

VISUOMOTOR ADAPTATION: CONTRIBUTIONS OF AWARENESS, ONLINE
CORRECTION, AND SENSE OF AGENCY

by

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Abstract

Our sensorimotor system constantly monitors its performance, checking that movements unfold as intended, and modifying motor commands when error creeps in. When a systematic change in the environment is imposed, such as a shift in the visual feedback of the limb, the sensorimotor system adapts to this change, such that when the perturbation is removed the system initially responds as though the perturbation were still present (so-called ‘aftereffects’). The current project investigates some of the factors that influence how the motor system responds when a systematic perturbation is introduced: How do awareness, explicit control, online control, and our sense of agency affect motor adaptation? To address these questions I apply two types of perturbation: perturbation of the target (Studies 1-3) and perturbation of visual feedback of the effector (Study 4). In Study 1, I investigate how a person’s awareness that a target has been perturbed influences how they learn from the reach error that this perturbation introduces. The study shows that awareness of a target perturbation dramatically undermines adaptation. In Study 2, I investigate how explicit control of a reaching movement influences adaptation to an unperceived target perturbation. The study shows that adaptation occurs even when participants are engaged in the explicit task of undershooting the target, suggesting that implicit motor processing can proceed while the system is busy with an explicit motor task. In Study 3, I investigate the influence of online error processing on reach adaptation, and I show that people adapt to a target perturbation regardless of whether error occurs during (online) or at the end of their reach. In Study 4, I investigate how a person’s agency over their movement influences how they learn from perturbed feedback. The study shows that a small amount of adaptation occurs when people have their limbs passively moved – a result of a shift in perceived limb location. The four studies, together, suggest that both error processing and sensory recalibration can contribute to aftereffects, but they also suggest that sensory feedback prediction during active reaching is the most important component of adaptation.

Preface

Chapters 2 through 5 contain work that was conducted under the supervision of Dr. Chua and in collaboration with Dr. Franks and Dr. Inglis. For each study, I was responsible for the majority of the experimental design, data collection, data analysis, and written reporting of the findings.

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1 Introduction

Motor adaptation is vital to our ability to successfully navigate and act upon the world. We have multi-component, multi-jointed bodies that change as we age and fatigue as we move. We operate in changing environments and upon a variety of objects. Motor adaptation allows us to refine our actions and to adjust control as conditions and objects change: Consider the tennis player's ability to alter grip strength as his or her hand grows sweatier, to maintain accuracy and power as the limb tires, to even adapt to a new, heavier, racket when the first one breaks. We rely on our motor system to detect and correct movement error; if it did not – if our motor system could not change its output and adapt to changed environments and limb dynamics – motor function would soon become pointless. If one's ability to adapt suddenly disappeared, walking in boots after wearing sandals would become a staggering challenge, and switching from a dinner to a salad fork would create not only a mess, but possible facial wounds. Indeed, if motor control were inflexible, the mere act of growing up and acquiring larger limbs would produce a population of non-motile (and probably non-replicating) individuals.

The present research focuses on some of the mechanisms of motor adaptation. When we reach for a target, for instance, and miss it, how is this error signal processed for future learning? How does our awareness of the source of reach error influence how we learn from it? How is learning influenced by such factors as whether we explicitly control our reach and whether we correct our reach online? If visual feedback of our limb is perturbed, do we alter the perception of limb location during exposure, and, if so, is this change in perception influenced by whether we are actively moving our limb or having it moved for us? As these questions suggest, my research will focus on the adaptation of reaching movements; however, many of the principles that govern adaptation of reaching should be common to other types of movement as well.

The present research approaches these questions behaviourally. That is, I attempt to uncover principles of motor function by measuring the system-level output of human participants engaged in motor tasks. These tasks, which will be described in more detail later, generally involve exposure to a

visual perturbation of some kind, either a perturbation of the reach target or a perturbation of limb feedback. By examining how people respond to these perturbations and, even more importantly, how they respond after the perturbations are removed, we can make inferences about how people learn and how strong the learning is. In Chapters 2 through 5 I will describe, in detail, how these techniques were applied in four different studies and what the results of those studies tell us about human motor control and learning. A more general discussion of those studies' results will be undertaken in Chapter 6.

