beers et al., 2002). Moreover, it has been argued that the ability to predict the consequences of one’s actions—an important component of sensorimotor control (Shadmehr et al., 2010; Wolpert and Flanagan, 2001)—can be impaired when efference copy and sensory feedback are inconsistent with a particular movement context (Blakemore et al., 1998). On the other hand, the benefit of haptic feedback is not obligatory. With the use of a task in which participants had to control the position of a ball on a rotating beam, Huang and colleagues (2006) found virtually no benefit of haptic information. Specifically, participants with vision only (V) began and finished training with comparable performance with those who also had haptic feedback. In addition, because interaction forces must be taken into account to achieve the desired
motion of the hand, it is also possible that the provision of appropriate haptic feedback degrades hand-motion control (and thus object control). Altogether, whether haptic feedback helps, hinders, or simply does not affect the control of nonrigid objects remains an open question.

We were also interested in how learning to control a non-rigid object without haptic feedback influences motor learning and control when haptic feedback is subsequently provided and vice versa. From an applied perspective, this question was motivated by the fact that provision of haptic feedback in virtual reality (VR) simulators is often difficult and costly. As a consequence, determining how training without haptic feedback (i.e., with vision only) influences performance when subsequently dealing with haptic feedback is important. From a theoretical perspective, we reasoned that if participants learn a direct mapping between arm motor commands and object motion, we might expect (bidirectional) negative transfer, because this mapping will change depending on whether interaction forces are present. However, it is also possible that participants could learn two distinct mappings when learning to control the object: a mapping between hand motion and object motion, which does not depend on the presence or absence of interaction forces applied to the hand, and a mapping between arm motor commands and hand motion, which does depend on interaction force. In the scenario, it is possible that bidirectional, positive transfer would occur, because the two conditions share a common mapping. However, bidirectional, negative transfer could also occur, because the mapping between arm motor commands and hand motion differs between tasks. Finally, independently of learning dynamics, it is possible that participants adopt different control strategies depending on the initial feedback condition they experience. If they persist with a given strategy
when the feedback condition changes, then transfer between conditions may either be positive or negative depending on the efficacy of the strategies selected.

We examined the role of haptic feedback using a task in which participants were asked to move a mass, attached to a hand-held handle via a slightly damped spring, to a target as quickly as possible (Dingwell et al., 2002, 2004; Nagengast et al., 2009). The object was simulated using a VR setup, allowing us to remove appropriate haptic feedback by turning off the forces applied to the handle (but not the simulated mass). Two groups of participants performed the task with visual and haptic feedback (HV task) and with visual feedback only (V task) but in different orders. We assessed initial performance, learning rate, and final performance in both nave participants, experiencing one of the two tasks for the first time, and participants who previously experienced the other task.

2.3 Materials and Methods

2.3.1 Participants

Twenty self-proclaimed, right-handed participants (six males and 14 females) took part in this study. Participants were split in two groups (group HV-V: age = 20.7 ±2.1 yrs, height = 1.70 ±0.11 m, mass = 58.6 ±10.5 kg; group V-HV: age = 21.5 ±2.5 yrs, height = 1.69 ±0.09 m, mass = 65.6 ±14.8 kg) who performed the same experimental conditions but in a different order. All participants were healthy and gave informed consent prior to the study. A local university ethics board approved the experiments, which complied with the Declaration of Helsinki.
2.3.2 Apparatus

In a fully illuminated room, participants were required to move a cylindrical object held between the tips of the thumb and the index finger of their right hand. The object had two parallel, horizontal grip surfaces (2.5 cm in diameter), located 6.4 cm apart, and was instrumented with two, six-axis force transducers (Nano force/torque, ATI Industrial Automation, Apex, NC), which measured forces (0.05 N resolution) and torques applied by the thumb and index finger in three dimensions. The two grip surfaces were covered with sandpaper and were free to spin about the long axis of the object, which was attached to a lightweight robotic manipulator (Phantom 3.0 haptic interface, Sensable, Wilmington, MA) via a joint that allowed rotation about all axes except the long axis of the object. Thus the combination of this joint and the spinning grip surfaces allowed free rotation of the object in three dimensions. Three optical encoders, placed on the three motors of the manipulandum, measured the object’s position in three dimensions (0.1 mm resolution). Cuffs mounted on air sleds supported the wrist and forearm and restricted motion of the hand to a horizontal plane (Fig. 2.1). All signals were recorded at a 1,000 Hz sampling frequency.
The positions of the hand (i.e., the grasped object), the virtual mass-spring object, the start position, and the target were all displayed in the horizontal plane of the center of the grasped object using a visual display system (Fig. 2.1). This system consisted of a 30-inch monitor positioned horizontally above a mirror located half-way between the monitor and plane of hand movement. Participants viewed the visual scene displayed on the monitor via the mirror, which blocked vision of the actual hand and grasped object. Filled circles were used to represent the positions of the hand (blue, 10 mm in diameter), object (yellow, 20 mm in diameter), start position (green, 20 mm in diameter), and target (green, 40 mm in diameter). The simulated properties of the mass-spring object were the following: mass = 3 Kg, stiffness = 120 N/m, damping = 1 N/m/s, resting length = 0 m. Note that these parameter settings are similar to those used in previous studies using this task (Dingwell et al., 2002, 2004; Nagengast et al., 2009). The resonant frequency of this mass-spring system
was close to 1 Hz. The dynamics of the mass-spring object were specified as two-dimensional, meaning that lateral displacements of the hand and object were also taken into account for the simulation.

2.3.3 Procedure

At the beginning of each trial, the participant had to first position the hand circle, without the mass-spring attached, over the start position for 300 ms. At this point in time, the target was displayed 15 cm away from the start position, the mass-spring object was displayed, and the simulation of the mass-spring was initiated. Initially, the mass-spring object was aligned with the hand position and the latter displayed on top of the object. Depending on the experimental condition, simulated interaction forces were either applied to the hand or not (see below). The participants were instructed to bring the circles representing the hand and object over the target circle as quickly as possible. However, they were free to initiate their movement when ready, once the target was presented. To complete a trial successfully, both the hand and object had to be within the target with their speed below 2 cm/s for at least 150 ms (Dingwell et al., 2002). At the end of each trial, the resulting movement time (MT) was displayed on the right side of the target. MT was defined as the time interval between the instant that hand speed first exceeded 2 cm/s and the instant at which the trial was completed. As soon as the trial was completed, the simulated mass-spring object was removed from view and turned off. Participants were given a maximum time of 10 s to complete each trial, after which, the trial was aborted. They were encouraged to explore various movements in an effort to minimize MT. However, no specific suggestions were provided.
2.3. MATERIALS AND METHODS

All participants started the experiment with 10 trials, without the mass-spring object attached to the hand so as to become familiar with the goal of the task, the location, and timing of the targets and receiving feedback about MT. Afterwards, participants in the HV-V group completed a block of 80 trials, in which both haptic and visual feedback was provided (HV task). Following a short break of 2–3 min, these participants performed another block of 80 trials, in which haptic feedback was removed, but visual feedback was preserved (V task). Participants of the V-HV group performed the same two blocks of trials but in the opposite order with a similar break in between. Before each block, the participant was informed about the nature of the task and the sensory context (haptic/no haptic). Overall, each participant performed a total of 170 trials (10 + 80 + 80), which on average, took about 45 min. Participants could request additional breaks at any time, but most of them only took the break offered between the two versions of the task.

2.3.4 Data analysis

All kinematic and kinetic signals were low-pass filtered at 20 Hz (fourth-order, no-lag, dual-pass Butterworth filter). For each trial or movement, we computed the MT, the average distance between the hand and object in the Y direction (aligned with the vector from the start position to the target), and the number of crossings between the Y positions of the hand and object. To assess the participants’ ability to predict the dynamics of the mass-spring system in the HV task, we measured the coefficient of correlation between grip force and load force (Danion and Sarlegna, 2007; Flanagan and Wing, 1997). Grip force was computed as the average of the normal forces at the two grip surfaces. To compute load force, we first determined, for each grip surface,
the resultant of the two tangential forces, and we then summed these resultant forces. ANOVA was used to assess the effects of task, group, and trial block (using eight blocks of 10 trials for each task). The Newman-Keuls technique was used for post hoc $t$-tests to correct for multiple comparisons. Since correlation coefficients do not follow a normal distribution, $z$ scores (Fisher transformation) were used for statistical analysis. A 0.05 significance threshold was used for all analyses.

To assess learning more specifically, we fit an exponential of the form $y = ae^{bx} + c$ to the MT data. To test for the effects of group, task, and interaction between group and task on the parameters of the exponential fits, we used nonlinear regression with dummy variables to code for group and task. The full model (including main effects and interactions) is given by equation 2.1 below.

$$MT = (a_0 + a_1 T + a_2 G + a_3 TG)e^{(b_0 + b_1 T + b_2 G + b_3 TG)block} + (c_0 + c_1 T + c_2 G + c_3 TG)$$

where $T$ and $G$ are dummy variables coding for task ($T = 0$ for the HV task; $T = 1$ for the V task) and group ($G = 0$ for the HV-V group; $G = 1$ for the V-HV group), respectively. Note that this 12-parameter model corresponds to fitting separate, three-parameter exponentials to each combination of group and condition. Benchmarking was used to determine the best-fit model (see section 2.4).

2.4 Results

2.4.1 MT analysis

There was no significant difference between the two groups of participants in terms of the mean MT computed over the 10 practice trials ($F_{1,18} = 0.09; p = 0.75$). This
result suggests that the two groups were similar in overall motor skill.

Figure 2.2: Movement time (MT) as a function of trial block. Data are presented on separate panels for each group and experimental condition. Hollow circles represent individual participant means for each block of 10 trials. The dashed and solid lines correspond to exponential curve fits of the data using equations 1 and 2, respectively.

Figure 2.2 shows MT as a function of trial block for each group and condition. Each point represents the mean MT, averaged across trials within a block, for a single participant. Benchmarking revealed that the best-fit exponential model (fit to all of
the data from both groups and both tasks), in which all parameters were significantly different (p < 0.05) than zero is shown in equation 2.2 (see section 2.3).

\[ MT = (a_0 + a_1 T + a_2 G) e^{(b_0 + b_2 G)block} + (c_0 + c_1 T + c_2 G) \]  
\[ (2.2) \]

This exponential model (2.2) revealed main effects of task (p < 0.001) and group (p = 0.029) on the leading value \(a\), main effects of task (p < 0.001) and group (p = 0.035) on the asymptote \(c\) of the exponential, and a main effect of group (p = 0.010) on the learning rate \(b\). There was no main effect of task on the learning rate and no interaction between task and group for any of the three parameters.

This best-fit model can be partitioned into the following four models for each combination of group and condition shown in equations 2.3–2.6.

\[ groupHV - V, taskHV : MT = a_0 e^{b_0 x} + c_0 \]  
\[ = 3.22 e^{-0.963 x} + 1.82 \]  
\[ (2.3) \]

\[ groupHV - V, taskV : MT = (a_0 + a_1) e^{b_0 x} + (c_0 + c_1) \]  
\[ = 5.32 e^{-0.963 x} + 2.94 \]  
\[ (2.4) \]

\[ groupV - HV, taskHV : MT = (a_0 + a_2) e^{(b_0 + b_2) x} + (c_0 + c_2) \]  
\[ = 1.104 e^{-0.455 x} + 2.10 \]  
\[ (2.5) \]

\[ groupV - HV, taskV : MT = (a_0 + a_1 + a_2) e^{(b_0 + b_2) block} + (c_0 + a_1 + c_2) \]  
\[ = 3.203 e^{-0.455 x} + 3.22 \]  
\[ (2.6) \]

These exponential fits are shown in Fig. 2.2, and for comparison, the figure shows the
exponential fits for the full model (see section 2.3). Consistent with the regression analysis, the additional parameters of the full model make little difference to the overall fit. In both cases, we found that final or asymptotic performance (i.e., MT at the end of learning) was significantly better in the HV task than in the V task and also that performance was significantly better for the HV-V group than for the V-HV group. A similar order effect was observed for the learning rate, which was approximately two times faster for the HV-V group than the V-HV group.

Consistent with the best-fit exponential model described above, repeated measures ANOVA revealed that for each combination of group and condition, MT decreased significantly from the first to the last block of 10 trials ($F_{1,9} = 15.9; p < 0.003$ in all four cases). Across conditions and groups, mean MT dropped by 37% (see Figs. 2.3, A and B).
2.4. RESULTS

Figure 2.3: Mean movement time (MT) results. A, Mean MT as a function of trial block and group in the Haptic-Visual task. B, Same as A but for the Visual Task. In A and B, the white and grey circles represent means averaged across participants in the V-HV and HVV groups, respectively. C, Mean MT time in the first block of trials as a function of group and task. D, Same as C but for the last block of trials. In C and D, the white and grey bars correspond to the V-HV and HVV groups, respectively. For all panels, error bars correspond to the standard error of the mean (SEM).

Two-way (task-by-group) ANOVA on MT during the first trial block (Fig. 2.3 C) revealed a significant effect of task ($F_{1,18} = 60.17; p < 0.001$) but no effect of group ($F_{1,18} = 0.10; p = 0.75$) and no interaction ($F_{1,18} = 0.98; p = 0.34$). Thus initial
2.4. RESULTS

performance on either the HV or V task was not affected by previous experience with the other task. Concerning final performance, two-way ANOVA on the last trial block (Fig. 2.3 D) showed a significant effect of task \((F_{1,18} = 79.5; p < 0.001)\). On average, MT was 63% longer when haptic feedback was absent (V task: \(M = 3.17\) s) than when haptic feedback was present (HV task: \(M = 1.95\) s). In addition, there was a significant effect of group \((F_{1,18} = 6.71; p = 0.018)\), demonstrating that prior experience influenced the ability of participants to manipulate the object. Specifically, the HV-V group, which started with full feedback, performed better overall \((M = 2.33\) s) than the V-HV group, which started with visual feedback only \((M = 2.79\) s). Finally, there was no task-by-group interaction, suggesting that starting with haptic feedback provided a final performance advantage in both tasks.

2.4.2 Trajectory analysis

Figure 2.4 shows two representative hand and object trajectories taken from the last 10 trials of the first session. That is, a participant in the HV-V group performed the trial from the HV task and a different participant in the V-HV group performed the trial from the V task. The figure shows the Y positions of the hand and mass (i.e., along the axis aligned with the start position and target), the Y distance between mass and object, and the Y velocities of the hand and mass. When haptic feedback was not available, the participant moved the hand slowly—making a series of submovements characterized by distinct hand velocity maxima (Fig. 2.4 F)—and kept the mass close to the hand (Fig. 2.4 D). In contrast, when haptic feedback was available, the participant moved the hand more quickly (Fig. 2.4 E), and the trajectory of the object was quite different than that of the hand (Fig. 2.4 C).
Figure 2.4: Examples of representative trials in each task. 

A and B, Hand and mass positions along the Y axis (main axis of movement) as a function of time. C and D, Y distance between hand and mass as a function of time. E and F, Hand and mass velocity along the Y axis as a function of time. In top and bottom panels, thick and thin lines refer to hand and mass kinematics, respectively. Dashed lines represent criteria that were used to assess when a trial was completed successfully (see section 2.3 for further information). Each trial was performed by a different subject, and was extracted from the last block of 10. Note the different movement strategies employed.
to displace the mass in the Haptic-Visual and Visual tasks.

Figure 2.5 shows mean hand and object Y positions (Fig. 2.5, A and B) and the mean hand-to-mass Y distance (Fig. 2.5 C) as a function of normalized time for each combination of task and group. These mean functions are based on participant means averaged over the last 10 trials. In both the HV and V tasks, the deviation between the hand and mass was greater for participants in the HV-V group compared with participants in the V-HV group. However, the difference between groups was far greater in the HV task than in the V task, revealing a strong effect of prior experience. Overall, the deviation between the hand and the mass was greater in the HV task, in which haptic feedback was provided, than in the V task. However, quite similar deviations were seen in the HV task performed by the V-HV group and the V task performed by the HV-V group (Fig. 2.5 C), again revealing the strong effect of prior experience.
Figure 2.5: Mean trajectories in the last block of trials. 

A, Mean hand (solid lines) and mass (dashed lines) positions as a function normalized time for each group in the Haptic-Visual task. 

B, Same as A, but for the Visual task. 

C, Mean hand-to-mass distance as a function of normalized time for each group and task. For all panels,
the mean trajectories are based on participant means averaged over the last 10 trials. Prior to averaging, trials were normalized with respect to movement time. Shaded areas correspond to 1 SEM.

Figure 2.6 shows mean values of the average absolute Y distance between the hand and mass over the movement, as well as the number of crossings between the hand and mass Y positions. (As a reference, in Fig. 2.4, there are two and seven crossings for the trials shown for the HV and V tasks, respectively.) Repeated measures ANOVA revealed that for each task, both measures changed significantly across blocks of trials ($F_{7,126} > 5.19; p < 0.001$). The average absolute distance between the hand and mass tended to increase across blocks in the HV task, whereas it tended to decrease across blocks in the V task. The number of crossings tended to decrease across blocks in both tasks.
Concerning final performance, two-way (task-by-group) ANOVA of the last trial block showed main effects of task ($F_{1,18} = 11.2; p = 0.004$) and group ($F_{1,18} = 11.8; p = 0.003$) on the average absolute distance between hand and mass (Fig. 2.7 A). Although the effect of group was larger for the HV task, the interaction between task and group did not reach significance ($F_{1,18} = 4.15; p = 0.056$). Thus in the
first session, participants who received haptic feedback tended to allow the mass to move away from the hand, whereas participants who only received visual feedback tended to keep the mass closer to the hand. However, the effect of haptic feedback on the average absolute hand-to-mass distance was much smaller when considering the second session. The number of crossing was about two times greater in the V task compared with the HV task ($F_{1,18} = 75.7; p < 0.001; 5.6 \text{ vs } 2.5$). There was also an effect of group ($F_{1,18} = 7.48; p = 0.014$) and a significant task-by-group interaction ($F_{1,18} = 7.09; p = 0.015$), due to the fact that the number of crossings was smaller for the HV-V group but only for the V task (corrected $t$-test; $p = 0.001$).

![Graph A](image1)

![Graph B](image2)
2.4. RESULTS

Figure 2.7: Means of kinematic variables in the last trial block. **A**, Average hand-to-mass distance in the Haptic-Visual task as a function of task and group. **B**, Same as A, but for the number of crossings between and mass along the Y axis. For all panels, grey bars correspond to the HV-V group and white bars correspond to the V-HV group. Error bars correspond to 1 SEM.

2.4.3 Gripload force coupling

To examine the coupling of grip force and load force in the HV task, in which substantial load forces acted on the object, we computed the coefficient of correlation between grip force and load force for each trial. Figure 2.8 shows mean correlation coefficients, averaged across participant means, as a function of trial block for each group. A two-way (trial block-by-group) ANOVA revealed significant effects of trial block ($F_{7,126} = 4.14; p < 0.001$) and group ($F_{1,18} = 5.01; p = 0.04$). The coupling between grip force and load force tended to increase with trial block and was consistently greater when haptic feedback was provided in the first session (HV-V group; $R = 0.66$) than when it was provided in the second session (V-HV group; $R = 0.46$). We also determined the maximum load force in each trial of the HV task. A two-way (trial block-by-group) ANOVA revealed that the maximum load force increased across blocks ($F_{7,126} = 2.06; p = 0.05$) and was greater for the HV-V group than the V-HV group (2.9 vs 1.1 N; $F_{1,18} > 10.48; p = 0.005$). These effects are consistent with earlier observations showing that MT was lower in the HV-V group than the V-HV group and that MT decreased across trials blocks.
Figure 2.8: Grip-load force coupling in the Haptic-Visual task. Average correlation coefficients of the correlation between grip force and load force as a function of trial block for both the HV-V (filled circles) and V-HV (open circles) groups. Each point represents the mean of participants means averaged across trials within the block. Error bars correspond to 1 SEM.