In the present chapter I will provide some background information on motor learning and adaptation, beginning with a brief discussion of the varieties of human learning and what it means to talk about motor skills and motor adaptation. I will go on to discuss some of the ways that motor adaptation has been investigated and some of the models that have been proposed for how the motor system adapts to certain kinds of perturbations. I will then present some of the previous research into motor adaptation and error processing that directly informs the research carried out here before, finally, providing an overview of each of the studies that I performed.

1.1 Motor learning, adaptation, and skill acquisition: defining terms

Finding a satisfying definition of motor learning can be surprisingly difficult. As for many constructs (e.g., attention, justice, intelligence), most people have a sense of what the term means and can engage in meaningful discussions about it, but are hard-pressed to provide a definition that captures its meaning without excluding phenomena that seem fitting or including ones that do not. I will try to avoid an extensive discussion of the 'best' definition of learning and will focus, instead, on how terms like motor learning, skill acquisition, and motor adaptation will be used in the present document. Prior definitions, however, may be a good place to start.

Schmidt and Lee (1999), authors of an influential undergraduate textbook on motor control and learning, describe motor learning as 'a set of internal processes associated with practice or experience leading to relatively permanent changes in the capability for motor skill'. This definition seems to focus largely on the acquisition of new and distinct skills (e.g., basketball dribbling,

juggling) and excludes phenomena such as adaptation (e.g., maintaining successful dribbling with a basketball that is slowly leaking air). Shadmehr and Wise (2005), authors of a computationally-oriented textbook on motor learning, opt for a less restrictive definition of motor learning. In fact, they explicitly avoid providing a rigid definition. Their idea of motor learning is one that includes skill acquisition, but also allows for phenomena such as adaptation, classical conditioning, and even changes in behaviour that occur across generations of organisms.

My use of ‘motor learning’ will fall somewhere between the foregoing definitions. Unlike Shadmehr and Wise, I will not consider behavioural changes that occur across generations to be a form of learning. Although I see no harm in considering cross-generational behavioural change as a form of learning, it is a form that would rely on fundamentally different processes than motor adaptation and skill acquisition, and so would only dilute the definition that serves the scope of the current project. More important is how my use of motor learning differs from that of Schmidt and Lee (1999). While I generally agree with their view that motor learning is a change in performance that arises from experience (a change that is not due to global factors like fatigue and arousal), I find their ‘relative permanence’ criterion too restrictive. The aftereffects of adaptation, for instance, may often be fleeting, possibly disappearing within a matter of a few trials, yet these effects suggest that the motor system has learned something very important about the relationship between its commands and their impact on the environment. Although this kind of learning may not involve the same processes as skill acquisition, it deserves to be considered learning nonetheless.

In short, I will treat adaptation as a form of motor learning. And, although this is not critical for the present work, I will also consider it to be closely linked to skill acquisition. The view I will adopt is one similar to Shadmehr and Wise’s (2005). They suggest that we might visualize the motor repertoire as an attractor landscape in which motor skills are attractors, and adaptation is the movement of attractors within that landscape. For example, a ‘reaching’ attractor might get shifted as one adapts to prisms, and then gradually shift back to its initial location once the prisms are removed. With practice, however, new attractors might be formed, such that, after repetition of a prism-

on/prism-off sequence, for example, one might develop a skill for reaching with those prisms. In other words, one maintains ‘skill attractors’ for prism-on and prism-off and can easily switch between them.

Having drawn a link between skill acquisition and adaptation, I should point out that certain kinds of skills, such as learning a sequence of actions for a motor task, may rely on very different regions of cortex than motor adaptations, with the former being linked to the striatum and the latter being linked to the cerebellum (Cohen and Eichenbaum 2001). Once a sequence has been learned, however, the refinement of the motor elements that make up that sequence probably relies on adaptive mechanisms in the cerebellum.

The focus of the present research, of course, is motor adaptation, and so skill acquisition will receive limited attention from here on. Motor adaptation is often understood as the reacquisition of normal motor function when one is exposed to altered conditions (e.g. Shadmehr and Wise 2005; Krakauer 2009). The term ‘adaptation’, then, focuses one’s attention on the altered conditions; it may give the impression of a special process that only occurs when a novel (perhaps, even, artificial) motor environment is introduced. However, the present work is motivated by the belief that the processes that underlie such adaptation are the same processes that are constantly operating to monitor and refine our motor output as we carry out everyday tasks in everyday environments with everyday objects. Using altered environments in an experimental setting simply allows us to probe these processes more effectively.

Operationally, adaptation is often defined by the presence of aftereffects. That is, in a typical adaptation protocol, motor performance is compared between a pre-test and a post-test, phases which involve normal action in an unperturbed environment. Between these phases is the exposure (or learning) phase, during which the participant experiences the perturbation of interest. Changes in motor performance between the pre-test and post-test are known as ‘aftereffects’. They are thought to reflect some sort of implicit change in the motor system as a result of the perturbation, for they occur

even when participants know that the perturbation has been removed and that they should simply perform the task as they normally would.

The present research uses aftereffects as a measure of adaptation; however, as will be discussed more extensively in Chapter 6, multiple processes may contribute to aftereffects. Depending on the nature of the perturbation and the nature of the task, exposure may produce error-based processing and/or sensory recalibration. Sensory recalibration might involve, for instance, a shift in one's proprioceptive sense of limb position after exposure to a visual perturbation. Although both error and sensory recalibration processes may lead to changes in motor performance, and thus be considered components of adaptation, I will only consider the first type of processing to be a form of motor learning. Thus, one might consider aftereffects to potentially be influenced by two kinds of adaptation: motor adaptation (a form of motor learning) and sensory adaptation (a form of perceptual learning). One of the issues that will be addressed in Chapters 5 and 6 is whether these processes operate independently.

I will be using the term 'adaptation' to refer to an associative type of learning, in which, for instance, the learner associates given motor commands with given sensory feedback, or, in the case of sensory adaptation, given proprioceptive feedback with given visual feedback. This contrasts with the way that adaptation is sometimes used (e.g., Squire 1987), where it refers to a non-associative habituation process, in which the neural response to a stimulus is simply attenuated, such as 'adapting' to the feel of the pebble lodged in one's shoe.

1.2 Kinds of memory and learning

Now that we have working definitions of motor learning and adaptation, it is worth briefly considering where these processes fit within the larger context of human memory and learning. Though memory researchers do not universally agree on how memory systems should be classified, one fairly influential model divides memory into declarative and procedural systems (Cohen and Squire 1980). Declarative memory underlies our explicit knowledge about the world; it stores information that we can consciously access and declare, such as the name of the person who taught us

to ride a bicycle. Of particular interest to the current research is the procedural memory system, which is thought to store, among other things, motor skills. So, while declarative memory would allow us to recall *who* taught us to ride a bicycle, the procedural memory system would allow us to implicitly recall *how* to ride a bicycle.

Subdivisions of the declarative and procedural memory systems have been proposed, wherein, for instance, the declarative memory system includes both semantic memory (factual knowledge about things) and episodic memory (knowledge about events in our own lives), and the procedural memory system includes memory involved in skills, priming, and classical conditioning (Eichenbaum and Cohen 2001). Unfortunately, most psychological research on memory has focused on non-motoric forms of learning and memory, so motor adaptation has not been explicitly placed within this framework, and whether it falls under the broad heading of ‘skills’ or should have its own category has not been addressed (e.g. Squire 1987; Eichenbaum and Cohen 2001; Budson and Price 2005). It seems clear, however, that motor adaptation should be considered a form of procedural learning (Fernandez-Ruiz and Diaz 1999).