2.5 Discussion

The current study yielded several key findings. First, in agreement with earlier studies, in which haptic feedback was provided (Dingwell et al., 2002, 2004; Nagengast et al., 2009), we found that people could improve their ability to control the movement of a nonrigid object. Second, improvements in control also occurred in the absence of appropriate haptic feedback, arising from interaction forces between the hand and object. Third, haptic feedback allowed greater dexterity in manipulating nonrigid objects as measured by MTs. Fourth, previous experience influenced the way participants manipulated the nonrigid object. Although positive transfer was found when appropriate haptic feedback was removed, quite unexpectedly, negative transfer was found when appropriate haptic feedback was added. Fifth, we found
that participants appeared to use distinct control strategies when moving the object with and without haptic feedback. With haptic feedback, considerable stretching of the spring, linking the hand and mass, was found in naive participants. In contrast, without haptic feedback, the mass was kept close to the hand in naive participants. Finally, we found that in the haptic version of the task, the coupling between grip force and load force improved across trials, suggesting that participants acquired an increasingly accurate representation of the interaction forces between the hand and mass.

2.5.1 Contributions of haptic and visual feedback

On the one hand, one might expect haptic feedback related to interaction forces to improve control, because such feedback should allow more accurate sensory estimates of the state of the object through multisensory integration (Ernst and Banks, 2002; Ernst and Bulthoff, 2004; van Beers et al., 2002). On the other hand, because interaction forces perturb the hand, one might expect haptic feedback to degrade control (Dingwell et al., 2002; Huang et al., 2006). Although previous experiments have examined the contributions of haptic and visual feedback in performing skilled object manipulation tasks (e.g., Sternad et al. (2001)), to our knowledge, only one study has addressed this issue explicitly in the context of learning to manipulate a nonrigid object. As mentioned in the introduction, Huang and colleagues (2006), who examined a task in which participants had to control the position of a ball on a beam, found virtually no benefit of haptic information; participants who received appropriate haptic feedback began and finished their training session with comparable performance with participants who received visual feedback only (see Table 3 in Huang et al. 2006). In
contrast, we found that haptic feedback facilitates both initial and final performance in naïve participants. In the absence of haptic feedback, initial and final MTs increased by 75% and 92%, respectively, and the number of crossings between the hand and mass increased by 260%. This comparison between these two studies suggests that the contribution of haptic information to the manipulation of objects with complex dynamics can vary substantially depending on the properties of the object and task. However, our observation that haptic feedback is helpful when manipulating a mass-spring system is consistent with another study by Huang and colleagues (2007), in which they examined the ability to oscillate and tune a mass-spring system at its resonance frequency. Future work will be required to determine which aspects and/or features of a mass-spring system make haptic feedback beneficial.

Although we found that haptic feedback improved performance, our participants were still able to complete the task and improve performance across trials when only visual feedback was provided. Overall, participants in the V task reduced their MT by ~40% between the first and the last block of trials—a reduction that was similar to that observed in the HV task. The fact that participants could control the mass-spring system based solely on visual information extends earlier observations made in the context of bouncing a ball on a racket (Sternad et al., 2001) or balancing an inverted pole (Mehta and Schaal, 2002).

2.5.2 Learning internal models of nonrigid objects

It has been argued that learning to control a nonrigid mass-spring object involves the acquisition of an internal model of the object’s dynamics (Dingwell et al., 2004). Internal models of object dynamics capture the mapping between the force applied
to the object and the motion of the object (or the mapping between arm motor commands and object motion). Such models enable the sensorimotor system to predict the consequences of motor commands, in which case, they are referred to as forward models (Wolpert and Flanagan, 2001; Wolpert and Ghahramani, 2000). Our results pertaining to the coupling between grip and load force support the idea that participants learned a forward model of the mass-spring system. To assess participants’ ability to predict dynamics of the mass-spring system in the HV task, we measured the correlation between grip force and load force (Danion and Sarlegna, 2007; Flanagan and Wing, 1997). We found that correlation coefficients (R values) were initially low but increased substantially over the first three blocks of trials. Interestingly, roughly parallel changes were observed in MT, which decreased substantially over the first three blocks (Fig. 2.3 A). Indeed, across trial blocks in the HV task, the correlation between mean R values and mean MT was -0.96 (p < 0.001). The rather gradual improvement in grip-load coupling observed in the current study may be contrasted with the rapid adaptation of grip forces reported for a task in which participants grasped and moved a rigid object with an unfamiliar load (Flanagan et al., 2003).

2.5.3 Transfer between tasks internal models and movement strategies

One aim of our study was to determine how learning to control a nonrigid object without haptic feedback influences control when haptic feedback is provided and vice versa. Our results provide clear evidence that previous experience in one version of the task influenced the ability to perform the other version of the task. However, those transfer effects were not symmetrical. Although earlier practice with haptic feedback improved the ability to perform the task without haptic feedback, earlier
practice without haptic feedback was detrimental to performing the task with haptic feedback. As noted above, there is evidence that learning to control a nonrigid object involves acquiring an internal model of the object’s dynamics. We reasoned that if participants learned a direct mapping between arm motor commands and object motion, then because this mapping depends on whether interaction forces between the hand and object are present, negative transfer should occur between the HV task and the V task and vice versa. Alternatively, we proposed that in principle, participants could learn two mappings: the mapping between motion of the hand and motion of the mass (i.e., between the states of the hand and mass) and the mapping between arm motor commands and hand motion. If so, it is not clear whether transfer would be positive or negative. On the one hand, because the former mapping is independent of interaction forces and is the same in both tasks, we might have expected positive transfer between the HV and V tasks in both directions. On the other hand, because the latter mapping changes between tasks, negative transfer might be expected between the HV and V tasks in both directions. However, none of these scenarios was supported, because negative transfer from the V task to the HV task was observed, whereas positive transfer occurred from the HV task to the V task.

Asymmetric transfer of learning could arise if participants adapted their arm motor commands to interaction forces more slowly than they de-adapted their arm motor commands when interaction forces were removed (Davidson and Wolpert, 2004; Shadmehr et al., 1998; Smith et al., 2006). However, although this scheme predicts that transfer of learning from the V task to the HV task will be poorer than the transfer in the opposite direction, it does not predict whether the transfer will be positive or
2.5. DISCUSSION

negative. Based on the above considerations, it seems difficult to explain the asymmetric transfer effects we obtained in the context of learning mappings or internal models.

As an alternative, we suggest that the asymmetric effects of previous experience can be understood in the context of control strategies, namely the process of optimizing/ selecting movement trajectories, which is distinct from learning dynamics. We observed that the hand-to-mass distance varied substantially depending on the experimental conditions. In the HV task, naïve participants allowed the mass to move quite far away from the hand. This resulted in movements characterized by a relatively low number of hand velocity peaks and crossings between the hand and mass. In contrast, in the V task, naïve participants kept the mass close to the hand, which resulted in movements featuring a large number of hand velocity peaks and crossings between the hand and mass. Altogether, it seems that in the HV task, naïve participants learned to control the degrees of freedom associated with the mass, whereas in the V task, naïve participants tended to do the opposite and froze the mass. Thus naïve participants used what might be referred to as a lead-lag strategy when haptic feedback was provided and a dragging strategy when haptic feedback was not available. The main advantage of the lead-lag strategy is that it allows faster hand movements. However, this strategy requires the ability to quickly damp the resulting oscillations of the mass. In contrast, the dragging strategy does not allow fast hand movements, but the ability to damp terminal oscillations is less crucial, since these oscillations are likely to be small. Last but not least, visual feedback processing is relatively slow compared with somatosensory feedback control (200 vs 80 ms), and this may have contributed to slower hand movements in the V task.
Our results indicate that when the two groups of participants exchanged tasks, they did not fully exchange strategies. Instead, they tended to stick, at least partially, with their initial strategy. As a consequence, both groups ended up adopting a rather similar, intermediate strategy. In other words, when participants had prior experience with haptic feedback, they allowed the mass to move more freely in the V task than naïve participants. Conversely, when participants had prior experience in the V task, they were reluctant to free the mass in the HV task, compared with naïve participants. Because fast completion times are possible only if the mass is moved away from the hand, this carryover effect (i.e., tendency to stick with the initial strategy) was beneficial to participants who started with haptic feedback, whereas it was detrimental to those who started without.

2.5.4 Implications for training in VR simulators

Our finding that haptic feedback as well as prior experience with haptic feedback enhance the ability to control a nonrigid object has implications for the design of teleoperation devices and VR simulators, such as those used in surgical training. This is particularly obvious for surgical simulators, because trainees will use these devices to learn how to handle a wide variety of soft tissues (Basafa and Farahmand, 2011; Lim et al., 2009). A typical issue when designing VR simulators is whether the provision of haptic feedback, which can be both difficult and costly, is necessary or justified. In line with our results, a number of studies have found that haptic feedback enhances performance in surgical simulator training (Panait et al., 2009; Ström et al., 2006; van der Meijden and Schijven, 2009). However, a novel finding brought by our study is that training without haptic feedback (i.e., with V) can lead to persisting
2.6. REFERENCES

detrimental effects if operators subsequently have to work with haptic feedback. This would typically be the case, when after simulated training, operators would then have to perform the real task.

2.6 References


Chapter 3

Separate contributions of kinematic and kinetic errors to trajectory and grip force adaptation when transporting novel hand-held loads

3.1 Abstract

Numerous studies of motor learning have examined the adaptation of hand trajectories and grip forces when moving grasped objects with novel dynamics. Such objects initially result in both kinematic and kinetic errors; i.e., mismatches between predicted and actual trajectories and between predicted and actual load forces. Here we investigated the contribution of these errors to both trajectory and grip force adaptation. Participants grasped an object with novel dynamics using a precision grip and moved it between two targets. Kinematic errors could be effectively removed using a force channel to constrain hand motion to a straight line. When moving in the channel, participants learned to modulate grip force in synchrony with load force and this learning generalized when movement speed in the channel was doubled. When the channel was removed, these participants continued to effectively modulate grip force
but exhibited substantial kinematic errors, equivalent to those seen in participants who did not previously experience the object in the channel. We also found that the rate of grip force adaptation did not depend on whether the object was initially moved with or without a channel. These results indicate that kinematic errors are necessary for trajectory but not grip force adaptation, and that kinetic errors are sufficient for grip force but not trajectory adaptation. Thus, participants can learn a component of the object’s dynamics, used to control grip force, based solely on kinetic errors. However, this knowledge is apparently not accessible or usable for controlling the movement trajectory when the channel is removed.

3.2 Introduction

Numerous studies of motor learning have examined the adaptation of hand trajectories and grip force when transporting objects with novel dynamics specifying the mapping between applied force and motion (Caithness et al., 2004; Crevecoeur et al., 2010; Danion et al., 2011; Flanagan et al., 2003; Nowak et al., 2004; Shadmehr and Mussa-Ivaldi, 1994). Initially moving such objects results in kinematic errors, i.e., mismatches between predicted and actual hand trajectories, as well as kinetic errors, i.e., mismatches between predicted and actual load forces acting on the hand that are revealed by poor modulation of grip force with load force. However, with practice, people adapt so as to generate approximately straight-line hand movements and modulate grip force in synchrony with load force (Flanagan et al., 2003).

Although kinematic errors are considered to be critical for trajectory adaptation (Shadmehr et al., 2010; Smith et al., 2006; Melendez-Calderon et al., 2011; Wolpert et al., 2011), it is not known whether kinetic errors also contribute. Likewise, although
it seems reasonable to assume that kinetic errors drive grip force adaptation, it is not known whether kinematic errors also contribute. Here we investigated the contributions of these errors to both trajectory and grip force adaptation. Importantly, the prediction of both load forces and hand trajectories relies on an internal model of object dynamics, and prediction errors can be used to update the internal model. A key question is whether kinematic and kinetic errors update a common internal model, or separate models used for trajectory and grip force adaptation, respectively.

In our task, participants grasped an object with a vertical precision grip and moved between targets in a horizontal plane. One robot, attached to the object, was used to create unusual object dynamics. A second robot, attached to the wrist, could implement a force channel that constrained hand motion to a straight line, effectively removing kinematic errors that would otherwise result from the unusual object dynamics (Scheidt et al., 2000; Smith et al., 2006). This setup enabled us to compare grip force adaptation with and without kinematic errors as well as test whether experiencing kinetic errors in the channel would benefit trajectory adaptation when the channel was subsequently removed.

If kinematic and kinetic errors update a common internal model of object dynamics, we would expect kinetic errors experienced in the channel to benefit trajectory control when subsequently moving without the channel. Moreover, we would expect grip force adaptation to be quicker when initially experiencing novel object dynamics without, compared to with, the channel because both kinematic and kinetic errors would update the internal model, as opposed to kinetic errors alone. However, if kinematic and kinetic errors update separate internal models, we would not expect kinetic errors experienced in the channel to benefit subsequent trajectory control.
Moreover, we would not expect grip force adaptation to be faster when first experiencing the novel object dynamics without the channel because kinematic errors experienced without the channel would not contribute to updating the internal model used for grip force control.

3.3 Material and Methods

3.3.1 Participants

Forty-five participants (21 women) were recruited from the population of undergraduate and graduate students at Queen’s University. Participants provided written informed consent and received monetary compensation for their time. The ethics committee of Queen’s University approved the study. The participants were randomly assigned to one of four groups, with 11 participants in Groups A, B, and C and 12 participants in Group D (Group A: age = 22.0 ±2.4 years, height = 1.72 ±0.09 m, mass = 73.2 ±15.5 kg; Group B: age = 23.3 ±4.6 years, height = 1.75 ±0.11 m, mass = 82.4 ±3.5 kg; Group C: age = 22.9 ±4.9 years, height = 1.70 ±0.07 m, mass = 67.6 ±17.0 kg; Group D: age = 20.8 ±2.3 years, height = 1.69 ±0.08 m, mass = 61.8 ±7.3 kg). All of the participants reported that they were right-handed.

3.3.2 Apparatus

While seated, participants moved a circular cursor (diameter 20 mm) representing the position of the right wrist between two circular targets (diameter 20 mm) presented in a horizontal plane (Fig. 3.1 A, B). The two targets were aligned in the participant’s midsagittal plane (y-axis) and separated by 15 cm. The wrist was strapped to the endpoint of a planar robotic manipulandum (WristBOT, Howard et al. (2009)) that
measured the position of the wrist (resolution 0.1 mm) and that could apply forces in the horizontal plane. In some trials, participants were required to grasp, with the right hand, a cylindrical object using a precision grip with the tips of the index finger and thumb contacting vertically aligned horizontal circular surfaces (diameter 25 mm) located on the top and bottom (64 mm apart), respectively. In these trials, a circular cursor (diameter 10 mm) representing the position of the object in the horizontal plane was displayed (Fig. 3.1 B). Each grip surface was mounted on a six-axis force transducer (Nano F/T, ATI Industrial automation) that measured applied forces (0.05 N resolution) and torques in three dimensions. The grip surfaces were covered with sandpaper and were free to spin about the long axis of the object. The object was attached to a lightweight robotic manipulandum (Phantom Haptic Interface, 3.0, Sensable Devices) via a joint that allowed rotation about all axes except the long axis of the object. Thus, the combination of this joint and the spinning grip surfaces allowed free rotation of the object in three dimensions. Three optical encoders, placed on the three motors of the manipulandum, measured the object’s position in three dimensions (0.1 mm resolution).
In some trials, a force channel, created with the WristBOT manipulandum, constrained the motion of the wrist to a straight line between the two targets (Fig. 3.1 B). The force channel was implemented as a damped spring (with a stiffness of 5 N/mm...
and a viscosity of 0.01 N/mm/s) that applied forces to the wrist perpendicular to the straight line between the targets if the wrist cursor veered off this straight line. In addition, the ends of the channel were capped such that the wrist cursor could not move >25 mm beyond the target centers. In force channel trials, a rectangle (width of 30 mm and length of 200 mm) was displayed representing the walls of the channel (Fig. 3.1 B). When moving in the channel, the cursor representing the wrist was positioned in the center of a visual slider (square of width 30 cm) that moved along the length of the channel. In channel trials, we displayed the position of the wrist projected onto the line between the targets. In other words, very small deviations of the wrist cursor off the line between the targets were not displayed such that the wrist cursor was always in the center of the channel.

A visual display system was used to present the two targets, the cursors representing the wrist and object, and the walls of the force channel in a horizontal plane at the height of the wrist. This system consisted of a 30-inch monitor positioned horizontally above a mirror located half way between the monitor and plane of wrist movement (Fig. 3.1 A). Participants viewed the visual scene displayed on the monitor via the mirror, which blocked vision of the arm and grasped object.

3.3.3 Procedure

A single trial involved moving the wrist cursor between the two targets (Fig. 3.1 B). In all cases, participants generated alternating outward and inward movements in successive trials. In a given trial, the movement could be generated either while grasping the object (in which case the cursor representing the object was displayed) or without the object in hand. In addition, in a given trial the force channel could
either be on (in which case the rectangle representing the channel was displayed) or off. In trials in which the object was grasped, the forces generated by the object on the fingertips depended on object velocity as shown in equation 3.1 below.

\[
\begin{bmatrix}
  f_x \\
  f_y
\end{bmatrix}
\begin{bmatrix}
  0 & -0.012 \\
  0 & 0
\end{bmatrix}
\begin{bmatrix}
  N \\
  \frac{\dot{N}}{mm/s}
\end{bmatrix}
\begin{bmatrix}
  \dot{x} \\
  \dot{y}
\end{bmatrix}
= \begin{bmatrix}
  \dot{N} \\
  \frac{\dot{N}}{mm/s}
\end{bmatrix}
= \begin{bmatrix}
  f_x \\
  f_y
\end{bmatrix}
\begin{bmatrix}
  \dot{x} \\
  \dot{y}
\end{bmatrix}
\begin{bmatrix}
  mm/s \\
  mm/s
\end{bmatrix}.
\] (3.1)

Thus, the object generated a velocity-dependent lateral force (x-axis in Fig. 3.1 B) on the fingertips proportional to the velocity of the object in the straight-ahead direction (y-axis in Fig. 3.1 B). The direction of the lateral force depended on the direction of object movement such that a leftward force was applied when the object was moved outwards (from the near target to the far target) and a rightward force was applied when the object was moved inwards (from the far target to the near target).

Before a trial could be initiated, the participant had to position the center of the wrist cursor within 5 mm of the center of the current start target for 200 ms. For the purpose of providing feedback about movement duration, movement onset was defined at the time at which the wrist velocity first exceeded 30 mm/s. In standard speed trials, the current end target changed color (from cyan to white) 400 ms after movement onset, and participants were asked to position the wrist cursor at the end target at the time at which the end target changed color. In fast speed trials, the duration was 200 ms.