1.3 Making predictions during adaptation

How we process sensory feedback during adaptation may depend, in large part, upon our expectations about the sensory feedback that our movements produce. Current models of adaptation implicate forward models and efference copy, which, together, are thought to allow the motor system to make predictions about sensory feedback. These predictions may also underlie our sense of agency over our actions, such that mismatches between our expectations and feedback lead to a reduced sense of action ownership. In this section, I will review some of the key concepts for understanding how prediction might play a role in learning and agency; I will also review some of the early research and thinking that led to the development of these ideas.

1.3.1 Reafference, exafference and efference copy

Von Holst and Mittelstaedt (1950) introduced the terms ‘reafference’ and ‘exafference’ to distinguish between sensory input that results from self-generated movement (reafference) and

sensory input that results from a change in the environment (exafference). The context for this distinction was Von Holst and Mittelstaedt's investigations into whether reflexive responses to sensory inflow are simply blocked during self-movement, or whether a different mechanism is at play (Von Holst 1954). At the time, it was known that a rotating visual environment would stimulate an insect to reflexively rotate in the same direction as the visual pattern. However, when the insect moved itself within a stationary environment, producing the same visual input as when the environment moved, the insect could move normally; the visual input would not cause it to reflexively move in the opposite direction. Prior to Von Host and Mittelstaedt's work this behaviour was attributed to a simple blocking of the reflex response during self-generated movement.

Von Holst and Mittelstaedt tested the reflex-blocking theory by rotating a fly's head 180 degrees, such that the flow of visual input across the retinas was opposite to the normal direction. If self-motion simply eliminated reflex responding, the head-rotated fly should be able to self-move without undue consequence (other than, perhaps, moving in the wrong direction). However, Von Holst and Mittelstaedt observed a breakdown in the fly's behaviour: it would rotate faster and faster in a given direction until exhaustion, caught, it would appear, in a positive feedback loop. Based on this evidence (and some related research on the righting reflex in fish (Von Holst 1954)) Von Holst and Mittelstaedt proposed the 'reafference principle'. They suggested that a copy of the motor command generated during self-movement (the efference copy) is stored and compared to the sensory feedback from the movement (the reafference). The efference copy is subtracted from the reafference, thereby canceling any sensation produced by the movement.

One can see how this principle might explain the fly's behaviour. A normal fly can move without reflexive anti-rotation because the visual pattern that would stimulate this reflex is cancelled by the efference copy. In the head-rotated fly, however, the efference copy and the reafference do not cancel each other. Instead, the reversed reafference and the incompatible efference copy have an additive effect because the two signals now have the same sign, rather than opposite ones. Von Holst

and Mittelstaedt proposed that the control system consequently increases the command signal in an attempt to compensate, but this only exacerbates the problem for the fly.

The reafference principle has been invoked to explain various perceptual phenomena in humans, such as the persistence of space constancy when we execute saccades. If the visual world rotates around us (imagine a pan shot during a film) we see a moving image. When the same retinal input is produced during a saccade, however, we perceive a stable visual scene. The reafference principle would imply that a saccadic efference copy is subtracted from the reafferent retinal input, thereby eliminating perception of world motion.

The possible role of efference copy during eye movements was raised by Helmholtz (1867/1925), who suggested that eye position sense was obtained from the motor outflow. The role of this outflow in maintaining space constancy across eye movements is sometimes demonstrated by comparing visual perception during active eye movement to visual perception during passive eye movement, which can be achieved by pushing the eye lightly with one's finger (Coren et al. 1999). In the first case the world appears stable, while in the latter it appears to move. This seems to be a compelling demonstration of the role of efference in the suppression of motion perception during saccades¹. Current evidence, however, suggests that saccadic suppression of motion relies mainly on a combination of magnocellular suppression (Burr et al. 1994), backward masking by the post-saccadic input (Matin et al. 1972), and the built-in assumption of world stability (Deubel et al. 1998) rather than a subtraction of efference copy from reafferent input. In sum, efference copy may be important for saccadic suppression (such as triggering some of the visual processing necessary for space constancy), but it does not appear to act in the purely subtractive fashion suggested by the reafference principle. (But see Cullen 2004; Pinel 2003).