The sequences of trials experienced by the four groups of participants are illustrated in Figure 3.1 C. Each group completed 3 blocks of trials. For all groups, block 1 consisted of 30 practice trials (15 outward and 15 inward movements interleaved) without the object and without the force channel. The primary aim of these trials was
to allow participants to practice moving between the targets in the prescribed duration. Participants in Groups A, B, and C performed these movements at the standard speed whereas participants in Group D performed alternating sets of standard and fast speed trials, with 6 trials per set, starting and ending with standard speed trials. These participants were told about the required speed at the start of each set. For all groups, block 3 consisted of 30 movements with the object in hand and without the force channel. The primary aim of the current study was to test whether moving the grasped object with the force channel (in block 2) would facilitate adaptation of movement trajectories when moving the object without the channel.

The four groups differed in terms of the trials they experienced in block 2. Participants in Group A, who served as controls, performed 30 trials without the object and without the force channel (as in block 1). Participants in Group B performed 30 trials with the object in hand and with the force channel. Participants in Group C performed alternating sets of 5 trials with and without the object in hand and with the force channel turned on throughout. This group was included in an effort to increase the salience of the forces generated by the object. Participants in Group D first performed 30 standard speed trials with the object and force channel. They then completed 6 fast speed trials in the force channel without the object, 20 fast speed trials in the force channel with the object, 6 standard speed trials in the force channel without the object, and 20 standard speed trials in the force channel with the object. The group was included to determine whether grip force adaptation, expected over the first 30 standard speed trials, generalized across movement speeds. The 6 no-object trials at the start of each change in required movement speed were included to ensure that participants were moving at the correct speed when first transporting
the object at the new speed.

As described above, participants in Groups B, C, and D first experienced the object with the motion of the wrist constrained by the force channel. To make the forces generated by channel versus the object as distinct as possible, all of these participants completed three channel exploration trials, without the object in hand, between blocks 1 and 2. Participants were told that the channel would act like a rail to which their wrist was attached (via the slider) and that they could move their wrist along the rail but not off the rail. To initiate the first exploration trial, participants were required to position the wrist cursor at a start position corresponding to the near target. The rectangle representing the walls of the channel and the slider were then displayed and the channel was turned on. Participants were given 10 s to explore the effects of the channel by moving along it and generating forces perpendicular to it. Participants were then given two additional 10 s trials to explore the channel. Following these exploration trials, participants were asked to move the wrist cursor to the near start position located within the channel and the object was handed to them. The object cursor was visible as the object was handed to the participant so that they could see it approaching. They were told to grasp the object with a precision grip and to keep the orientation of the grip axis vertical. Participants were told that the object would generate forces on their fingertips when it was moved but that their wrist would be secured to the rail. Participants were also informed that they would be required to transport the same object without the help of the channel following the current block of channel trials. At this point, block 2 was initiated.

Participants in Groups B, C, and D also completed a similar transition trial between block 2 (with the channel) and block 3 (without the channel). Specifically,
following the last trial of block 2, participants were asked to move the wrist cursor to the start position and the object was then taken from them and moved such that the object cursor was out of view. The rectangle representing the walls of the channel and the slider were then removed from view and participants were told that the channel had been removed. Participants were then given 10 s to move around the workspace as they wished so that they could appreciate that the channel had been removed. Participants then returned the wrist cursor to the start position and the object was handed back to them. Participants were told that they would now be required to make movements between the targets while holding the object and with the channel removed.

One of the two experimenters who were always present monitored the orientation of the object during object trials and encouraged the participant to keep the orientation of the grip axis vertical. The orientation of the object was also assessed during data analysis (see section 3.3.4). Participants were debriefed after completing the experiment. They were asked to comment on the forces exerted by the object both when moving in the channel and when subsequently moving without the channel. They were also invited to provide any additional comments.

3.3.4 Analysis

Force signals from the force sensors and position signals from the robotic devices (indicating the positions of the object and wrist) were recorded at 1000 Hz and digitally smoothed using a fourth-order, zero-phase lag Butterworth filter with a cutoff frequency of 14 Hz. A first order central difference equation, applied to the smoothed position signals, was used to compute the x and y velocities of the object.
3.4. RESULTS

and wrist. Grip force was computed as the average of the normal forces, applied by the index finger and thumb, at the two grip surfaces. Load force was computed as the sum of the tangential forces at each grip surface (i.e., the load force at each surface). To assess whether the object was held in a vertical orientation, for each trial we computed the correlation between the load forces exerted by the index finger and thumb. In general, these forces were very similar, yielding an average correlation of 0.97. Trials in which the correlation was <0.50 were removed from the analysis of grip force adaptation. This resulted in the removal of 2.6% of the trials.

To assess the coupling between grip force and load force we computed the correlation coefficient (at zero phase lag) between the two forces. To quantify the trajectory of the wrist, we computed the peak-to-peak lateral deviation of the wrist path. That is, we determined the difference between the largest and smallest x positions observed during the movement (see x coordinates in Fig. 3.1 B). Movement onset was taken as the time at which the wrist velocity exceeded 20 mm/s, and movement offset was taken as the time at which wrist velocity went below 20 mm/s. To quantify grip force and trajectory adaptation, we fit an exponential of the form $y = ae^{bx} + c$ to the grip-load force cross-correlation coefficients and the lateral trajectory deviations. We tested for the effects of group on all three parameters of the exponential using nonlinear regression. A 0.05 significance threshold was used for all analyses.

3.4 Results

3.4.1 Grip force adaptation in the channel

Figure 3.2 A illustrates grip and load forces and movement kinematics from the first trial in the force channel (block 2) for a single participant from Group B. Note that
the load force scaled with the velocity of the object in the y direction (i.e., along the channel). As expected, the coupling between grip force and load force on this initial trial with the object in hand was poor, yielding a correlation coefficient of 0.52. This indicates that the participant failed to predict the load force (and modulate grip force appropriately). The motion path of the wrist was constrained to a straight-line path between the two targets. The path of the object was also quite straight. However, a small amount of curvature occurred due to the load force applied to the fingertip. Because the load force acted orthogonal to the direction of movement, the velocity profiles of the wrist and object were similar to what one would expect without a load or with a standard inertial load; i.e., they were approximately bell-shaped (Atkeson and Hollerbach, 1985; Flanagan and Wing, 1997; Hogan and Flash, 1987; Morasso, 1981; Ruitenbeek, 1984).
Figure 3.2: Representative trials. A, First trial while moving the unfamiliar object in the channel. B, First trial, after prior experience in the channel, while moving the same object without the channel. The same participant, from group B, performed both trials. Note that although arm and object movements were relatively straight in A, the coupling between grip force and load force was weak. Conversely, in B, movements were altered but the coupling between grip force and load force was strong.

The average maximum absolute lateral deviation of the wrist, based on means from all participants in Groups B and C, was 2.7 mm (SE = 0.2 mm). Thus, the channel was effective in maintaining an approximately straight-line wrist path. However, we
found that the maximum absolute lateral deviation of the wrist increased slightly over the first 10 trials across trials performed in the channel and then remained steady. The average deviation was significantly greater ($p < 0.05$) over the last two trials combined [mean ($M$) = 3.3 mm, SE = 0.32 mm] than over the first two trials combined ($M = 1.2$ mm, SE = 0.08). This indicates that participants learned to exploit the channel, allowing forces applied by the channel to counteract the load force applied by the object. The average maximum absolute lateral deviation of the grasped object, based on means from all participants in Groups B and C, was 15.7 mm (SE = 0.8 mm). Thus, on average, the maximum lateral motion of the object relative to the wrist, which in the direction of the load applied by the object to the hand, was $\sim 13$ mm. Although the load acting on the object slightly perturbed the trajectory of the object and hand when moving in the channel, as will be shown below, this perturbation was much smaller than that observed in participants who first experienced the load without the channel.

Figure 3.3: Mean grip-load force coupling as a function of trial and group. A, Average correlation coefficients between grip force and load force while experiencing the object in the channel. B, Average correlation coefficients between grip force and load force
3.4. RESULTS

when moving the object without the channel. Dashed lines represent exponentials fit to the data. The comparison between the 3 groups indicates that prior experience moving in the channel (groups B and C) benefited grip-load coupling. Error bars correspond to 1 SE.

Figure 3.3 A presents the evolution of the correlation coefficient (R) between grip force (GF) and load force (LF) over successive object transport trials performed in the channel (block 2) by participants from Groups B and C. In both groups, as the number of trials increased, the correlation between GF and LF increased. To assess grip force adaptation, we fit exponentials to both groups. For each group, all three parameters of the exponential were significantly different (p < 0.05) than zero. Nonlinear regression revealed no significant differences between Groups B and C in terms of the leading value (–0.243 vs –0.261) or the learning rate (–0.175 vs –0.370). However, the asymptote was significantly greater (p < 0.05) for Group B (0.737) than for Group C (0.660). These results indicate that participants in Groups B and C learned to modulate grip force in synchrony with load force while moving the grasped object in the channel.

3.4.2 Transfer of grip force adaptation outside the channel

Figure 3.2 B illustrates grip and load forces and movement kinematics from the first trial with the force channel removed (block 3) for the same participant shown in Figure 3.2 A. In contrast to the first trial performed in the channel (block 2; Fig. 3.2 A), good coupling between grip force and load force was seen in the first trial outside the channel, yielding a correlation coefficient of 0.89. Importantly, the path of the wrist (as well as the path of the object) was strongly deflected by the load force applied to the object. This required the participant to generate arm movement
correction, which is also evident in the y velocity profiles of the wrist and object. Thus, whereas predictive grip force control was maintained when the channel was removed, the participant was seemingly unable to exploit knowledge of object dynamics, gained when moving in the channel, to compensate for the effects of the load on the movement trajectory.

Figure 3.3 B presents the evolution of the correlation coefficient between grip force and load force over successive trials outside the channel (block 3) for Groups A, B, and C. When the channel was removed, participants from Groups B and C were able to maintain good coupling between grip force and load force, as indicated by relatively high correlation coefficients observed in the initial trials. This view was confirmed by a two-way ANOVA that compared mean $R$ values over the 4 initial trials performed outside the channel and the mean $R$ values over the last 4 trials performed in the channel for both Group B and C. There were no main effects of GROUP or TRIAL BLOCK (first 4 vs last 4) and no interaction ($p > 0.22$ in all three cases), indicating that both groups had no difficulties in maintaining accurate grip force control when the channel was removed (block 3). In contrast, participants from Group A exhibited lower $R$ values during initial trials. A one-way ANOVA examining the first trial outside the channel revealed that the $R$ value was smaller in Group A than in Groups B and C combined ($p < 0.02$). Thus, in terms of grip force control, participants from Groups B and C appeared to benefit from prior exposure to object dynamics in the channel (block 2). However, due to the nature of the load acting on the object, good transfer of grip force control would be expected if participants keep modulating grip force in the same way once the channel is removed in block 3.

For Group A, $R$ values improved across trials in block 3 in much the same way that
they improved for Groups B and C when moving in the channel (block 2). Fitting an exponential to the $R$ values for Group A revealed that all three parameters ($a = 0.221$, $b = 0.192$, $c = 0.726$) were significantly different from zero ($p < 0.05$). Nonlinear regression was used to compare the exponential fit to the $R$ values of Group A (outside the channel; block 3) with the exponentials fit to the $R$ values for Groups B and C when moving inside the channel (block 2). This analysis failed to reveal significant differences among the three groups in terms of the leading value and learning rate. The asymptote was greater for Group B than Group A ($p < 0.05$) but there was no difference between Group C and Group A. Thus, overall the adaptation of grip force control did not seem to benefit from kinematic errors associated with arm movements without the channel.

### 3.4.3 Trajectory adaptation outside the channel

A central aim of the current study was to assess whether prior exposure to object dynamics in the channel would benefit trajectory adaptation when the channel was removed. Figure 3.4 shows the peak-to-peak lateral deviation of the wrist path as a function of trial in block 3 for Groups A, B, and C. As expected, for participants in Group A, who were experiencing the novel dynamics for the first time, the wrist path was substantially deviated in initial trials. However, these participants gradually adapted to the perturbation over $\sim 15$–$20$ trials. As can be appreciated visually in Figure 3.4, participants in Groups B and C did not seem to benefit from prior exposure to object dynamics when moving in the channel (block 2). That is, the lateral deviation functions observed for these groups were similar to that observed for group A. To quantify trajectory adaptation, we fit exponentials to the lateral
deviations for each group. For each of the three groups, all three parameters of the exponential were significantly different ($p < 0.001$) than zero. Nonlinear regression revealed no significant differences ($p > 0.05$) among the three groups in terms of the leading value (37.1, 47.2, and 45.0 for Groups A, B, and C), the learning rate (-0.280, -0.259, and -0.335), or the asymptote (15.63, 17.92, and 16.67). Thus, this analysis indicates that all three groups exhibited similar trajectory adaptation and that there was no benefit of prior exposure to object dynamics in the channel.

![Graph](image.png)

Figure 3.4: Mean peak-to-peak lateral deviation of the wrist, as a function of trial and group, when moving without the channel. The dashed lines represent exponentials fit to each series of data points. Error bars correspond to 1 SE.

### 3.4.4 Generalization across speeds within the channel

The fact that participants in Groups B and C adapted their grip force to the novel load force experienced in the channel (block 2) suggest that they learned that this load was velocity dependent. To evaluate whether this is the case, we ran an additional group of participants (Group D) who manipulated the object at various speeds in
the channel (block 2). These participants first performed 30 movements at the same speed as participants from Groups B and C and were then instructed to double their movement speed for 20 trials before completing 20 trials at the initial, regular speed.

The instruction to double movement speed led to an approximate doubling of the magnitude of peak LF. Overall, the mean load force peak was $4.8 \pm 0.3$ N (average based on participant means $\pm$SE) during the first 30 trials, then reached $8.2 \pm 0.4$ N during the subsequent 20 faster trials, and finally decreased to $5.1 \pm 0.3$ N during the last 20 trials performed at normal speed. One-way ANOVA showed significant variation in the load force peak among the three sessions ($p < 0.001$). Post hoc analyses confirmed that load force peaks during the intermediate session were greater than in the first and last sessions ($p < 0.001$), but that there was no significant difference between the load force peaks in the first and the last sessions ($p = 0.29$). Note that transitions in peak load force across sessions were brisk. Indeed the peak load during the very first trial performed at fast speed was 7.8 N, a value very close from the overall mean of the trials. Similarly, the peak load force dropped immediately to 4.6 N during the first trial of the last session. These immediate transitions were possible because our protocol included practice trials without the object at the start of each session so that participants moved at the intended speed when first moving the object.

To assess generalization in grip-load force coupling across movement speeds, we focused on the correlation coefficient in the first trial and the last four trials performed at each speed (i.e., the initial regular speed, the fast speed, and the second regular speed). Figure 3.5 shows the mean correlation coefficients averaged across participants for each of these three sessions. As expected, the correlation between grip force and
load force was relatively poor in the first trial performed with the object (session 1) and the $R$ value was similar to the initial $R$ values observed for Groups B, C, and D (Fig. 3.3). Two-way ANOVA showed a TRIAL by SESSION interaction ($p < 0.05$). Post hoc analyses of the interaction revealed that $R$ values during the first trial in session 1 were significantly smaller than all the other $R$ values ($p < 0.01$ in all 5 cases), and that there were no significant differences between the remaining five $R$ values. This indicates that the good coupling between grip force and load force, observed at the end of session 1, did not deteriorate with successive changes in movement speed. This suggests that, once updated, predictive grip force control generalized well across movement speeds.

![Graph showing grip-load force correlation](image)

**Figure 3.5:** Mean grip load-force coupling as a function of trials for group D when moving in the channel. The correlation between grip force and load force is presented at the beginning and end of each session (each one requiring a different movement speed). Note that grip-load force coupling generalized well across movement speeds. Error bars correspond to 1 SE.

When the channel was subsequently removed (block 3), participants of Group D
were able to maintain a good coupling between grip force and load force ($r = 0.73$ in the first trial without the channel), as previously shown for participants of Groups B and C. To assess whether the coupling of grip force and load force changed over trials performed outside the channel, we compared $R$ values averaged over the first 4 and last 4 trials. A two-way BLOCK (first 4 versus last 4 trials) by GROUP (Groups B, C, and D) ANOVA failed to show main effects of BLOCK ($p = 0.57$) or GROUP ($p = 0.40$), and there was no interaction ($p = 0.61$). This indicates that all 3 groups maintained efficient grip force control throughout the trials performed without the channel.

In terms of trajectory control when the channel was removed (block 3), participants from Group D did not benefit from exposure to object dynamics in the channel. All three parameters of the exponential fit to the lateral deviations for Group D (leading value = 36.78, learning rate = -0.180, asymptote = 18.91) were significantly different from zero, thereby confirming the reduction of lateral deviations across trials. Nonlinear regression comparing all four groups revealed that the asymptote was slightly but significantly greater for Group D than Group A ($p < 0.05$) and that the learning rate was slightly but significantly slower for Group D than Group C ($p < 0.05$). No other significant differences between groups were observed. Thus, experiencing the novel object dynamics at different movements speeds in the channel clearly did not facilitate trajectory adaptation after the channel was removed.

3.5 Discussion

The goal of this study was to investigate the contribution of kinematic and kinetic errors to grip force and trajectory adaptation when learning to manipulate objects
with unusual dynamics. To achieve this goal, we developed a novel setup that enabled us to compare grip force adaptation with and without kinematic errors and to test whether experiencing kinetic errors in the channel benefits trajectory control when subsequently moving without the channel. We found that participants successfully adapted their grip force when moving in the channel (Groups B, C, and D, block 2) and that grip force adaptation was no quicker when initially experiencing the object without the channel (Group A, block 3). We also found that prior experience moving the object in the channel did not benefit trajectory adaptation when moving without the channel.

3.5.1 Updating and generalization of grip force control

Previous studies (Danion et al., 2011; Flanagan et al., 2003; Nowak et al., 2004) have shown that people can learn to modulate grip force in synchrony with load force when manipulating objects with unfamiliar dynamics. In all of these studies, both kinetic and kinematic errors were available and thus the separate contributions of these errors could not be assessed. Our finding that grip force control can be updated when moving in the channel (Groups B, C, and D, block 2) and thus in the absence of significant kinematic errors, suggests that kinetic errors are sufficient for driving grip force adaptation. Although kinematic errors, in principle, can provide information about object dynamics, our finding that grip force adaptation was no quicker when first experiencing the object without the channel (Group A, block 3) suggests that these errors are not key inputs for grip force control. This conclusion fits well with observations showing that tactile information at the fingertips dominates over proprioceptive information in terms of controlling grip force responses to unexpected
load force perturbations (Cole and Abbs (1988); Häger-Ross and Johansson (1996); see also Danion (2007)).

We found that learning to modulate grip force in synchrony with load force, when moving in the channel, generalized across movement speeds (Group D, block 2). This result suggests that participants did not simply learn to compensate for a specific temporal profile of load force, but rather acquired an internal model capturing the object dynamics. Previous studies have shown that trajectory adaptation to novel, velocity-dependent loads also generalizes across movement speeds (Goodbody and Wolpert, 1998; Joiner et al., 2011). Thus, it appears that grip force adaptation, which seems to be driven by kinetic errors, and trajectory adaptation, thought to be driven by kinematic errors, both involve the acquisition of an internal model of object dynamics.

### 3.5.2 Updating of arm movement control

Although the grip force results showed that participants learned a component of the object’s dynamics when moving in the channel (Groups B, C, and D, block 2), this knowledge was apparently either not relevant or not accessible when subsequently controlling the motion of the hand and object without the channel. Although we cannot rule out the possibility that kinetic errors contribute to trajectory adaptation when combined with kinematic errors, our results indicate that kinetic errors alone are insufficient to drive learning that can be exploited for trajectory control. Instead, kinematic errors appear to be necessary for trajectory adaptation.

Previous studies of arm movement adaptation to novel hand held loads have shown
that people primarily attribute the load to the object such that relatively small after-effects are observed when the object is released from grasp (Berniker and Kording, 2008; Cothros et al., 2006; Kluzik et al., 2008; Lackner and DiZio, 2005). One possible explanation for our results is that, despite our efforts to provide explicit contextual information about the channel, object, and perturbation (see section 3.3), participants failed to link the load forces experienced at the fingertips to the object when moving in the channel. However, the fact that participants continued to modulate grip force in synchrony with load force on the first trial after the channel was removed (Groups B, C, and D, block 3) indicates that they expected the same object dynamics, at least at the level of grip force control. Interestingly, when participants were debriefed after the experiment, they indicated that the forces applied by the object when moving in the channel were much weaker than those experienced when the channel was removed and were generally unable to describe the forces experienced in the channel (i.e., that they scaled with movement speed and were leftward and rightward for outward and inward movements, respectively). This suggests that the grip force adaptation was based on implicit rather than explicit processes (see Mazzoni and Krakauer (2006) for a discussion of these processes). Previous work suggests that people can use cognitive strategies, based on explicit knowledge of kinematic errors experienced when moving a novel load in one context, to compensate for the same load experienced in a new context (Criscimagna-Hemminger et al., 2003; Malfait and Ostry, 2004). Had our participants been able to explicitly appreciate the kinetic errors experienced in the channel, it is possible that they could have developed similar strategies to generate compensatory arm motor commands when the channel was removed.

One interpretation of our results is that participants relied on distinct internal
models of object dynamics for grip force and trajectory control. We previously suggested that grip force adaptation involves rapid learning of a forward model mapping arm motor commands onto predicted load forces, whereas trajectory adaptation involves slower learning of an inverse model mapping desired movements onto arm motor commands (Flanagan et al., 2003). However, a limitation of that study is that grip force and trajectory control were measured using different dependent variables, making the comparison of learning rates problematic. The current study does not suffer from this limitation and it therefore provides more convincing evidence that distinct neural processes drive grip force and trajectory adaptation. This possibility was raised in a recent study that investigated the ability of participants to move a manipulandum while controlling explicitly the contact forces at the handle (Chib et al., 2009). Based on the observation that transcranial magnetic stimulation over the parietal cortex selectively disrupted arm motion control but not the control of contact forces, the authors argued that object manipulation involves independent control of hand motions and interaction forces between the object and hand.

In most studies of arm movement adaptation to novel loads, the load is applied to the hand via a vertical handle that is grasped in a power grip (Davidson, 2005; Diedrichsen et al., 2005; Izawa et al., 2008; Lackner and DiZio, 2005; Malfait et al., 2002; Shadmehr and Mussa-Ivaldi, 1994; Shadmehr et al., 2010). It is an open question whether such adaptation, which is thought to be driven by kinematic errors, would benefit grip force control when subsequently moving the load using a precision grip. It has been shown that adapting arm movements to novel object dynamics while seated, enables participants to appropriately scale anticipatory postural adjustments when subsequently performing the same movements in a standing position (Ahmed
3.5. DISCUSSION

and Wolpert, 2009). Because grip force adjustments can be viewed as postural adjustments that compensate for forces arising from arm movements (Wing et al., 1997), we might expect that learning object dynamics when using a power grip would benefit grip force control when subsequently using a precision grip.

3.5.3 Concluding comments

Object manipulation and transport tasks are among the most widely used to study how people learn novel mappings between their motor commands and their behavioral consequences (Flanagan et al., 2006; Shadmehr et al., 2010; Wolpert et al., 2011). Whereas many studies have focused on the adaptation of arm movement trajectories, relatively little attention has been paid to the adaptation of grip force control, which is a key component of skilled object manipulation (Johansson and Flanagan, 2009). Our results further document the crucial role of kinematic errors for arm movement adaptation (Shadmehr et al., 2010; Smith et al., 2006; Wolpert et al., 2011), but also highlight the key role of kinetic errors for grip force adaptation, as well as the ability of grip force to generalize across multiple contexts. More generally, these results suggest that arm movement control and grip force control are mediated by distinct internal representations of object dynamics. Previous studies have shown that learning of dynamics is state-dependent such that adaptation in one movement direction or orientation of the object in hand shows limited generalization to other directions or orientations (Mah and Mussa-Ivaldi, 2003; Shadmehr and Moussavi, 2000; Thoroughman and Shadmehr, 2000; Ingram et al., 2010, 2011). Our results suggest that such learning also depends on the motor response required to compensate for the dynamics. That is, learning of object dynamics associated with adapting
grip force commands in the channel does not generalize to the control of arm motor commands when the channel is removed.

3.6 References


3.6. REFERENCES


Chapter 4

Grip-load coordination during rapid arm movement corrections in response to visuomotor perturbations

4.1 Abstract

When reaching with a hand-held object, people modulate grip force in phase with—and thus anticipate—movement-dependent load forces. This anticipatory coupling, which stabilizes the object in hand while avoiding unnecessary force, has been documented for both familiar object loads, such as inertial loads, and is also observed following adaptation to novel loads. Reaching behaviour also incorporates online control mechanisms to rapidly counter unexpected and sudden changes in the viewed position of the reach target or moving limb. While reaching with a hand-held object, these motor responses can cause sudden changes in object load force. Here we investigated whether the close anticipatory coupling between grip and load force is preserved during rapid responses of the limb. Participants made reaching movements with a hand-held object that was linked to a rotary, position dependent load. On
random trials, the position of either the target or a cursor representing the hand was displaced laterally by 1.5 cm early in the movement, evoking a rapid corrective response of the limb within approximately 150 ms. We found that these corrective movements were accompanied by similarly rapid adjustments of grip force that were coupled to the change in load force associated with the hand movement. These results indicate that grip force adjustments, coupled to changes in load force, are integrated into sensorimotor control policies that support rapid, or automatic, visually driven hand movement corrections during reaching.

4.2 Introduction

When transporting a grasped object with familiar dynamics, people modulate grip force in phase with—and hence in anticipation of—movement-dependent load force, allowing them to prevent the object from slipping while avoiding unnecessary grip forces (Danion et al., 2011; Flanagan and Wing, 1993; Flanagan et al., 1995). Moreover, people quickly learn to modulate grip force in phase with the load force when transporting an object with unfamiliar movement-dependent dynamics (Danion et al., 2011, 2013; Flanagan et al., 2003; Flanagan and Wing, 1997). These studies provide strong evidence that the brain learns and makes use of accurate internal models of the dynamics of grasped objects, as well as the dynamics of the limb, to determine the mapping between arm motor commands and the load forces applied by the object to the hand (Franklin and Wolpert, 2011; Kawato, 1999; Miall and Wolpert, 1996; Wolpert and Flanagan, 2001).

The aim of the current study was to determine whether the close coupling between grip force and load force is also observed during rapid, automatic hand movement
corrections observed in visually guided reaching when either the target or the viewed hand, or cursor representing the hand, unexpectedly changes position. These rapid corrections, which typically occur with 105–180 ms (Franklin and Wolpert, 2008; Oostwoud Wijdenes et al., 2011; Prablanc and Martin, 1992; Saunders and Knill, 2003, 2004), appear to be incorporated into the control policy implemented during reaches to handle errors that could reasonably arise from sensory and/or motor noise (Pruszynski and Scott, 2012; Scott, 2004; Todorov and Jordan, 2002). To date, only a single study, by Danion and Sarlegna (2007) has examined grip force adjustments during corrective movements made while reaching. However, large target jumps were employed in this study and the hand movement response latencies were more representative of voluntary reaction times (e.g., 280 ms or longer) than rapid, automatic corrections.

Work on precision grip lifting has documented rapid corrective actions, involving coupled changes in grip and load force, triggered by mismatches between expected and actual tactile signals (Johansson and Flanagan, 2009). For example, when an object being lifted is heavier than expected, tactile signals linked to lift-off mechanics do not occur at the expected time, and this mismatch triggers a coupled increase in grip force and load force within ~90 ms (Johansson and Westling, 1988b). However, to our knowledge, no study has examined the coordination of grip and load force during rapid responses to a purely visual perturbation. We designed an object transport task where small displacements of the target or cursor representing the grasped object evoked rapid arm movement corrections that resulted in substantial increases or decreases in load force. We hypothesized that these rapid changes in load force would be accompanied by coupled changes in grip force. Confirmation of this prediction would
indicate that knowledge about the dynamical properties of the arm-object system are integrated into rapid motor responses of the limb triggered by visual perturbations.

4.3 Methods

4.3.1 Subjects

Seven men and 6 women between the ages of 19 and 32 years of age (M = 26.5 years) participated after providing written, informed consent. All participants self-reported having normal or corrected-to-normal vision, being right handed, and being free of sensorimotor dysfunction. The experimental protocol was approved by the General Research Ethics Board at Queen’s University in compliance with the Canadian Tri-Council Policy on Ethical Conduct for Research Involving humans. All participants completed the same experimental conditions and the experimental session lasted approximately one hour. Participants were compensated $10 per hour of participation.

4.3.2 Apparatus and Stimuli

Participants performed an object transport task that required them to move a grasped object from a start position to visual target, located at one of two possible positions, in the horizontal plane. The object consisted of two parallel circular grip surfaces (2.5 cm in diameter) separated by 6.4 cm (i.e., reflecting the grasp aperture) and covered in sandpaper. Each grasp surfaces were instrumented with a six-axis force-torque transducer (Nano force/torque, ATI Industrial Automation, Apex, NC), which measured linear forces (0.05 N resolution) and torques in three dimensions. Participants grasped the object using a precision grip in which the thumb and index finger each contacted a grip surface. Participants were instructed to hold the object in a vertical
orientation, with the index finger on top and the thumb below, such that the grip surfaces were in a horizontal plane. Therefore, we could dissociate horizontal load forces tangential to the surfaces, and vertical grip forces normal to the grip surfaces. The experimenter carefully monitored the orientation of the object to ensure participants held the object upright throughout the experiment.

The center of the object itself was attached to a lightweight robotic device (Phantom 3.0 haptic interface, Sensable, Wilmington, MA) through a two-joint linkage and the grip surfaces could freely rotate around the long axis of the object. This combination allowed full three-dimensional rotation of the object. Optical encoders in the manipulandum recorded the position of the object with at a spatial precision of 0.1 mm. Two air-sleds fitted with cuffs were used to support the arm slightly below the elbow and at the wrist. The air sleds moved across a horizontal glass surface with near-zero friction.
Figure 4.1: Apparatus and experimental design. **A**, Drawing of the experimental setup; see text for details. **B**, Configuration of the start position, occluder and the 10 practice targets. The red force vectors denote the position-dependent force field applied to the grasped object. **C**, Configuration for the experimental trials with targets at -10° and 5° and the same force field as shown in panel B (illustrated with fewer red arrows). Shown only for the 5° target, but also present for the -10° target, are the cursor jumps (filled coloured circles) and target jumps (open coloured circles). Red
4.3. METHODS

and blue circles indicate perturbations requiring a rightward and leftward movement response, respectively. **D**, Average object paths in the practice block for a single participant. The shaded regions represent ±1 SD. **E, F**, Average object paths for each target and perturbation type for the same participant as in panel D. Red and blue traces represent perturbation trials requiring a rightward and leftward movement, respectively, and the grey traces represent unperturbed trials (with the same unperturbed trials shown in E and F). **G**, Procedure for calculating arm movement response latency, illustrated for a single participant and target jumps involving the -10° target. We first determined when the p-value from a running t-test comparing the average object perpendicular velocity (at right angles to the vector from the start position to the target) for right (red trace) and left (blue trace) target jumps dropped below 0.001 (vertical grey dash-dotted line), and then backtracked to the first minima (vertical black dashed line) in the rate of change of the p-value. The thin black line at 0 ms shows the time of the perturbation.

A display system consisting of a 30-inch computer monitor and a mirror was used to present visual images (Fig. 4.1 A). The mirror was positioned halfway between the monitor and the plane of hand movement such that these images appeared in the hand movement plane. In each trial, the participant moved a circular cursor (yellow, 1 cm in diameter) from a circular start position (green, 1 cm in diameter), located 30 cm in front of the participant at midline, to a circular target (blue, 1.6 cm in diameter) located 20 cm from the start position at various angles. A grey arc was presented that occluded the view of the object cursor while the cursor passed beneath it (see Fig. 4.1 C). The arc had an inner radius of 2.5 cm and an outer radius of 5.5 cm and spanned from -55° to 55°.

The robotic device was used to create a rotary position-dependent load applied by the object to the hand (see red arrows in Fig. 4.1 B). The load was rotated 90° counter clockwise from the vector from the start position to the object. The magnitude of
the force \( F \) was determined by equation 4.1 below:

\[
F = \begin{cases} 
K2\pi R\left(\theta + \frac{5\degree}{360\degree}\right), & -5\degree < \theta < 90\degree \\
0, & -90\degree < \theta \leq -5\degree
\end{cases}
\]  

(4.1)

where \( K = 0.12 \text{ N/mm} \), \( R \) is the distance (in mm) from the start position to the object position, and \( \theta \) is the angle (in degrees) of the object relative to \( 0\degree \) (see figure 4.1 B). That is, for \( \theta > -5\degree \), the magnitude of the load force was proportional to the arc length, from \( -5\degree \) to \( \theta \), of a circle with radius \( R \) centered at the start position. For \( \theta \leq -5\degree \), no load force was applied.

### 4.3.3 Procedure

**Task**

Each trial began with the presentation of the start position, occluder, and the target; there were no object load forces applied at this time. The participant was first required to move the hand-held object to the start position, at which time the force field was activated. After a delay of 150 ms, the target changed from blue to red, instructing participants to move to the target when ready. The participant was encouraged to reach the target between 450 and 750 ms after movement onset and text was displayed at the conclusion of each trial indicating whether the movement was “too fast”, “too slow”, or “good”. To aid the participant, a tone sounded 600 ms after movement onset and the participant was instructed to time their movements so that to have the cursor arrive at the target simultaneously with the tone.
4.3. METHODS

Practice Block

The practice block was designed to give participants experience with the task and an opportunity to learn the force field specifying the load forces applied by the object to the hand. In each trial, a target was presented at one of 10 possible locations, 20 cm from the start position at angles of -12.5°, -9.7°, -1.4°, 1.4°, 4.2°, 6.9°, 9.7°, and 12.5° (Fig. 4.1 B). The three most leftward targets fell within the no-force region and the remaining 7 fell within the force region. The load forces when the object was located at these targets ranged from 0 to 7.3 N. Each target was presented 15 times in random order for a total of 150 practice trials.

Test Block

In the test block only two targets were used, a left target at -10°, where the load was zero with the object positioned at the target, and a right target at +5° where the magnitude of the load force was 4.19 N with the object positioned at the target (Fig. 4.1 C). The test block contained 10 different conditions, 8 that involved visual perturbations and 2 that did not. The 8 perturbation trial types included movements towards either of the two targets, two perturbation types (cursor or target displacements), and two perturbation directions (left or right). The two non-perturbation trial types were used as control reaches to the two targets and did not contain perturbations. All conditions were randomized throughout the test block with each condition presented 50 times for a total of 500 trials.

On perturbation trials, the position of either the target or the object cursor was displaced 1.5 cm orthogonal to the vector from the start position to either the cursor
(for cursor displacements) or the target (for target displacements), and this displacement could be either leftward or rightward (Fig. 4.1 C). The cursor displacements occurred when the object cursor passed beneath the occluder, and therefore information related to the cursor displacement was available only once the cursor emerged from the beneath the occluder. Participants were consistently unaware of the cursor displacements, as indicated by self-reports following the experimental session. Target displacements were triggered when the cursor emerged from beneath the occluder and, on average, the target displacement occurred when the cursor was 0.9 cm beyond the outer radius of the occluder. In contrast to the cursor displacements, participants were aware of the target displacements. Note that leftward cursor displacements and rightward target displacements required a rightward movement of the hand in order to bring the object cursor to the target, whereas rightward cursor jumps and leftward target jumps required a leftward movement of the hand. All of the figures are colour coded with red representing conditions involving rightwards movement responses and blue representing conditions involving leftwards movement responses. For the 5° target, rightward and leftward hand movement corrections resulted in substantial increases and decreases in load force, respectively (see section 4.4.3 below). In contrast, for the -10° target, such corrections did not result in appreciable changes in load force.

**Analyses**

Position and force signals were sampled at 1000 Hz and then digitally smoothed, offline, using a fourth-order, zero-phase lag Butterworth filter with a cutoff frequency of 14 Hz. Using the smoothed position signals, we computed the component of object
velocity in the target direction (i.e., the direction of the vector from the start position to the target) as well as the object velocity perpendicular to the target direction, which is particularly sensitive to movement corrections in response to target and cursor displacements. Grip force was calculated as the average normal force applied by the thumb and index finger to the two force sensors. Load force was calculated using the total tangential force applied by the thumb and index finger. The programmed force specified for the robotic device provided a second measure of load force, which closely resembled the load force calculated from the force sensors. In cursor displacement trials, the perturbation occurred at the time at which the cursor emerged from the occluder (i.e., when information about the displacement was available). In target displacement trials, the target was displaced when the cursor emerged from the occluder. Thus the point at which the perturbation occurred during the movement was similar in cursor and target displacement trials. All trials were aligned in time relative to the time of the perturbation for our analyses. Non-perturbation trials were aligned to the point when the cursor emerged from beneath the occluder.

Latencies of corrective arm movement responses, relative to the perturbation, were determined using the object velocity in the direction perpendicular to vector from the start position to the target direction (Franklin et al., 2012; Knill et al., 2011). For each perturbation type, target, and participant, we compared: (1) leftward and rightward displacement trials, (2) leftward displacement trials and control trials, and (3) rightward displacement trials and control trials, to determine the point of divergence. This involved two steps. First, for each comparison we performed a running independent samples t-test and determined the point when the p-value first dropped below 0.001 and remained below 0.001 for 30 consecutive samples (i.e., 30
4.3. METHODS

ms). As illustrated in Fig. 4.1 G, which compares responses to right and left jumps of the 5° target for a single participant, the mean perpendicular velocity profiles were clearly separated at this point, shown by the dash-dotted grey vertical line at 176 ms relative to perturbation onset. To determine the time at which the two mean profiles first deviated from one another, we searched backward in time (from the p < 0.001 point) to the first minima in the rate of change of the p-value, which occurred 14 ms earlier and is shown by the dashed black vertical line. This time of this minima, which consistently corresponded to the point at which the mean profiles visibly first separated, was taken as the response time. Similar approaches are standardly used in signal detection (Nashed et al., 2012, 2014; Thompson et al., 1996) and have also been previously used to determine corrective movement response times (Nashed et al., 2012, 2014). For movements directed to the 5° target, where movement corrections gave rise to appreciable changes in load force, we used the same two-step procedure to determine corrective grip force response latencies. In addition, for these movements we also used the procedure to determine load force latencies, which provide another measure of arm movement correction latencies (Danion and Sarlegna, 2007).

We excluded trials on the basis of initial movement angle, endpoint accuracy, and movement time. Specifically, individual trials were excluded from our analysis if the cursor was outside of ±10° from the target location at 25% of the movement amplitude or if the cursor did not come within 0.5 cm of the target center within 400 to 800 ms after movement onset. In total, an average of 17% of trials were excluded from our analysis per condition.