¹ Bridgeman (2007) argues that the finger pressing manipulation does not, in fact, produce meaningful passive eye movement but, to the contrary, actually triggers efferent signals designed to stabilize the eye in the face of the perturbing pressure, and these signals produce the perceptual effect. Accordingly, the 'eye push' demo may not demonstrate what it is often purported to. However, it would still indicate that efference (in the absence of eye movement) has a perceptual effect.

However, the reafference principle may be an effective explanation of people's inability to tickle themselves (Weiskrantz et al. 1971). Blakemore et al. (2000) showed that people were better at tickling themselves when a delay was introduced between their movement and the tickle applied to them by a yoked robotic arm. The delay would theoretically reduce the ability of efference copy to cancel the reafference. Furthermore, when Blakemore and colleagues altered the spatial mapping between the participant's movement and the movement applied by the robot arm, the tickle effect increased. These results suggest that the degree of tickle is inversely related to the temporal and spatial correspondence between the motor command and the reafference, consistent with Von Holst and Mittelstaedt's theory that an efference copy cancels reafference.

Some of the strongest empirical support for the reafference principle is found in the electric fish (Bell 1982). These fish emit an electric signal into their surroundings but this signal presents potential interference to the processing of signals that are not self-produced. Efference copy allows them to cancel the reafference of their own signal such that it does not interfere with the processing of external signals. In his experiment, Bell deactivated the electrical discharge from the fish with curare, but was still able to record the efferent signal sent to the electrical discharge organ, a motor command that the fish spontaneously generates approximately 2 to 4 times per second. He was then able to manipulate the pairing of an artificial electric signal to the fish's motor command. In other words, the design allowed Bell to manipulate the presence/absence of reafference, the timing of reafference with respect to the command, and the magnitude of reafference. Critically, Bell simultaneously recorded the neural activity in a sensory processing center of the fish's brain. He could, accordingly, examine the response of these cells when no reafference was presented and thereby observe the effect of the efference copy on the cells' activity.

Bell found that the efference copy produced a response in the cells that was opposite to their response to sensory input alone, strong evidence for a canceling effect of the efference copy. Furthermore, Bell demonstrated remarkable plasticity in the cells' responses. They would only modulate their response to the efference if there had been previous pairing between the motor

command and sensory input. During these pairings, the lag between the command and the efference (the artificial electric stimulus) could be changed, and this lag would then be reflected in the test response². The test response was when no electric stimulus was presented and only the neural response to the efference copy was measured. In other words, if the lag was varied during the pairings, the delay would be reflected in the timing of the efference copy's dampening effect. Moreover, when the magnitude of the artificial stimulus was increased during the pairings, the magnitude of the efference copy's effect was also increased. These results illustrate the reafference principle in action, and they simultaneously demonstrate that sensory prediction (efference copy) can be trained by the reafference. Such 'prediction training' may be a critical process in human motor learning, as well.

What is the efference copy? Its name suggests that it is simply a copy of the command signal, implying that it codes a motor representation. However, for the reafference principle to work, the efference copy has to be capable of canceling the reafference, and this suggests that it needs to have the same representational format as the reafference, which is sensory. Accordingly, either the efference copy must be converted into sensory format or the reafference must be converted into motor format. Some computational approaches to motor behaviour, which are discussed in the next section, solve this problem with a 'forward model'. A forward model is an internal representation of an effector that allows the system to estimate the effect of a motor command on the output of the system. In so doing, it converts an efference copy into a sensory prediction. Such a model can have important implications for biological systems, not only for learning, but for rapid online control as well. Indeed, the idea that forward model predictions that occur during online control might concurrently impact learning is taken up in the 3rd study of this thesis (Chapter 4).

² However, the lag could not exceed 80ms. Outside of this window, the stimulus was, presumably, no longer interpreted as reafference by the fish.