We used repeated measures ANOVAs to assess experimental effects with Bonferroni corrected post-hoc comparisons. P-values < 0.05 were considered to be significant.
4.4 Results

4.4.1 Practice trials

Participants first completed a total of 150 practice trials with 10 different target locations (10 targets × 15 reaches). In the first few trials, reach trajectories were markedly deviated. However, participants quickly adapted so as to produce relatively straight movement paths within a few trials. Figure 4.1 D shows the average object path towards each of the 10 different targets for a representative participant. These trajectories were aligned to perturbation onset and the shaded regions represents ±1 SD orthogonal to the target direction. To assess the coupling of grip and load force during the practice trials, we computed the mean correlation coefficient (at zero phase lag) between grip and load force for each participant. Overall, grip and load force was highly correlated, with an average correlation of 0.97 (SE = 0.005) based on participant means. These findings indicate that participants learned the position dependent rotary load. We also evaluated the average movement time for each participant. On average, participants reached the target in 562 ms (SE = 10 ms), based on participant means.

4.4.2 Arm movement corrective responses

As expected, participants compensated for the visual perturbations by moving their hand, and hence the object cursor, either leftward or rightward (relative to the target direction) to reach the target. These corrections are illustrated in Figs. 4.1 E and F, which show, for a representative participant, average trajectories of the object in perturbation trials requiring a leftward response (blue traces), perturbation trials requiring a rightward response (red traces), and unperturbed trials (grey traces).
4.4. RESULTS

![Graph showing velocity and response times for cursor and target jumps.](image)

**Left (-10°) target**
- Cursor jump: A
- Target jump: C

**Right (5°) target**
- Cursor jump: B
- Target jump: D

- Left response
- Unperturbed
- Right response

**Velocity perpendicular to target direction (cm/s)**
- Left response
- Unperturbed
- Right response

**Velocity in target direction (cm/s)**
- Left response
- Unperturbed
- Right response

**Cursor jump**
- Left (-10°) target
- Right (5°) target

**Target jump**
- Left (-10°) target
- Right (5°) target
4.4. RESULTS

Figure 4.2: Object velocity profiles for each target and perturbation type for a single participant. **A–D**, Average perpendicular velocity profiles for unperturbed trials (grey) and perturbed trials requiring a leftward (blue) or rightward (red) correction. Positive indicates rightward relative to the movement direction. The dashed blue, red and grey vertical lines represent the times at which the blue and grey, red and grey, and blue and red velocity profiles, respectively, could be differentiated (see section 4.3.3), with these times included as colour-coded text. The solid blue, red and grey vertical lines represent the mean times the participant reached the target for each trial type. The dash-dotted red and blue vertical lines in B depict, for perturbations requiring right and left responses, respectively, the difference between the peak average velocity in perturbation trials and the average velocity in unperturbed trials. Prior to averaging, profiles were aligned to perturbation onset, or the corresponding time in unperturbed trials (dash-dotted lines). The heights of the shaded regions represent ±1 standard deviation. **E–H**, Corresponding plots for velocity in the same direction as the vector connecting the start position and target.

To assess arm movement corrective responses, we computed the velocity of the object perpendicular to vector from the start position to the target; i.e., the component of velocity inline with the perturbation. Figures 4.2 A–D show, for a representative participant, the average perpendicular velocity for perturbed trials requiring either a leftward (blue traces) or rightward (red traces) and unperturbed trials (grey traces), with trials aligned in time to the perturbation (t = 0). Separate traces are shown for each target (-10° or 5°) and perturbation type (cursor or target jump). Figures 4.2 E–H show the corresponding average velocities in the direction from the start position to the target.

To assess the speed of the corrective movement responses we determined, for each participant, perturbation type, target, and response direction, the absolute difference between the maximum of the average perpendicular velocity in perturbed trials minus the average perpendicular velocity in unperturbed trials, taken at the same time (see dash-dotted red and blue vertical lines in Fig. 4.2 B). We then submitted the absolute
values of these difference scores to a 2 perturbation type (cursor, target) × 2 target ($-10^\circ, 5^\circ$) × 2 response direction (leftward, rightward) repeated measures ANOVA. This analysis uncovered a main effect of perturbation type, $F_{1,12} = 24.6, p < 0.001$, and target, $F_{1,12} = 5.4, p < 0.05$, with the absolute difference scores being greater for target displacements ($M = 7.4 \text{ cm/s}, \text{SE} = 0.2 \text{ cm/s}$) compared to cursor displacements ($M = 6.3 \text{ cm/s}, \text{SE} = 0.2 \text{ cm/s}$), and greater for movements towards the left target ($M = 7.0 \text{ cm/s}, \text{SE} = 0.3 \text{ cm/s}$) compared to movements towards the right target ($M = 6.6 \text{ cm/s}, \text{SE} = 0.2 \text{ cm/s}$). The ANOVA also uncovered a perturbation type by response direction interaction, $F_{1,12} = 5.2, p < 0.05$, where the effect of perturbation type was slightly larger for leftward versus rightward responses. There was no main effect of response direction and no further interactions. As can be appreciated in Figs. 4.2 E–H, the visual perturbations has relatively little effect on the object velocity in the direction of the target, indicating that the movement responses were largely confined to the perpendicular direction as we intended and participants performed a single continuous movement.

The vertical dashed lines in Figs. 4.2 A–D represent the response latencies for this participant, with the blue and red lines showing the latencies obtained by comparing the leftward and rightward responses to baseline, respectively, and the grey line showing the latency obtained by comparing the leftward and rightward responses. Overall, it can be seen that these latencies are short, consistent with automatic responses. Averaging across the three latency measures, this participant responded earlier to cursor jumps (134 ms) compared to target jumps (161 ms) whereas the average latencies for the left (151 ms) and right (144 ms) targets were similar. When
considering the latencies determined by comparing the leftward and rightward response trials to unperturbed trials, the latencies of leftward responses (147 ms) were similar to the latencies for rightward responses (153 ms). This pattern of results was similar to that observed at the group level, which will be described below.

### 4.4.3 Grip and load force responses

Figure 4.3 shows, for a representative participant, average grip force (panels A–D) and load force (panels E–H) for perturbed and unperturbed trials, with separate traces shown for each target and perturbation type. To quantify the magnitude of grip and load force responses, we computed, for each trial, the mean force over the last 50 ms prior to reaching the target. For each participant, perturbation type, target, and response direction, we then computed the difference between the average mean force in perturbation trials and the average mean force in unperturbed trials. These difference scores enabled us to examine how grip and load force, in perturbation trials, changed relative to baseline.
Figure 4.3: Grip and load force profiles for each target and perturbation type for a single participant.  
A–D, Average grip force profiles for unperturbed trials (grey)
and perturbed trials requiring a leftward (blue) or rightward (red) correction. The dashed blue, red and grey vertical lines, shown for the right target only, represent the times at which the blue and grey, red and grey, and blue and red grip force profiles, respectively, could be differentiated, with these times included as colour-coded text. The solid blue, red and grey vertical lines represent the mean times the participant reached the target for each trial type. Prior to averaging, profiles were aligned to perturbation onset, or the corresponding time in unperturbed trials (dash-dotted lines). The heights of the shaded regions represent ±1 standard deviation. \( E-H \), Corresponding plots for load force.

We submitted these difference scores to a 2 perturbation type (cursor, target) \( \times \) 2 response direction (left, right) \( \times \) 2 target (-10°, 5°) repeated measures ANOVA. As expected, for load force we found a main effect of response direction, \( F_{1,12} = 2724, p < 0.001 \), as well as a response direction by target interaction, \( F_{1,12} = 4261.7, p < 0.001 \). For the right target, perturbations requiring rightward and leftward responses resulted in large increases (\( M = 1.7 \) N, \( SE = 0.04 \) N) and decreases (\( M = 2.0 \) N, \( SE = 0.04 \) N) in load force, whereas minimal changes in load force were observed during perturbation trials involved the left target.

A similar pattern was found for grip force. There was a main effect of response direction, \( F_{1,12} = 198, p < 0.001 \), as well as a response direction by a target interaction, \( F_{1,12} = 181, p < 0.001 \). Post hoc comparisons showed this effect was attributed to the greater grip force responses—both increases and decreases—for movements towards the right target compared to the left, \( p < 0.05 \). On average, for the right target, participants increased their grip force by 2.3 N (\( SE = 0.2 \) N) and decreased their grip force by 1.6 N (\( SE = 0.1 \) N), relative to baseline, during rightward and leftward movement corrections, respectively. This contrasted with an increase of 0.4 N (\( SE = 0.1 \) N) and a decrease of 0.2 N (\( SE = 0.1 \) N) for rightward and leftward movement responses, respectively, for movements towards the left target.
For movements directed to the right target, where corrective responses resulted in appreciable changes in grip and load force, we could quantify grip force and load force response latencies. As in Fig. 4.2, the vertical dashed lines in the right hand panels of Fig. 4.3 represent the response latencies, with the blue and red lines showing the latencies obtained by comparing the leftward and rightward responses to baseline, respectively, and the grey line showing the latency obtained by comparing the leftward and rightward responses. Note that the load force latencies provide an additional measure of hand movement latencies because load force is mapped to position. Averaging across the three latency measures and two perturbation types (i.e., cursor and target), this participant’s grip force responses were slightly later (178 ms) than the load force responses (149 ms), but still within the automatic range of response times to visual perturbations. Averaging across the three latency measures, the grip force latency was shorter for cursor jumps (166 ms) than target jumps (190 ms) and, likewise, the load force latency was shorter for cursor jumps (144 ms) than target jumps (153 ms), suggesting grip and load force latencies may be correlated. This pattern of results was similar to that observed at the group level, which will be described below.

4.4.4 Movement and grip force response latencies

To assess and compare hand movement (i.e., perpendicular velocity of the object), grip force, and load force response latencies, we focused on movements directed to the right (5°) target. The bars in Figs. 4.4 A–C show these response latencies, averaged across participants, for each perturbation type (i.e., cursor or target) and latency measure (i.e., left response vs baseline, left response vs right response, and right response vs baseline). The circles in Fig. 4.4 C also show the movement response
latency for left (-10°) target.

Figure 4.4: Grip force and movement response latencies. **A–C**, Average response latencies, based on participant means, for grip force, load force, and perpendicular velocity. The coloured bars show the 3 latency measures calculated by comparing leftward response and unperturbed trials (blue), rightward and leftward response trials (grey), and rightward response and unperturbed trials (red). Error bars represent ±1 standard error. **D**, Grip force response latency versus movement response latency, where the latter was computed from the average of the load force and perpendicular velocity latencies. Each circle represents a single participant and all three latencies are based on averaging the three latency measures. The open and filled circles show latencies for the cursor and target jump trials, respectively. The dashed line represents the unity line and the solid line represents the regression slope computed using all points.

To quantify response latency effects, we performed a 3 response measure (grip
force, load force, perpendicular velocity) × 2 perturbation type (cursor, target) × 3 latency measure (left response vs right response, left response vs baseline, right response vs baseline) repeated measures ANOVA. This analysis showed a main effect of response measure, $F_{2,24} = 27$, $p < 0.001$. Post hoc comparisons showed grip force latencies ($M = 179$ ms, SE = 4 ms) were slightly but significantly longer, $p < .05$, than both load force ($M = 163$ ms, SE = 3 ms) and perpendicular velocity ($M = 157$ ms, SE = 3 ms) latencies, but that there was no significant difference between load force and perpendicular velocity latencies, both of which are measures of arm movement response latencies. The analysis also uncovered a main effect of perturbation type, $F_{1,12} = 108$, $p < 0.001$, with responses to cursor displacements ($M = 156$ ms, SE = 3 ms) preceding responses to target displacements ($M = 176$ ms, SE = 3 ms), on average. Finally, we found a main effect of latency measure, $F_{2,24} = 4.1$, $p < 0.05$. Post hoc comparisons showed that latencies obtained by comparing leftward vs rightward responses ($M = 158$ ms, SE = 3 ms) were shorter, $p < 0.05$, than those obtained by comparing rightward vs baseline responses ($M = 172$ ms, SE = 6 ms) and marginally shorter than those obtained by comparing leftward vs. baseline responses ($M = 169$ ms, SE = 3 ms), $p = 0.08$. However, there were no differences between latencies obtained by comparing leftward vs. baseline responses and those obtained by comparing rightward vs. baseline responses, indicating that participants responded equally quickly to leftward and rightward perturbations (i.e., increases and decreases in force). The ANOVA did not uncover any interactions among response measure, perturbation type, or latency measure. Finally, we carried out a separate paired t-test to compared movement response latencies, derived using perpendicular velocity, for the two targets and did not find a significant difference.
4.4. RESULTS

To assess the temporal coupling between grip force and arm movement responses, we examined the correlation, across participants and perturbation type, between grip force response latency (based on the average of the three latency measures) and the average of the perpendicular velocity and load force response latencies (each based on the average of the three latency measures), both of which measure the arm movement response. The slope and intercept of the best bit regression line (see Fig. 4.4 D) were 1.1 and 0.005 ms, respectively, and the correlation was 0.75 (p < 0.001). Thus, although the grip force response slightly lagged the arm movement response, on average, these responses were tightly coupled in time.

4.4.5 Grip-load force coordination during corrective actions

The coordination between grip and load force in unperturbed and perturbed trials for the right target is illustrated in Figs. 4.5 A and B for cursor and target jumps, respectively. Each figure shows average grip force plotted against average load force—where the averages are based on participant means—for unperturbed trials (grey traces) and perturbed trials requiring leftward (blue traces) and rightward (red traces) corrective movements. The open blue and red squares indicate where, on average, the perturbations requiring leftward and rightward responses occurred, and the open circles blue, red and grey circles indicate where, on average, the object reached the target. The dashed line shows the line of unity. Overall, grip force was modulated in phase with load forces both during both the initial, uncorrected portion of the movement and during the corrective portion of the movement. To quantify the coupling between grip and load force we determined, for each participant, the mean correlation coefficient for unperturbed trials and for the 4 types of perturbation trials depicted in Figs. 4.5
4.4. RESULTS

A and B (i.e., cursor and target jump trials requiring either leftward or rightward corrections). Planned comparisons showed no significant differences between the unperturbed trials and any of the perturbation trials, $p > 0.05$. Overall, the average correlation coefficient was 0.97 (SE = 0.04).

![Diagram](image)

Figure 4.5: Coordination of grip and load force. **A, B**, Average grip force plotted against average load force for movements to the right target involving either cursor (A) or target (B) jumps. Average force based on participant means. Blue and red traces represent trials requiring rightward and leftward movement corrections, respectively, and the grey traces represent unperturbed trials. The dashed line represents the unity line. The open squares show the average point at which the perturbation occurred and the open circles show the average point at which participants reached the target. **C, D**, Grip and load forces, averaged over the 50 ms prior to reaching the target, as a function of the arc length of the target position relative to 5°. Each
4.4. RESULTS

circle represented an average based on participant means. The blue and red circles represent perturbation trials requiring leftward and rightward responses, respectively, the grey circles represent unperturbed trials, and the black circles represent practice trials. Error bars represent ±1 standard error.

Figures 4.5 C and D show, for cursor and target jumps respectively, grip (filled circles) and load (open circles) forces averaged over the last 50 ms of the movement prior to reaching the target, as a function of the arc length of the target position relative to -5°. Each circle represented an average based on participant means. The blue and red circles represent perturbation trials, with either the -10° or 5° target, requiring leftward and rightward responses respectively, the grey circles represent unperturbed trials, with either the -10° or 5° target, and the black circles represent practice trials with each of the 10 practice targets. As expected given the force field applied to the object, the final load forces (i.e., when the object reached the vicinity of the target) for all experimental and practice trial types fall along the same function. To a first approximation, the same is true of the final grip forces. However, the final grip forces in perturbation trials involving the right target—and especially the perturbation requiring a left response—were slightly greater than would be predicted from the practice trials given the arc length. The slightly elevated final grip forces in perturbations requiring a leftward correction can also be appreciated in Figs. 4.5 A and B (see blue traces). The tendency not to fully decrease grip force during corrections involving a decrease in load force is consistent with previous work on precision grip lifting where the object is lighter than expected (e.g., Flanagan and Beltzner (2000); Johansson and Westling (1988b)), and is perhaps unsurprising given that a slightly greater grip force does not threaten task success. Overall, these findings indicate that participants integrate knowledge of the position-dependent load
profile into rapid corrective grip force responses.

4.5 Discussion

The aim of this study was to test the hypothesis that the close coupling between grip force and load force, observed during object lifting (Johansson and Westling, 1984, 1988a) and transport movements (Danion et al., 2011, 2013; Flanagan and Lolley, 2001; Flanagan et al., 1995; Flanagan and Wing, 1993, 1995, 1997), is also present during rapid hand movement correction made in response to visuomotor perturbations involving cursor or target displacements. In support of our hypothesis, we found that rapid changes in load force resulting from fast hand movement corrections were closely coupled—in time, direction, and magnitude—with grip force responses. The results indicate that knowledge about the dynamical properties of the grasped object, together with the dynamics of the arm, can be integrated into rapid motor responses to adapt to rapid changes in object load force triggered by visual perturbations.

Numerous studies have used displacements of the viewed hand position or target to study how vision is used in the online control of reaching behaviour (Elliott et al., 2001; Goodale, 2004). Although reported response latencies vary, many of the studies—typically involving small amplitude target or cursor displacement—have reported fast hand movement corrections between 120–180 ms (Franklin and Wolpert, 2008; Goodale et al., 1986; Grafton et al., 1999; Gritsenko et al., 2009; Pisella et al., 2000; Prablanc and Martin, 1992; Saunders and Knill, 2003; Sarlegna et al., 2003; Saunders and Knill, 2004). These rapid movement responses, which can occur without conscious awareness of the perturbation (Goodale et al., 1986; Saunders and Knill, 2003) and are often termed automatic responses (to distinguish them from slower,
volitional corrections) and are thought to be governed by feedback control policies, implemented during goal-directed movements (Scott, 2004; Shadmehr et al., 2010; Todorov and Jordan, 2002; Wolpert et al., 2011), which not only counter unexpected perturbations but also function to compensate for natural variation in movement (Hamilton et al., 2004; Harris and Wolpert, 1998; Todorov and Jordan, 2002; van Beers, 2009). Importantly, we observed movement correction latencies within this fast, automatic range, allowing us to evaluate our hypothesis concerning grip force responses. However, a priori, it was not a certainty that such rapid hand movement responses would be generated when transporting a grasped object. Specifically, if the motor system was unable to generate rapid, context appropriate changes in grip force, hand movement corrections could have been delayed in order to maintain good grip-load coupling.