1.3.2 Forward models in motor control and learning

One of the difficulties that our sensorimotor system must overcome, particularly during on-line control of a rapid movement, is the inherent delay in receiving sensory feedback. Due to relatively slow neural conduction speeds, biological systems receive delayed reafference from the moving limb (Wolpert et al. 2001; Jordan 1996; Desmurget and Grafton 2000). Interestingly, this is one area where robotic movement control, which profits from almost instantaneous signal conduction, has an advantage over human control (Jordan 1996). In humans, the delayed feedback introduces a control problem: by the time it is processed, the limb has moved to a new location and the feedback is no longer viable. Control theories have proposed the forward model as a means of redressing this problem.

The forward model is an internal representation of an effector system. The forward model uses a copy of the command signal to estimate the impact that it will have on effector output. This estimated output can then be used to inform the system about the current and upcoming state of the effector, ahead of the delayed reafference. Current theories of limb control in humans suggest that efference copy is fed into a forward model and then combined with available sensory information to obtain an optimal estimate of the limb's current state (Wolpert et al. 1995). It has been suggested that this prediction can be used to drive rapid on-line corrections of aiming movements (Desmurget and Grafton 2000; 2003) by estimating not only the current state of the limb, but also its future state. At very early stages of the movement, the forward model could be used to compare the predicted endpoint of the effector to the current target position. The error between these points could then drive online control.

Empirical support for the role of efference copy in online control can be found in a study involving a deafferented patient who was able to make on-line corrections to a perturbed target without vision of the limb (Bard et al. 1999). In the absence of proprioception, vision of the limb, and knowledge that the target had jumped (the displacement was saccadically suppressed), forward

modeling of the efference copy may be the only signal that would have enabled an estimate of limb position with respect to the target and permitted the patient to modify the limb's trajectory.

The forward model serves another purpose. By converting a motor signal into a state estimate, it allows direct comparison between the motor signal and the reafference, which are initially in different representational formats. This would not only permit the efference-based cancellation of reafference, as alluded to in the previous section, but would also allow the system to directly learn about error in the prediction (due to the forward model) and/or error in the motor command (due to the inverse model). These error signals could then be used to train the internal models (Ramnani 2006).

The inverse model, like the forward model, is an internal representation of an effector system. However, it works in the opposite direction; rather than predicting the sensory outcome of a motor command (the job of the forward model), the inverse model designs a motor command to achieve a desired outcome. The inverse model, accordingly, operates during the earliest stages of motor control. Its input is the desired outcome of the movement and its output is a motor command plus an efference copy. The motor command operates on the effector, while the efference copy is fed into the forward model. Figure 1.1 provides a schematic of such a control system, with the inputs, outputs, internal models and error signals that are potentially involved in goal-directed action.

1.3.3 Sensory predictions and sense of agency

One of the roles of efference copy and the accompanying forward model predictions of sensory feedback may be to help us determine whether the feedback we receive is a result of our own actions or from some external source. In the electric fish, for example, the cancelling of self-produced electrical impulses by the efference copy is thought to allow the fish to detect impulses that arise from the environment. And, as mentioned earlier, humans' inability to tickle themselves is thought to reflect a similar type of efference copy-based cancellation of self produced feedback (Weiskrantz, et al. 1971).

The reafference principle suggests, in other words, that how we label feedback (self/other) is dependent on how well it matches our internally-generated feedback prediction. Of course, sense of agency is a relatively complex phenomenon that may rely on multiple processes, only one of which might involve comparing sensory prediction to sensory feedback (Synofzik et al. 2008). For instance, a conceptual judgment about whether or not movement feedback is or is not our own may rely on factors such as knowledge about whether anyone else is present who may be a plausible external source for the feedback (Synofzik et al. 2008). Still, the reafference principle does appear to provide a reasonable hypothesis for how a component, at least, of our sense of agency may arise (Frith et al. 2000; Frith 2005).

Sense of agency is potentially an important factor during motor learning, for whether or not an actor attributes the error in a movement to themselves or to an external source should impact if and how much they learn from it. As an example, consider the simple act of swatting a fly. If we see the fly jump while we reach for it (and miss it) we probably learn differently from our error than if we reach for, and miss, a fly that appears to remain stationary. In the first instance, we would presumably attribute the error to an external source (the fly), whereas in the second instance we would attribute it to ourselves. Even though the magnitude of the terminal error might be equivalent in both cases, one might expect internal model updating to occur only in the latter instance. A test of this hypothesis is taken in up Study 1 (Chapter 2).

If the foregoing claims about motor learning and sense of agency are correct, then not only would efference copy potentially play a role in both motor learning (Figure 1.1) and sense of agency, but its role in sense of agency would, in turn, influence learning. This does, however, lead to somewhat of a paradox: If sensory feedback that is not cancelled by efference copy is labeled as externally-derived and if externally-derived error is not relevant to learning, then relevant error signals should never arise (and motor learning should never occur). Clearly, there must be some flexibility within the system, by which it allows for a certain amount of error between prediction and outcome while still labeling the action as self-generated. Indeed, the system probably rarely operates

in an all-or-none fashion, but rather may weight the learning signal based on how much of the error it attributes to itself versus the environment (Wei & Kording, 2009). The next section discusses this idea in more detail.