We found that during the initial practice trials without visual perturbations that participants quickly learned the novel force field applied to the hand-held object, such that they were able to generate roughly straight line movements to a range of targets (with and without rotary load forces) with grip force modulated in phase with load force. This result is consistent with previous studies showing that people can learn novel position dependent force fields (Danion et al., 2013; Flanagan and Wing, 1997; Sing et al., 2009; Tong et al., 2002). In addition, we found that participants produced appropriate hand trajectory and grip force responses to the visuomotor perturbations experienced in the force field. That is, participants moved their hand in the correct direction to compensate for the perturbation and increased or decreased grip force when the response to the perturbation resulted in an increase or decrease in load force.
In support of our hypothesis, we found that rapid changes in object load, associated with fast hand movement corrections, were accommodated by similarly rapid grip force responses. Furthermore, these grip force responses were tightly coupled—in time, direction, and magnitude—to load force changes. Importantly, participants did not simply increase grip force in response to rapid arm movement corrections, a strategy that would prevent slip but lead to unnecessarily high grip forces. Instead, grip force adjustments predicted the direction of the associated change in load force. Our results differ in several key ways from those reported by Danion and Sarlegna (2007), who examined grip force adjustments during corrective hand movements made in response to large target jumps (8 cm) that occurred as participants moved a grasped object attached to an elastic. First, the average latency of hand movement corrections reported by these authors was 284 ms, which suggests that the corrective movements were entirely ‘reprogrammed’ voluntary movements rather rapid, automatic responses. Second, although grip force increases and decreases were found for corrective movements results in increases and decreases in load force, respectively, significant decoupling of grip and load force response latencies was reported. On average, grip force decreases and increases occurred 346 ms and 209 ms after the target jump, respectively. Thus, although the grip force increase occurred at relatively short latency (but still much longer than the grip force changes reported here), these do not appear to form part of a coordinated response that maintains grasp stability, with adequate but not excessive grip force.

Previous work on the sensorimotor control of object manipulation tasks has demonstrated fast corrective force adjustments driven by mismatches between expected and actual tactile feedback (Flanagan et al., 2006; Johansson and Flanagan, 2009). For
example, when lifting an object that is heavier (or lighter) than expected, coordinated increases (or decreases) in grip force and load force occur around 90 ms after the absence (or presence) of expected (or unexpected) tactile feedback signaling liftoff (Johansson and Westling, 1988b). Similar rapid adjustments occur in response to imperceptible slips during lifting (Johansson and Westling, 1984, 1987). These fast and flexible corrective responses are ‘task-protective’ in that they support the attainment of task goal; i.e., successful lifting while maintaining grasp stability. The current results demonstrate that similarly flexible and task-protective corrective responses—involving coordinated grip and load force adjustments—can be driven purely by visual feedback about hand position. The fact that the latency of these responses is approximately 60 ms greater (i.e., 150 ms compared to 90 ms) is perhaps not surprising given that they are driven by visual rather than tactile signals. (Note that the fast grip force responses we observed are not driven by changes in load force. If this were the case, changes in grip force would have lagged behind changes in load force by some 90 ms, rather than changing in concert with load force changes.)

Recently, Leonard and colleagues (2011) examined postural responses during visual perturbations delivered while standing participants made target directed reaching movements. The visual perturbation, a target jump, evoked rapid arm movement responses, occurring on average at 178 ms, that brought the cursor controlled by the hand to the target. The authors found that postural adjustments in the legs, measured using a force platform, preceded changes in the reach trajectory by ~80–85 ms (Leonard et al., 2011). Note that grip force responses can be viewed as postural adjustments that provide stability during goal directed movement (Wing et al., 1997). Both the current findings and those reported by Leonard and colleagues (2011)
indicate that the anticipatory postural adjustments observed during voluntary arm movements are also observed during rapid, automatic arm movements triggered by visuomotor perturbations.

The rapid and intelligent grip force responses observed in our task are impressive given that the visual perturbations used in the current study were arbitrarily linked to the load force change via the novel force field applied to the object. That is, participants could not rely on well-established priors linking the visual stimulus to load force change and instead, had to make use of an internal model of the force field learned through recent (and limited) experience (i.e., during the practice trials). Previous work has shown that rapid feedback responses to mechanical loads applied to the arm, mediated by long-latency reflexes, incorporate an internal model of the arm itself (Kurtzer et al., 2008), and also intelligently adapt following adaptation of reaching movements to novel loads applied to the arm (Cluff and Scott, 2013) as well as to visuomotor adaptation (Dimitriou et al., 2013). The latter finding and the current results highlight an important link between feedforward and feedback control mechanisms and indicate that modulation of feedback responses is a key part of motor adaptation. However, not all perturbations can be integrated into rapid corrective responses. Gritsenko and Kalaska (2010) examined hand movement responses to target jumps while reaching under a visuomotor reversal. Although their participants could learn to launch their initial reaching movements in the correct direction (reaching to the right of midline for targets located on the left of midline), they were unable to integrate this learning into rapid arm movement corrections in response to target jumps. This inability presumably arises because the visuomotor reversal requires responses in the opposite direction of the responses normally required for the
In conclusion, we have shown that coordinated grip force responses are linked to rapid movement responses to visuomotor perturbations applied during reaching movements. This result indicates that participants could not only learn—and make use of—knowledge of object (and limb) dynamics for feedforward control but could also implemented a sensory feedback control policy that incorporated this knowledge.

4.6 References


4.6. REFERENCES


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Chapter 5

Rapid target foraging with reach or gaze: the hand looks further ahead than the eye

5.1 Abstract

Real-world tasks typically consist of a series of target-directed actions and often require choices about which targets to act on and in what order. Such choice behaviour can be assessed from an optimal foraging perspective whereby target selection is shaped by a balance between rewards and costs. Here we evaluated such decision-making in a rapid movement foraging task. In a given trial, participants were presented with 15 targets of varying size and value and were instructed to harvest as much reward as possible by either moving a handle to the targets (hand task) or by briefly fixating them (eye task). The brief trial duration enabled participants to harvest about half the targets, ensuring that total reward was due to choice behaviour. We developed a probabilistic model to predict target-by-target harvesting choices that considered the rewards and movement-related costs (i.e., target distance and size) associated with the current target as well as future targets. Because the time and energy costs are greater for hand than eye movements, we predicted that in the hand
task, in comparison to the eye task, target choice would be more strongly influenced by movement-related costs and would take into account a greater number of future targets. The model results confirmed both predictions. In a constrained version of the hand task in which choices could only be based on target positions, participants consistently chose among the shortest movement paths. Our results demonstrate that optimal foraging theory offers a useful framework for understanding choice behaviour in target-directed movements.

5.2 Introduction

Studies of reach planning and control have focused on movements towards single targets, with theoretical accounts focusing on the minimization of various movement-related costs (for reviews see Diedrichsen et al. (2010); Scott (2004); Shadmehr et al. (2010); Todorov (2004); Wolpert et al. (2011)). However, real-world tasks often involve choosing targets from among multiple alternatives, and therefore not only involve decisions about how to move but also where to move. Moreover, such tasks often involve a sequence of actions in which choices are made at each step. Although decision-making related to target selection has been extensively studied in the context of eye movement preparation (Churchland et al., 2008; Najemnik and Geisler, 2005; Platt and Glimcher, 1999; Schall, 2001) and in more cognitive tasks such as the traveling salesperson problem (MacGregor and Ormerod, 1996; MacGregor et al., 1999; Vickers et al., 2003, 2001), comparatively little work has been done on reaching, in which movement-related costs are likely to play a more critical role (Resulaj et al., 2009; Wolpert and Landy, 2012). Although a handful of reaching studies have examined how values and costs influence the selection of targets in single movements
(e.g., Gepshtein et al. (2007)), and fixed sequences of movements (Safstrom et al., 2013; Wu et al., 2009; Zhang et al., 2010), to our knowledge no study has investigated the selection of targets during a sequential reach task.

In performing a task involving the selection of a series of targets, each successive choice decision could be made *de novo* in order to maximize rewards and minimize costs associated with only the next target selection. However, by "looking ahead" and considering the rewards and costs across future potential targets, it may be possible to further optimize performance.

Here we assessed sequential decision-making using a movement foraging task in which participants could choose the order in which they harvested from a set of targets of varying size, value and position across the workspace, either by moving their hand to the targets (hand task) or briefly fixating them (eye task), with the goal of maximizing reward. The trial duration was such that on any given trial participants could only harvest around half of the targets, placing a premium on efficient decision-making. We evaluated performance using a probabilistic model, inspired by optimal foraging theory (Charnov, 1976; Stephens and Krebs, 1987), that predicts target-by-target harvesting probabilities based on rate of reward, costs associated with target distance and size, and decision noise. A key feature of the model is that it can incorporate a number of future successive harvests with temporal discounting; i.e., it can ‘look ahead’. Because moving the hand is more costly, in time and energy, than moving the eyes, we predicted that target choice in the hand task, in comparison to the eye task, would be more strongly influenced by movement-related costs and would take into account a greater number of future targets so as to optimize the route through the targets.
5.3 Methods

5.3.1 Participants

Eight women and seven men between 20 and 28 years of age participated in the present study after providing written, informed consent. All participants self-reported having normal or corrected-to-normal vision, being right handed, and being free of sensorimotor dysfunction. Participants were assigned to one of two groups: the hand foraging group (n = 8) or the eye foraging group (n = 7). The experimental protocols were approved by the General Research Ethics Board at Queen’s University in compliance with the Canadian Tri-Council Policy on Ethical Conduct for Research Involving humans. Each experimental session lasted approximately one hour. Participants received $10 in compensation and an additional monetary sum based on the total points harvested during the experiment. Specifically, a $0.05 bonus was provided for every 250 points harvested, resulting in an additional payoff of between $4 and $5.

5.3.2 Apparatus and Stimuli

Seated participants viewed 15 circular targets located in 3 rows by 5 columns (see examples in figure 5.1). To specify the locations of the targets on each trial, we began with the targets arranged in a perfect $3 \times 5$ grid with equal 6 cm spacing between targets (in both dimensions), providing 15 initial grid locations. The 15 targets were then offset from their initial positions in the perfect grid by adding random vertical and horizontal offsets to each initial target location, independently drawn from a uniform distribution over $\pm 11$ mm. Thus, the positions of the targets, relative to the grid locations, changed from trial to trial. Targets in the display could be one of three sizes—5, 8, or 11 mm in radius—and have one of three point values—10, 12,
or 15 points (Fig. figure 5.1 B). Participants also viewed a circular start position, 5 mm in diameter, located 6 cm closer to their body than the first row of targets and at the participants’ midline. All stimuli were presented using a visual display system, consisting of a CRT projector (Electrochrome 9500 Ultra) with a refresh rate of 120 Hz and a horizontal mirror through which participants viewed the images on a horizontal surface.

Figure 5.1: **A**, Schematic of the experimental setup and stimuli configuration. In the hand task, participants harvested targets by moving a handle and pressing a button instrumented to the handle. In the eye task, participants harvested targets by fixating gaze over a target. **B**, Target size and value pairings featured in the 4 experimental conditions. Five of each target type (size-value pairing) was displayed
for a given block and the position of each of the 15 targets was randomized on each trial. Representative traces of hand movements or eye movements in each of the three foraging tasks, where grey targets represent those that have been successfully harvested. The numbers indicate the order of harvests.

In the hand foraging task, participants selected targets by moving a circular cursor (5 mm in diameter) linked to the position of a grasped handle to each target. A successful harvest occurred when participants pressed a button fitted to the side of the handle with their index finger when the cursor overlapped with any portion of the target. The handle, which was attached to a lightweight manipulandum (Phantom 3.0, Sensable Technologies, Cambridge, MA), could freely rotate about its vertical axis and was mounted on an air sled allowing participants to move the handle by sliding over a horizontal surface. Optical encoders in the manipulandum measured the handle position at 1000 Hz and the state of the button was also recorded at 1000 Hz.

In the eye foraging task, participants selected targets by fixating their gaze on the targets. An infrared video-based eye-tracker (ETL 500 pupil/corneal tracking system, ISCAN, Burlington, MA, USA) was used to record gaze position of the left eye in the plane of the target display at 240 Hz. A bite bar was used to help stabilize the head. Gaze position was calibrated to the plane of the target display (see Bowman et al. (2009) for details) at the beginning of the experiment and recalibrated if drift in the recorded gaze signal occurred. In practice, gaze was recalibrated approximately once per participant, typically at around 75% of the duration of the experiment. The gaze signal was smoothed, on-line, using a running average filter computed over the last 50 samples (samples at 1000 Hz), which introduced a small time delay of 24.5 ms. In performing the gaze foraging task, participants almost always fixated one of
the targets and very few corrective gaze shifts were observed. That is, participants shifted their gaze directly from one target to the next. To determine which target was fixated, we simply took the closest target to the gaze position. A successful target selection was achieved when gaze was at a given target for 150 ms. With this fixation duration, the time between successive harvests was similar to the hand foraging tasks.

5.3.3 Procedure

For a given trial, participants were instructed to harvest as many points as possible (which translated to a monetary bonus). At the start of each trial, the participant had to position the cursor, or fixate, the start position for a random time period of between 0.3 and 2.3 s. The target display then appeared, and the participant then had a fixed duration of 3.25 s to harvest targets. This duration was chosen so that on average subjects could average about half the targets on any given trial. At the moment a target was successfully harvested, the target turned grey and a brief tone (1000 Hz) was sounded for 50 ms. At the end of each trial, the total number of harvested points was presented on the target display. Participants completed one practice block of trials, consisting of a set of targets that were all of medium size (8 mm radius) and value (12 points). Participants then completed four experimental blocks of 50 trials, in counterbalanced order, with a 3–5 minute rest between blocks.

The four experimental blocks differed in how target size and value were combined (see Fig. 5.1 B). In the size condition, only target size was varied, with 5 targets of each size, while target value (12 points) was held constant. In the value condition, only target value was varied, with 5 targets of each value, while target size (8 mm) was held constant. For this condition, the low, medium, and high value targets were
5.3. METHODS

colored blue, green, and orange, respectively (in all other conditions, all of the targets were blue). In the small-high condition, the target size was negatively correlated with target value with the smallest targets being the most valuable. Participants were presented with 5 small targets of high value, 5 medium-sized targets of medium value, and 5 large targets of low value. Lastly, in the small-low condition, the size of the targets were positively correlated with value with the larger targets being the most valuable. Participants were presented with 5 small targets of low value, 5 medium-sized targets of medium value, and 5 large targets of high value. Before each block, participants were explicitly told the size-value pairing of the upcoming block. These blocks were completed in both the hand and eye foraging tasks.

Participants in the hand foraging group performed an additional constrained hand foraging task in which they were required to harvest targets in order of decreasing value. That is, participants were required to harvest all of the high value targets first, followed by the medium value targets, and then the low value targets. Participants could not harvest a target out of order; if a participant attempted to harvest a target out of sequence, no tone was sounded and the target did not change to gray. In this task, participants typically harvested between 6 and 7 targets and therefore we could assess their route-selection efficiency by comparing the actual route they selected through the first 5 (high value) targets to all possible 5-target routes (n = 120). In this task, participants performed three blocks of 50 trials, counterbalanced across participants, corresponding to the value, small-high, and small-low conditions described above.
5.3.4 Analyses

For each harvest, we determined the duration from the previous harvest (i.e., duration between successive successful button presses) as well as the distance from the previous harvest, defined as the distance between successive target centers. In the hand foraging task, participants occasionally missed the target by pressing the button while the cursor was slightly off the target. Participants on average missed the target on 7% (SE = 0.01%) of harvest attempts in the free task and 8% (SE = 0.01%) in the constrained task. This analysis was not carried out in the eye task because misses were not classifiable using our technique for capturing target harvests in this condition (see section 5.3.3). An alpha level of 0.05 was used for statistical tests and a Bonferroni correction was used for post hoc tests.

5.3.5 Model

We developed a model that assigned, to each available target, a probability that that target would be chosen next. Each selection made by the model began from the most recently harvested target, $i$ and considered the sizes, values and positions of the remaining targets, $j \in H$, where $H$ represents the set of remaining non-harvested targets. We defined the distance from target $i$ to target $j$ as $d_{ij}$, the value of target $j$ as $v_j$ and the size of target $j$ as $s_j$. An estimate of the time required to move from target $i$ to target $j$, $t_{ij}$, was derived from linear regressions, relating movement time to movement distance, that were computed separately for each participant and target size. The rate of reward for selecting target $j$ was calculated as $r_{ij} = v_j/t_{ij}$. A pure reward based model would only consider rate of reward. In this case, target distance and size can only influence choice via effects on movement duration. However,
distance and size may also influence target choice via other costs. For example, distance may be associated with a physical effort cost whereas target size may be associated with a cost linked to planning and controlling more precise movements. To capture this possibility, the cost, \( c_{ij} \), of choosing target \( j \) as the next harvest was calculated as:

\[
C_j = c_{ij} = -r_{ij} + w_1d_{ij}^\gamma - w_2s_j
\]  

That is, the cost depended on the negative reward rate, a penalty associated with distance and a penalty for reaching to smaller targets. The penalty associated with distance captures possible movement-related energy costs. We included the exponent gamma in this term to accommodate the possibility of a non-linear mapping between energy and distance. We then used a probabilistic softmax selection rule so that the probability of choosing target \( j \) became:

\[
P_j = \frac{e^{-\beta C_j}}{\sum_j e^{-\beta C_j}}
\]  

The parameter \( \beta \) determined the combined noise in perceptual and decision processes, with infinite noise assuming a value of \( \beta = 0 \). For very large values of \( \beta \), the probability of choosing the target with the lowest cost approaches 1. For intermediate values the probabilities are always ordered according to the cost (highest probability for lowest cost) but allow higher cost targets to be selected occasionally.

We also considered models that look more than one harvest ahead. When looking \( n \) harvests ahead (where \( n = 1 \) corresponds to the model already described), we consider each potential next harvest target \( j \) and all possible subsequent sequences of \( n - 1 \) harvests \((k, l, m, \ldots)\). For each harvest we calculated the cost with different
weightings, $\lambda$, applied to future harvests. For example, when looking $n = 4$ steps ahead (i.e., $j, k, l, m$) the cost of choosing $j$ as the next harvest is given by:

$$C_j = \min_{H(k, l, m, n)} (c_{ij} + \lambda_1 c_{jk} + \lambda_2 c_{kl} + \lambda_3 c_{lm} + \lambda_4 c_{mn})$$  (5.3)

where the minimum is taken over all triplets $H(k, l, m)$ of potential harvested targets after the first harvest. Therefore $C_j$ represents the smallest cost associated with making the next harvest target $j$ when considering the next 3 targets. Again we used the softmax function to select the next harvested target. We modeled look aheads, $n$, from 1 to 5 targets (due the combinatorial nature of the problem it was not possible to consider look aheads of 6 or more).

We did not analyze the first harvest of each trial because, in the hand task especially, participants tended to rapidly launch their initial movement in a relatively fixed direction and choose between the one or two targets located in this direction (e.g., the center target in the first row and the target to its left). By limiting decision-making in the initial movement, participants could initiate the task quickly while bringing their hand (or gaze) towards the grid of targets and giving themselves time to select the next target or targets. In addition, we only considered up to 8 harvests because as the number of harvests increased beyond 8, the number of trials decreased sharply (see section 5.4.2). We used maximum likelihood (MATLAB fminsearch) to fit the model to the entire dataset of 200 trials by 8 harvests (max) for each participant separately. For a look ahead of $n$, the model had $n + 4$ parameters. We also fit reduced models in which one of the three components in Eqn. 5.1 was set to zero.
5.4. Results

5.4.1 Representative trials

Figures 5.1 C–E shows hand or gaze paths for single trials performed, by different participants, in each of the three foraging tasks in the small-high condition. These trials illustrate several general features of the performance we observed in these tasks. Participants exhibited a strong tendency to move between adjacent targets in the hand task but also tended to make relatively small movements in the eye task. Even in the constrained hand task (in which the targets had to be harvested in order of decreasing value), participants moved to close-by targets where possible. In the hand task, participants also tended to minimize changes in movement direction between successive harvested targets whereas, in the eye task, sharper changes in direction
were often observed. One strategy that participants employed to limit changes in hand movement direction was to harvest targets along a roughly circular route. In all three tasks, participants typically harvested most, if not all, of the high value targets. In the hand task, they often harvested medium or, less frequently, low value targets in between the high value targets. In contrast, in the eye task, there was a stronger tendency to harvest the high value targets prior to lower valued targets. The pattern observed in the hand task suggests that participants were aware that they could typically obtain 8 or 9 targets and could therefore harvest some less valuable targets while ensuring that most, if not all, high value targets were harvested. Harvesting a few less valuable targets en route between high value targets often allowed participants to avoid large amplitude hand movements.

5.4.2 Target preferences

Figure 5.2 shows the mean number of harvests for each condition of the hand and eye foraging tasks. Overall, the number of targets harvested in the hand (M = 8.4, SE = .16) and eye (M = 8.2, SE = .18) tasks were similar (F_{1,13} = .12, p = 0.73), allowing us to reasonably compare target preferences across tasks. In both tasks large targets were preferred when only size was varied and high value targets were preferred whenever value was varied (i.e., in the three other conditions). However, in the small-high condition, in which value and size traded off, the preference for high value targets was weaker in the hand task than the eye task. To quantify these results, for each condition we carried out a two-way mixed model ANOVA to assess the effects of target (3) and task (2) on the number of harvests. In no condition was there a main effect of task (p >0.05 in all 4 cases). A main effect of target size was
found in the size condition \( (F_{2,26} = 48.8, p < 0.001) \) but there was no target by task interaction. A main effect of target value was observed in the value \( (F_{2,26} = 104.7, p < 0.001) \), small-high \( (F_{2,26} = 91.6, p < 0.001) \), and small-low \( (F_{2,26} = 280.6, p < 0.001) \) conditions. A target value by task interaction was found for the value \( (F_{2,26} < 5.5, p < 0.05) \), small-high \( (F_{2,26} < 91.6, p < 0.001) \), and small-low \( (F_{2,26} < 4.6, p < 0.05) \). In these three conditions, participants in the eye task harvested more high value targets than participants in the hand task, possibly because smaller movement-related costs in the eye task allowed participants to harvest targets according to their value, with limited influence of their sizes and/or distances.
5.4 RESULTS

Figure 5.2: Average number of harvests per trial for the hand task (left column) and the eye task (right column) for each condition and target type. The bars show the average number of harvests computed from participant means, with error bars representing ±1 SE, and the lines show individual participant means. All bars represent targets of a given size shown for a given value (X-axis), with white, skinny bars representing the smallest target size, light grey, thicker bars representing the medium target size, and thick, dark grey bars representing the largest target size.

Although size similarly influenced hand and gaze target selection in the size condition, when size was paired with value, size had a substantial influence on hand target selection (compare the small-high and small-low conditions) but little influence on gaze target selection. Thus, whereas participants in the eye tasks exhibited a clear preference for large targets when only size varied, this preference was largely superseded by value when value also varied.

5.4.3 Movement times

For the probabilistic model, we estimated the time required to move to any given target based on its distance and size. Specifically, for each participant, we performed separate regressions between recorded movement time (i.e., time between harvests) and target distance for each target size, where regressions in the arm task were obtained after pooling data from the free choice and constrained tasks. Two-way mixed model ANOVAs were carried out to assess how the slope and intercept varied with task and target size. There was no significant difference (F$_{1,13} = 2.3, p = 0.2$) between the slopes in the eye (M = 0.9 s/m; SE = 0.2 s/m) and hand (M = 1.0 s/m; SE = 0.1 s/m) tasks. However, the intercepts were slightly greater (F$_{1,13} = 15.8, p = 0.002$) in the eye task (M = 0.3 s; SE = 0.02 s) than the hand task (M = 0.2 s; SE = 0.01 s). The slope (F$_{2,26} = 18.6, p < 0.001$) and intercept (F$_{2,26} = 6.0, p = 0.007$) also
depended on target size. Specifically, the slope and intercept tended to decrease and increase, respectively, as a function of target size.

5.4.4 Model comparisons

In this section, we first evaluate the contribution of reward rate, target distance, and target size using the 1-look-ahead version of the model, which only considers the next or immediate harvest when predicting which target will be selected. After establishing that the full model (with all three of these parameters) provides the best overall fit in both the hand and eye tasks, we then compare versions of this model with 1 to 5 look-ahead steps. Finally, we evaluate the performance of the best-fit N-look-ahead model by comparing model predictions against actual data. In all cases, the models are fit to each individual participant, with all harvests (except for the first harvest in each trial) from all trials in all four conditions (i.e., size, value, small-high, and small-low) fit together.
Figure 5.3: Model performance and look-aheads. 

A–B, Bayesian Information Criterion (BIC) used to compare models having different number of parameters, where smaller BIC scores are preferred, shown for each participant. Three different models are presented, involving either no reward rate (dark grey bars), no target size (white bars), or no distance (medium grey bars). C–D, shows the BIC scores for each participant as a function of look-ahead for the hand and eye task, with BICs normalized to the mean score for the 1 look-ahead model. E, histogram showing the number of participants in the hand (black bars) and eye (grey bars) task whose best fitting model incorporated a given number of look-aheads. F, Average weights computed
from participant means assigned to each look-ahead number in the model for the hand (black line) and eye (grey line) task taken from the 5 look-ahead model. Error bars represent ±1 SE.

To assess the contribution of reward rate, target distance, and target size, we compared the full model against the three submodels, obtained by removing each individual factor, using the Bayesian Information Criterion (BIC), with a lower BIC indicating a better fit. Figures 5.3 A and B show the change in BIC score (Δ BIC) going from the full model to each of the three submodels, for the hand and eye tasks respectively. The full model provided the best fit for all 8 participants in the hand task and for 4 of 7 participants in the eye task. In the other 3 participants who performed the eye task, the best model included reward rate and distance but not target size. However, this model and the full model had very similar BIC scores in all participants in the eye task (i.e., Δ BIC was very close to zero). For all participants in the hand task, the model omitting target distance was the poorest predictor of target choice by a large margin, and this model was also the poorest predictor in 5 of 7 participants in the eye task (with the model omitting reward rate being the poorest predictor in the other 2 participants). Overall, these results indicate that, in both the hand and eye tasks, all three parameters of the full model—i.e., reward rate, target distance, and target size—influence choice behavior.

Using the full model, we then evaluated how many future harvests are considered when selecting the current target to harvest. Figures 5.3 C and D show BIC scores as a function of the number of look-ahead harvests for each participant in the hand and eye tasks, respectively. Note that these scores have been normalized (by subtraction) to the mean BIC score, across participants, for the 1-look-ahead model. In the hand
task, the BIC score tended to decrease (indicating a better fit) as a function of look-ahead steps whereas, in the eye task, the BIC score tended to increase for the majority of participants. The histogram in Figure 5.3 E shows the number of participants best fit by models with 1 to 5 look-aheads. In the hand task, the best-fit model for all participants contained at least 3 look-aheads and, in 5 of the 8 participants, the 5-look-ahead model provided the best fit. As noted above, we could not examine models with more than 5 look-aheads due to the combinatorial nature of the model. However, with the exception of one participant, the BIC scores appeared to level off somewhat as the number of look-aheads increased. In the eye task, the 1-look-ahead model provided the best fit in 5 of 7 participants, with the other two participants’ choice behaviour best fit by models the 3 and 5 look-aheads. These results indicate that in the hand task participants consider a sequence of forthcoming target choices when selecting the next target whereas, in the eye task, participants chose targets on a harvest-by-harvest basis.

When considering the best-fit models for each participant, the average power exponent on the distance term (gamma in equation 5.1) was 0.36 (SE = 0.09) for the eye task and 1.14 (SE = 0.23) for the hand task. Thus, the influence of target distance in determining target choice was close to linear in the hand task but compressive in the eye task, consistent with the idea that the additional cost of making larger eye movements was less than the additional cost of making larger hand movements.

In the model, different weights are assigned to the costs associated with each look-ahead step. To further assess the contribution of future harvests to the choice of target in the current harvest, we fit the 5-look-ahead full model to each participant. Figure 5.3 F shows the average weights assigned to each look-ahead step in the hand and eye
tasks. (Note that the weights for a given participant sum to one.) For both tasks, the largest weight was assigned to the immediate choice option (i.e., 1-look-ahead), with this weight being higher in the eye task than the hand task, consistent with the finding that the 1-look-ahead model provided the best fit for most participants who performed the eye task. These effects were confirmed by a two-way ANOVA, which revealed a main effect of look-ahead number ($F_{4,52} = 130.0, p < 0.001$) as well as a look-ahead by task interaction ($F_{4,52} = 4.6, p < 0.05$).

5.4.5 Model performance

To evaluate the best-fit model for each participant (i.e., the full model with the number of look-aheads that provided the lowest BIC), we compared the actual target selections to those predicted by the model. At each harvesting step, the model assigns a probability of selection to each available (i.e., non-harvested) target. The black traces in Figures 5.4 A and B show, for each participant in the hand and eye tasks respectively, the probability that the participant selected the target assigned the highest probability of selection by the model, as a function of harvest number. Overall, participants selected the highest probability target 61 percent of the time in the hand task and 53 percent of the time in the eye task. As is evident from the figure, across all harvests in both tasks, the probability of selecting the highest probability target was well above chance (dashed grey traces), which increases from $1/14$ (0.071) to $1/8$ (0.125) from the second to the eighth harvest.
Figure 5.4: Target selection probabilities.  \(A–B\), The black lines show, for each participant in the hand and eye tasks, respectively, the average probability that the participant selected the target assigned the highest probability by the model for harvests 2–8. The dashed grey line shows the probability that the target was selected by chance, which increases slightly as targets are harvested.  \(C–D\), Black lines show the average probability, assigned by the model, to the target selected by each participant in the hand and eye tasks, respectively, for harvests 2–8. The grey lines show the probability of the most probable target minus the probability of target selected by...
the participant.

The black traces in Figures 5.4 C and D show the probability, assigned by the model, to the actual target selected by the participant, and the grey traces show the difference between the highest assigned probability and the probability assigned to the selected target. Although participants did not always select the target with the highest assigned probability, they generally selected a high probability target. Overall, the average ranking—from highest to lowest probability—of the selected target was 1.61 in the hand task and 1.96 in the eye task. These results are indicative of the fact that the probabilities assigned to the most probable few targets were often similar. Note that both the probability of selecting the highest probability target (black traces in Figs. 5.4 A and B) and the probability assigned to the selected target (black traces in Figs. 5.4 C and D) increased over the initial few harvests in the hand task, but were quite constant in the eye task. This observation is consistent with the fact that, in the eye task, the influence of target distance is relatively weak, which yields more target options with similar probabilities of selection.

5.4.6 Features of selected targets over harvests

To examine how participants prioritized targets of varying value and size across harvests, for each participant and condition we calculated the proportion of targets, of a given size or value, that were selected on each successive harvest. Figure 5.5 shows these proportions, averaged across all participants, for harvests 2 through 8 in both the hand and eye tasks. The figure also shows the predicted proportions, averaged across participants, obtained with each participant’s best-fit model. (Note that the data from all four conditions the predicted together.) Qualitatively, it is evident that
the model was able to capture the choice behaviour of the participants in both tasks and in all four conditions.
Figure 5.5: Proportion of targets of a given size or value selected from harvests 2–8. Proportions averaged across all participants in the hand (left column) and eye (right column) tasks. The red, green and blue traces show proportions for high, medium and low value harvests, respectively, or in the case of the size condition (top row), large, medium, and small target harvests, respectively. These proportions are shown for the experimental data (solid lines) as well as the model data (dashed lines). Shaded regions represent ±1 SE.

In the eye task under conditions in which target value varied (i.e., the value, small-high, and small-low conditions), participants had a strong tendency to initially select high value targets right from the start (i.e., from harvest number 2 onwards), and largely ignored the size of the targets. When most or all of the high value targets were harvested, they then strongly favoured the middle value targets. In contrast, under the corresponding conditions in the hand task, the influence of value on target selection was weaker, and varied considerably across conditions. Thus, although high value targets were always preferred, this preference was weaker when the high value targets were small (small-high condition) and stronger when the high value targets were large (small-low condition). A modest influence of target size was observed under the size condition in both tasks, even though size had little influence on choice behaviour in the eye task in the other conditions. These results are consistent with the finding that movement related costs play a more significant role in shaping choice behaviour in the hand task than the eye task. Participants in the hand task appeared to exploit the fact that they had enough time to harvest most, if not all, of the high value targets without having to harvest the high value targets first. Presumably, they were willing to harvest lower value targets in order to reduce movement related costs. In contrast, participants in the eye task tended to select the high value targets, presumably because they can do so without incurring large movement related costs.
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5.4.7 Movement Distance

Figure 5.6 shows, for each of the conditions, frequency distributions of target-to-target distances for all actual and predicted harvests in both the hand and eye tasks averaged across participants. In both tasks, participants most often harvested targets that were directly adjacent (up, down, left, or right) to the previously harvested target and were therefore on average 60 mm away (corresponding to the mode of the distributions). Participants less frequently harvested adjacent but oblique targets, located on average 90 mm away, and targets located 2 or, even less frequently, 3 targets away. Although the distributions for the hand and eye tasks were similar in that adjacent targets were strongly preferred, a greater number of larger distances were seen in the eye task (blue traces) than the hand task (red traces). Two independent samples Kolmogorov-Smirnov tests revealed significant differences (p < 0.05) between the two tasks in the three conditions where target value varied (bottom three row of Fig. 5.6), but not in the size condition where only target size varied (top row). Presumably, participants were more willing to move greater distances in the eye task, when value was manipulated, because of the lower movement-related costs involved. However, target size alone did not drive participants to move greater movement distances in the eye task.
Figure 5.6: Frequency distributions of target-to-target distances for all actual (solid line) and predicted (dashed line) harvests in both the hand (red traces) and eye (blue traces) tasks for each condition averaged across participants. The pronounced peak at 60 mm reflects the separation distance of adjacent targets and the most common movement.

5.4.8 Constrained Hand Task

We included a constrained hand task, in which participants were required to harvest targets in order of decreasing value, for two reasons. First, comparing performance on the constrained and unconstrained (or ‘free’) hand tasks enables us to test whether sometimes selecting lower value targets before harvesting all high value targets (as in the unconstrained hand task), improves performance. Second, by focusing on the first 5 harvests (i.e., harvests of the high value targets) in the constrained task, we could assess how effectively participants minimize movement path distance. Figures
5.4. RESULTS

5.7 A and B show the average number of points and harvests, respectively, per trial for both the free and constrained hand tasks in the three conditions examined in the constrained hand task. (Note that the size condition was not performed since the targets all had equal value.) On average, participants harvested all 5 high value targets and one or two mid-value targets in the constrained hand task. Two 2 task (free versus constrained hand task) × 3 condition repeated measures ANOVAs showed that participants harvested more points (F$_{1,7} = 68.0$, p < 0.001) and more targets (F$_{1,7} = 72.4$, p < 0.001) in the free choice task than the constrained task. These findings indicate that participants’ inclination to sometimes forgo high value targets in the free task led to more optimal performance. The analysis also uncovered a task by condition interaction for both the number of harvested points (F$_{2,14} = 43.3$, p < 0.001) and targets (F$_{2,14} = 6.2$, p = 0.012). As shown in the figure, for both variables, the largest discrepancy between tasks is seen in the small-high condition, where high value targets were small. In the constrained task, fewer targets were harvested when participants were required to harvest the small targets first. This could reflect a speed-accuracy trade-off, more challenging visual search, or both. However, even when the high value targets were large, the number of targets harvested in the constrained task was less than in the free choice task.
Figure 5.7: Performance in the constrained hand task.  

\(A\)–\(B\), Average number of points and harvests, respectively, per trial across the three conditions examined in the constrained hand task. Error bars represent ±1 SE.  

\(C\), Mean distributions, averaged across participants, of possible path distances (dashed line) and actual path distances (solid line) that participants chose. Shaded areas represent ±1 SE.  

\(D\), The bars show the proportion of trials in which participants selected the shortest possible path (rank 1), the next shortest path (rank 2), and so on up to the 20th shortest path. The grey line shows the total path as a function of rank.

To assess how effectively participants minimized hand path distance, we computed, for each trial in the constrained task, the distance between successive targets for all 120 possible harvest orders of the first five targets. Figure 5.7 C shows the distribution of possible path distances (dashed line) together with the distribution of actual path distances that participants chose. It is evident that participants selected harvest paths from the lower end of the distribution of all possible paths. The histogram in Fig. 5.7 D shows the proportion of trials in which participants selected the shortest
possible path (rank 1), the next shortest path (rank 2), and so on up to the 20\textsuperscript{th} shortest path. (The gray solid line shows the average total distance of the ranked paths.) Participants chose the shortest path on close to 40\% of trials and selected one of the 5 shortest paths on approximately 75\% of trials. These data show that participants were efficient at rapidly harvesting a sequence of targets the resulted in a relatively short cumulative distance.

5.5 Discussion

We examined sequential decision-making within the context of a rapid motor foraging task in which participant briefly harvested targets—of vary value, position, and size—either by moving the hand to the targets (hand task) or fixating the targets (eye task). A probabilistic ‘look ahead’ model in which target choice depended on rate of reward, target distance, and target size of up to the next 5 targets was fit to the data. We found that in hand task, in comparison to the eye task, target choice was more strongly influenced by target distance and size, and took into account a greater number of future targets. In a constrained version of the hand task, we also found that participants were capable of selecting efficient routes through the targets that reduced total distance travelled.

Until recently, research in the fields of decision-making and action has, for the most part, progressed independently. On the one hand, studies of decision-making have focused on cognitive and perceptual factors without considering costs associated with acting on decisions. On the other hand, studies of action, including goal-directed reaching, have focused on motor factors (e.g., accuracy and energy; Scott (2004); Todorov (2006)) without often considering decision-making processes related
5.5. DISCUSSION

... to choosing what movement to make and when to make it (for reviewers see Cisek (2012); Cisek and Pastor-Bernier (2014); Wolpert and Landy (2012)). However, in situations in which decisions are implemented in terms of actions, one might expect that certain movement factors might be integrated into decisions, an idea supported by the observation that elements of decision-making and motor control share some common neural circuits (Cisek, 2007a,b; Cisek and Kalaska, 2005, 2010; Gold and Shadlen, 2007; Hernández et al., 2010). In fact, it has been posited that decision-making capabilities developed first to support movement-type decisions, e.g., fight or flight, eat or do not eat, which later evolved to support abstract cognitive decision-making (Cisek and Kalaska, 2010).

A number of studies have recently examined the interplay between motor control and decisions about where and when to reach during single movements. For example, it has been shown that people factor into account their spatial movement variability to optimize performance when reaching towards target configurations with different reward and penalty regions (Battaglia and Schrater, 2007; Trommershäuser et al., 2003, 2008) and similar optimization has been shown for temporal variability (Dean et al., 2007; Hudson et al., 2008; Safstrom et al., 2013). Real-world tasks often consist of a series of target directed actions, requiring sequential decisions about which targets to act on and in what order. In such tasks, we might expect target choice to be determined by a trade off between various movement-related costs (Diedrichsen et al., 2010; Harris and Wolpert, 1998; Scott, 2004; Todorov, 2004; Wolpert et al., 2011) and value, a factor known to bias cognitive decision-making (Glimcher, 2004; Kahneman and Tversky, 2000). This trade-off between costs and rewards can be related to optimal foraging theory, which posits that foraging organisms attempt...
to maximize net energy intact per unit time by harvesting as much food energy as possible as quickly as possible while minimizing the energy expended (Charnov, 1976; Stephens and Krebs, 1987). Although there are obviously many differences between natural foraging and the reaching task we examined, foraging theory can nevertheless provide a framework for studying movement decisions in the context of competing costs and rewards (see Hayden et al. (2011); Kan (2011); Kolling et al. (2012)).

Recent work has shown that activity in sensorimotor areas of the brain encodes multiple potential reach targets prior to deciding between, and then reaching towards, one of these targets (Cisek and Kalaska, 2005). One provocative interpretation of this activity is that it reflects competing movement plans prepared for multiple potential targets (Cisek and Kalaska, 2010). Recent behavioural studies showing ‘spatial averaging’ when reaching towards multiple potential reach targets (Chapman et al., 2010a,b; Stewart et al., 2013; Wood et al., 2011) are consistent with the idea that the brain represents multiple possible movements (see also Stewart et al. (2014)).

With respect to multiple targets, other studies have shown that motor effort and movement variability influences the choice about which of two competing targets to reach to (Burk et al., 2014; Marcos et al., 2011; Trommershäuser et al., 2006). For example, in an elegant series of studies, Cos and colleagues evaluated whether participants incorporated knowledge of limb biomechanics, affecting energy and limb stability, to determine which of two movements to perform (Cos et al., 2014; Marcos et al., 2011; Cos et al., 2012). The task was structured so that movements to one target were more effortful than movements to the other target based on the configuration of targets and via points. The authors showed that participants chose the shorter of the two movements and were able to predict and thus choose, within 200 ms, movements
also requiring less effort. This was true even in conditions where distance was held constant (Marcos et al., 2011). Furthermore, Trommershäuser et al. (2006) showed that participants were able to choose which of two goal configurations yielded greater reward, which was based on participants’ knowledge of their own motor variability. Overall, these findings demonstrate that people can make movement-decisions about what targets to reach to based on knowledge of their own biomechanics and motor performance.

The present results extend the previously mentioned findings by showing that movement related costs together with target value interact to influence decisions about where to move. Furthermore, we show these decisions are made amidst numerous target options in the context of a free-choice sequential task. Although sequential decision-making has been previously studied in the context of eye movements using visual search paradigms (Najemnik and Geisler, 2005; Navalpakkam et al., 2010), our study is the first to probe this behaviour during reaching movements where movement costs associated with limb motion can be exploited. One of our principle findings was that participants in the hand foraging task weighted movement-related costs more heavily in their decisions about what targets to select compared to participants in the eye foraging task, which reflects the greater energy and time requirements of hand movements. Consistent with this finding, we found that participants in the hand task took into account a greater number of future harvests compared to in the eye foraging task. Such ‘looking ahead’ may have enabled participants in the hand task to effectively trade-off the distance travelled by the hand and the total value of the targets harvested. Our look-ahead findings are in support of previous findings
from Todorov (1998), who showed that participants altered their movement trajectory towards an intermediate target when a future was displaced during a sequential target task. Other examples of such look-ahead behaviour are observed during typing (Flanders and Soechting, 1992) and coarticulation in speech (Fowler and Saltzman, 1993). Overall, these studies show that motor behaviour, at least with respect to sequential tasks, is influenced by future movements or task constraints.

The model results also showed that participants placed the most weight on the current target option with each subsequent target option having progressively less weight in the decision; though participants in the hand task looked further ahead than the eye task overall. This finding can be linked to the phenomenon of ‘temporal discounting’ shown for saccades (Hwang, 2009; Shadmehr, 2010; Shadmehr et al., 2010), where the value of a foveated stimulus decreases parabolically with duration of movement. This means that movements offering immediate reward are preferred over those movements where reward might be delayed.

The results of the fixed order task showed that subjects chose the optimal—or near optimal—routes through the first 5 harvests. Given the temporal constraints of the task, optimal route choices enabled subjects to maximize the number of harvests—and also the number of harvested points. Therefore, the capacity to rapidly select minimal path distance forms a fundamental requirement for optimal harvesting performance. Recent evidence indicates that human performers are quite capable of generating efficient solutions (MacGregor and Ormerod, 1996; MacGregor et al., 1999; Vickers et al., 2003, 2001) to the travelling salesman problem (TSP). For instance, MacGregor and Ormerod (1996) showed that subjects effortlessly found minimum—or near—minimum solutions to problems of 10 and 20 nodes; and these solutions were generated
in less than 5 minutes (although it was not a timed task). Furthermore, Vickers et al. (2003) showed that subjects could generate near optimal solutions to open-ended versions of the TSP, albeit often less optimal compared to their closed counterparts, which is similar to the problem presented by our constrained task. Overall, the effortless and near optimal human solutions for TSPs has been well documented and is consistent with our observation that our subjects optimize the order of harvests (i.e., minimize distance).

### 5.5.1 Summary

The influence of movement costs and rewards have been previously studied during single movements (Harris and Wolpert, 1998; Scott, 2004; Shadmehr et al., 2010; Todorov, 2004; Wolpert et al., 2011), involving one or two targets, and using perceptual tasks (Glimcher, 2004). Here, we pitted these two factors against each other in a foraging task where participants made sequential decisions about what targets to harvest. Using a probabilistic model that predicted target-by-target harvesting choices, we found that movement-related costs were weighted more heavily in the hand task compared to the eye task and participants took into account a greater number of future harvests, or ‘look-aheads’, in the hand task than did participants in the eye task. These results indicate that participants intelligently incorporated movement-related costs when deciding which movements to perform. Finally, in a variant of the hand task where we fixed the order of harvests, we found that targets were selected using the shortest, or one of the shortest, harvesting paths, adding further evidence that movement-related costs were incorporated into target selection, specifically by minimizing distance travelled. Overall, our findings extend previous
accounts of movement decision-making, which focus almost exclusively on how costs or value influence single movements, by showing how they combine to drive choice behaviour.

5.6 References


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Chapter 6

General Discussion

A large body of research on motor control and motor learning focuses on studies of upper limb control, involving pointing movements in free space (Elliott et al., 2001; Goodale et al., 1986; Milner and Goodale, 2008; Prablanc and Martin, 1992) and reaching movements with forces applied to the hand (Caithness et al., 2004; Gandolfo et al., 2000; Mattar and Gribble, 2005; Shadmehr and Mussa-Ivaldi, 1994) or arm (Krakauer et al., 1999; Nashed et al., 2012, 2014). These studies place little emphasis on manipulation itself. This is perhaps surprising given that the overwhelming majority of movements we make with our upper limbs are object-oriented. Thus, in our daily lives we are constantly making decisions about which objects to interact with and then perform reaches towards these objects and grasp them and move them about. The study of object manipulation therefore represents an important avenue for understanding motor behaviour, particularly related to movements of the upper limb.

Numerous studies have used lifting tasks or reaching tasks with hand-held objects to gain insight into the mechanisms supporting these basic behaviours. This work has shown that manipulation tasks can be broken down into various action phases, such as
grasping, lifting, and transporting of objects (Johansson and Edin, 1993; Johansson and Westling, 1984, 1987, 1988a,b; Westling and Johansson, 1987). Moreover, it has shown that such phases, and the transitions between phases, are well defined by stereotyped sensory feedback, which the brain exploits to afford flexible and adaptable manipulation (Johansson and Flanagan, 2009). Thus, the sensorimotor mechanisms underlying object manipulation has been an area of focus for researchers interested in understanding how the nervous system represents and organizes manual tasks. Within this framework, this thesis was designed to extend the scope of object manipulation studies by focusing on functional, object oriented tasks.

**6.1 Summary of studies and principle findings**

In study 1 we assessed the contributions of haptic and visual feedback when learning to manipulate a non-rigid object with internal degrees of freedom. We also assessed how learning with haptic feedback subsequently affected movements when haptic feedback was removed and vise versa. With this aim, we used a virtual environment where participants moved a mass via a simulated damped spring to a target as quickly as possible. The results from this study showed first, that participants could learn to move the object with or without haptic feedback; however, final performance was superior when haptic feedback was provided. Second, learning to move with haptic feedback improved subsequent movements without haptic feedback, yet the reverse was not true, where learning to move without haptic feedback adversely affected subsequent movements with haptic feedback. Indeed, these findings have implications for simulated training, such as for surgery, where haptic feedback is typically not provided.
In study 2 we assessed whether kinetic errors, represented by mismatches between predicted and actual load forces, were sufficient for learning the dynamics of a novel object. Participants made reaching movements to a target while grasping an object with novel dynamics. Errors in movement trajectory, i.e., kinematic errors, were reduced to near zero using a force channel, which confined movements to a straight path. Yet despite the absence of kinematic errors, participants still experienced kinetic errors that provided information about the object’s dynamics. During channel trials, it was found that participants learned to modulate grip force with load force indicating that successfully predicted the load force; however, the movement trajectories of subsequent movements in free space did not show improvement compared to initial movements in free space. These findings demonstrate the importance of kinematic errors for learning and also show that information about the object’s dynamics used for trajectory control cannot be extracted from grip kinematic errors.

In study 3 we assessed whether rapid, intelligent grip force responses could be elicited by visual perturbations that evoke rapid corrective responses of the limb. Participants performed reaching movements with a hand-held object attached to a position dependent load. On random trials, the cursor representing the grasped object or the target position could be displaced a short distance. These perturbations evoked rapid movement responses of the limb to bring the object cursor towards the target within approximately 150 ms. By design, these corrective movements also resulted in appreciable increases or decreases in object load force depending on the perturbation direction. We found that these rapid corrections of the limb were accompanied by similarly rapid grip force responses tuned to both the increase and decrease in object load force. These findings indicate that grip force adjustments, coupled to changes
in load force, are integrated into sensorimotor control policies that support rapid, or automatic, visually driven hand movement corrections during reaching.

In study 4 we assessed how movement costs and value influenced what targets to reach to. Using a virtual display, we presented participants with 15 targets composed of three different sizes and explicitly assigned point values. Participants were assigned the task of acquiring as many points as they could, in a fixed 3.25 s time period, by either reaching using a manipulandum (hand task) or by visual fixations (eye task). We developed a probabilistic model to predict target-by-target harvesting choices that considered rate of reward and costs associated with target distance and size for up to five future harvests in succession. We found that movement factors, such as target distance and size, were weighted more heavily in target choice for the hand task than the eye task. In addition, a greater number of future targets were taken into account in the hand task than in the eye task. These results indicate that decisions about what targets to move to, or harvest, were influenced by motor factors. As well, using a version of the hand task in which participants were required to acquire the targets in order of value, we found that participants were exceptionally skilled at choosing from amongst the shortest possible routes. Our results demonstrate that optimal foraging theory offers a useful framework for understanding choice behaviour in target-directed movements.

6.2 WHAT CONSTITUTES AN OBJECT?

6.2.1 Reaching with hand-held objects versus robotic handles

One of the motivating factors underlying this thesis was that developing object manipulation tasks is important for understanding motor behaviour, especially that of
the upper limb. This is because the majority of actions people perform with their hands are object-oriented. Therefore, a logical question that stems from this observation is what constitutes an object? For instance, numerous studies have used tasks where forces are applied to the hand via a robotic device (Caithness et al., 2004; Gandolfo et al., 2000; Mattar and Gribble, 2005; Shadmehr and Mussa-Ivaldi, 1994). Here the question arises as to whether these forces are interpreted by the nervous system as a change in arm dynamics (Shadmehr and Mussa-Ivaldi, 1994) or whether people learn to associate the forces with the grasped handle, effectively treating the handle as they would a grasped object. If the latter were true then many of these studies could be considered manipulation tasks to some degree. Other studies have applied novel forces, via cuffs, to the upper and lower arms (Krakauer et al., 1999; Nashed et al., 2012, 2014). Here again one can ask whether the nervous system interprets these forces as a change in arm dynamics or links the forces to the robotic device delivering these forces to the arm.

Davidson (2005) assessed whether loads applied to the hand, by gripping a handle, or arm, via cuffs, were represented separately. The authors showed that adaptation to a force field applied to the hand interfered with the previous adaptation of an opposing force field applied to the arm (and vice versa), and that this interference was just as strong as when both force fields were applied to either the arm or hand (Brashers-Krug et al., 1996; Caithness et al., 2004; Gandolfo et al., 1996; Shadmehr and Brashers-Krug, 1997). The authors concluded that the sensory cues associated with grasping were insufficient to separately encode the two opposing forces, thus supporting an internal representation of the dynamics that is independent of whether the forces were applied to the hand or arm. However, other studies have provided
evidence that novel force fields applied to the hand are attributed, at least in part, to the handle of the robotic device. Cothros et al. (2006) showed that loads applied to a gripped handle were not attributed to a change in arm dynamics, as demonstrated by a limited aftereffect following force field adaptation when reaching in free space without grasping the handle. Unlike Davidson (2005), where sensory cues of the robotic device were still present in both the hand and arm conditions, Cothros et al. (2006) eliminated contact forces completely by having participants reach in free space without contact with a robotic device, which produced aftereffects smaller than those produced during reaches with the robot in a null field. This finding suggests that the nervous system can largely attribute movement errors to the correct source, i.e., the robotic device and not changes in arm dynamics. Kluzik et al. (2008) further demonstrated support for this notion using a task where contextual features of the reaching task were more tightly controlled. Here, the authors found partial generalization to reaches in free space, indicating that there is likely some overlap between an internal model that captures object dynamics and one that captures limb dynamics. The authors note that while this question has fundamental implications for how the nervous system represents perturbation tasks, it also has implications for rehabilitation where robotic devices are used to teach people how to move (Patton et al., 2006a,b; Reinkensmeyer and Patton, 2009).

In summary, it is clear that force perturbations that involve a moveable handle are at least partly attributable to a change in overall limb dynamics. Furthermore, the extent to which this generalization occurs is influenced by contextual properties associated with the task.
6.2.2 Harvesting objects versus visual targets

The fourth study was performed to better understand the factors influencing decisions about what targets to move to, and in what order, when selecting among alternatives. This study was developed within the context of object manipulation. Furthermore, we framed the study by explaining that manipulation tasks are composed of linked actions (Bowman et al., 2009), requiring movement decisions about where to move and when. This context begs an important question that is whether the visual targets used in the foraging study were represented by the nervous system as objects. First and foremost, our foraging task did not involve haptic cues, specifically associated with the objects themselves, which are fundamental to natural manipulation tasks. Second, our task did not involve any grasping of objects, with the exception of the manipulandum used to harvest the targets and that was used more as a tool and was not used to simulate the qualities of the objects themselves. Despite these limitations, we feel that the foraging task nevertheless captured an important aspect about manipulation tasks that has not often been studied; namely, decisions about the selection of targets to act on. Specifically, the decisions probed using the hand foraging task were explicit movement-decisions where different choice options required very different biomechanical requirements. Furthermore, these decisions needed to be successively linked to accomplish an overall goal (in this case gather as many points as possible), similar to natural manipulation tasks.
6.3. Future directions

6.3.1 Quality of haptic feedback

In study 1 we assessed the contributions of haptic feedback to the learning of non-rigid objects. One of the principle findings was that initially learning without haptic feedback had persisting detrimental effects even when subsequently learning with haptic feedback. In our study, we posited this has potential implications for virtual reality training systems such as those used in surgical training (Basafa and Farahmand, 2011; Lim et al., 2009), for example, if trainees train on a simulator without the provision of haptic feedback and then perform the real task. However, what our results do not cover is whether the quality of haptic feedback affects this generalization from virtual reality to the real world. Therefore, it is useful for future studies to manipulate not only whether haptic feedback is present or absent, but also the quality or extent to which haptic cues simulate real world sensation. This consideration is important because constructing a virtual environment with haptic feedback is both difficult and costly. Therefore, if only certain haptic cues, e.g., contact events, are necessary to afford generalization to real tasks then this may make the development of such devices more cost effective and less complex to construct.

6.3.2 Grip force clamp trials

Study 2 we exploited force channels to create trajectory error clamp trials that removed errors in the movement path by constraining the path to a straight line. However, there is no equivalent technique for clamping errors in grip force; i.e., there is currently no experimental manipulation to generate load forces equivalent to the expected load forces of the participant; e.g., to apply a load force that is appropriate
6.3. FUTURE DIRECTIONS

for the grip force applied by the participant. For this reason, and in the context of study 2, we were unable to assess the sole contribution of kinematic errors, in the absence of kinetic errors, to trajectory adaptation. A technique that allows one to clamp grip force errors would be a very useful tool for 1) assessing the contribution of kinematic errors to trajectory adaptation and 2) for probing feedforward grip force control independent of error-based learning (Wolpert et al., 2011).

There are several challenges for developing a protocol where grip force errors can be successfully clamped. First, it is difficult to predict what load forces participants expect. In contrast, participants tend to move straight so confining participants to straight ahead movements during channel trials successfully conform to participants’ intentions of moving straight (Shadmehr and Mussa-Ivaldi, 1994; Thoroughman and Shadmehr, 2000). Second, the load applied to the arm must be successfully dissociated from the load applied through the hand-held object. Although this was achieved in study 2 using our two-robot system, it could not easily be applied in the reverse direction so as to clamp grip force; i.e., supply object load force to a level expected by the participant with one robot, while applying a load to the arm with the other robot. Third, the simulated load force would have to be servo controlled, taking into account both grip force and friction. For instance, if the applied grip force was too high, subjects may increase their grip force, leading to an increase in load force, which would perpetuate this cycle and likely create a highly unstable situation.

6.3.3 Foraging tasks to probe neural mechanisms in decision-making

Previous decision-making tasks have tended to focus on perceptual tasks involving choices between competing options (Glimcher, 2001, 2004; Kahneman and Tversky,
6.4. CONCLUSIONS

1979, 1984; Trommershäuser et al., 2006; Tversky and Kahneman, 1974, 1981). However, these studies do not offer insight into movement decisions, such as what targets to move to, which presumably are linked to motor factors, such as the duration or difficulty of the movement. In study 4 we presented a laboratory foraging task that involved trading off movement factors, such as distance and size, against value. Because foraging theory was established in behavioural ecology, which examines behaviour in the real world, there is limited knowledge about the neural mechanisms supporting these behaviours. However the fact that foraging behaviour is found within a wide variety of species and contexts (Hills et al., 2012; Pyke et al., 1977; Stephens and Krebs, 1987; Thompson and Fedak, 2001) suggests there may be common neural elements supporting such behaviour. Foraging tasks such as ours have the advantage of being able to be applied in fMRI studies or studies involving non-human primates to probe the neural mechanisms supporting foraging type movement-decisions (Hayden et al., 2011; Kan, 2011; Kolling et al., 2012). Thus future research on decision-making would benefit from developing integrative tasks, such our foraging task that involves movement-decisions, which can be brought into the laboratory.

6.4 Conclusions

Most actions people perform on a daily basis involve interactions with objects, whether lifting, transporting, or choosing what to grasp. The study of such object-oriented behaviours is thus necessary for understanding motor behaviour, especially that of the upper limb. This is despite the dominance of aiming and reaching movements in the literature, which do not explicitly employ manipulation tasks per se. This thesis presents a series of studies that directly probe manipulatory function, or certain
components of manipulatory function, using integrative goal-oriented tasks that deal with how people cope with novel objects or decisions about what objects to move to. Together these studies extend the scope of what we know about how the nervous system organizes and represents object-oriented behaviours.

6.5 References


6.5. REFERENCES