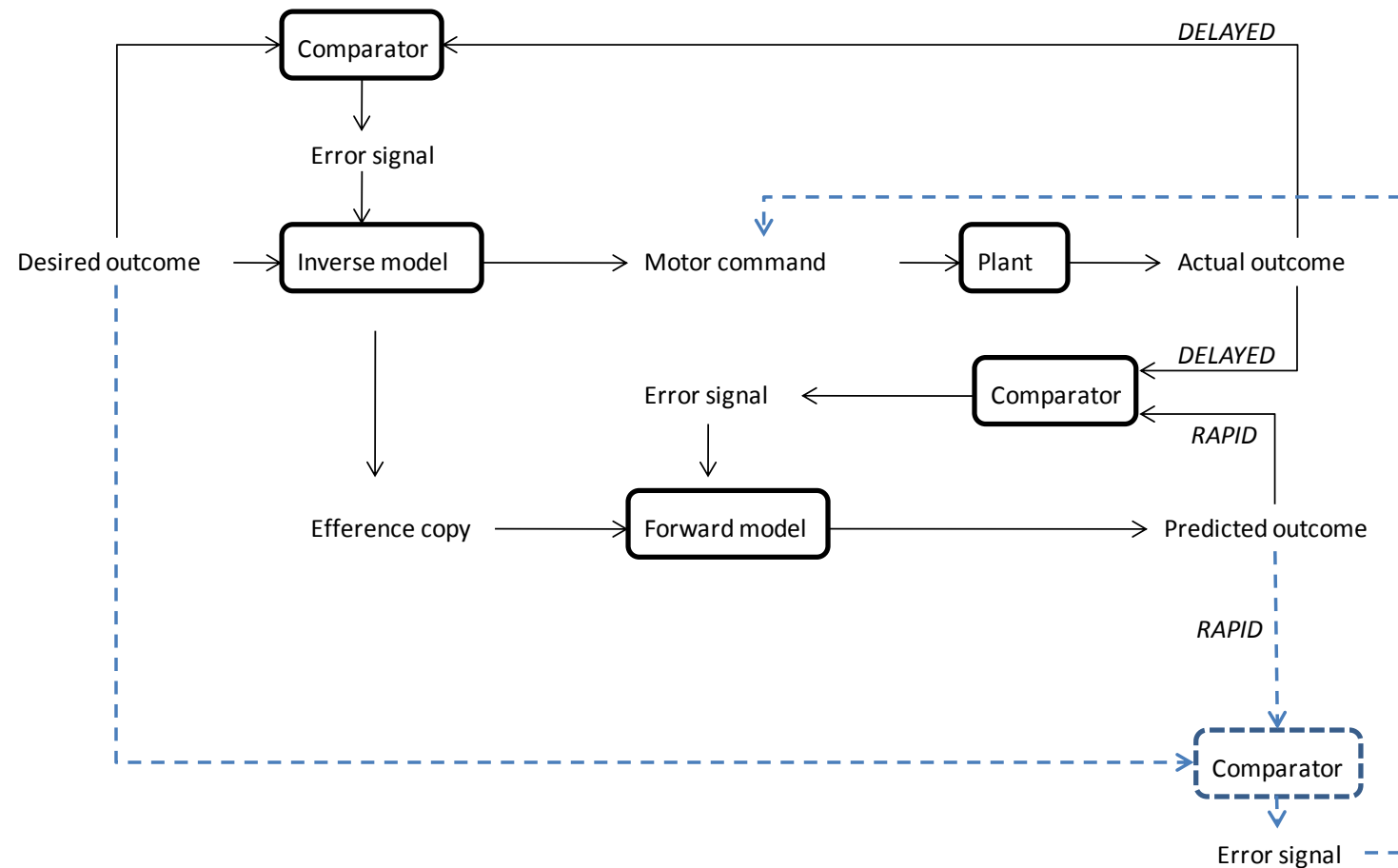


Figure 1.1 Possible functional components of a human motor control system. The solid lines indicate a mechanism by which the inverse and forward models would be trained by the motor output. The dashed lines indicate a mechanism for rapid online modification of the command signal, in which the predicted outcome of the movement (derived from the forward model) is compared to the desired outcome. Note that this process avoids the sensory delays incurred when the system relies on the actual movement outcome for error feedback. [This schematic is informed by Gauthier et al. (2007), Sabes (2000), and Desmurget and Grafton (2000).] Although I have drawn separate learning routes for the forward and inverse models, it is possible that inverse model training operates via the forward model (i.e., a single error signal trains the forward model and then the inverse model) (Gauthier et al. 2007; Wolpert et al. 2001).

1.3.4 Feedback expectation and error attribution

One of the themes of the present document is that our expectations about movement feedback influence how we learn. In the case of error attribution, the degree that we attribute error to ourselves versus the environment should be reflected in how we adaptively respond to the error. Recent work by Wei and Kording (2009) examined this idea by manipulating the size of the error in a goal-directed aiming task. Effector location was represented by a cursor, and the separation between the cursor and the target at the end of the movement (i.e., the error) could vary among 1, 2, 4 and 8 cm. If the relevance of the error signal were not a factor (i.e., if degree of adaptive response was simply related to the size of the error and not at all to considerations of agency), the adaptive response should have linearly increased with increasing perturbation size. However, Wei and Kording showed that the weighting of the error signal was reduced when the error became larger, consistent with the idea that people are less inclined to treat larger errors as entirely self-generated.

That finding is consistent with research by Michel et al. (2007), in which it was shown that participants exposed to the sudden onset of a large prism perturbation adapted less effectively than did those who were exposed to incremental increases in the size of the prism perturbation. The large prism perturbations made participants aware that their vision was being displaced, presumably causing the participants to attribute less of the reach error to themselves.

1.4 Prism adaptation: method and theory

1.4.1 An introduction to prism adaptation

We can investigate motor adaptation by perturbing the system's established relationship between motor commands and sensory feedback and then observing how the system responds to the new relationship, and one of the ways that this can be accomplished is by having people view the reaching environment through displacing prisms. Although none of the experiments in the present thesis employ prisms, prisms have been used extensively in prior research on motor adaptation, and so a brief overview of how prisms influence reaching is worthwhile.

When people wear displacing prisms, the prisms shift the visual scene by a certain number of degrees to the right or left. For example, if you view an apple through rightward displacing prisms, you will perceive the apple's position as rightward of its actual position. Then, when you reach for the apple, your arm will move as though the apple *were* to the right, and your reach will miss the actual apple, which lies to the left of where you reached (Figure 1.2).

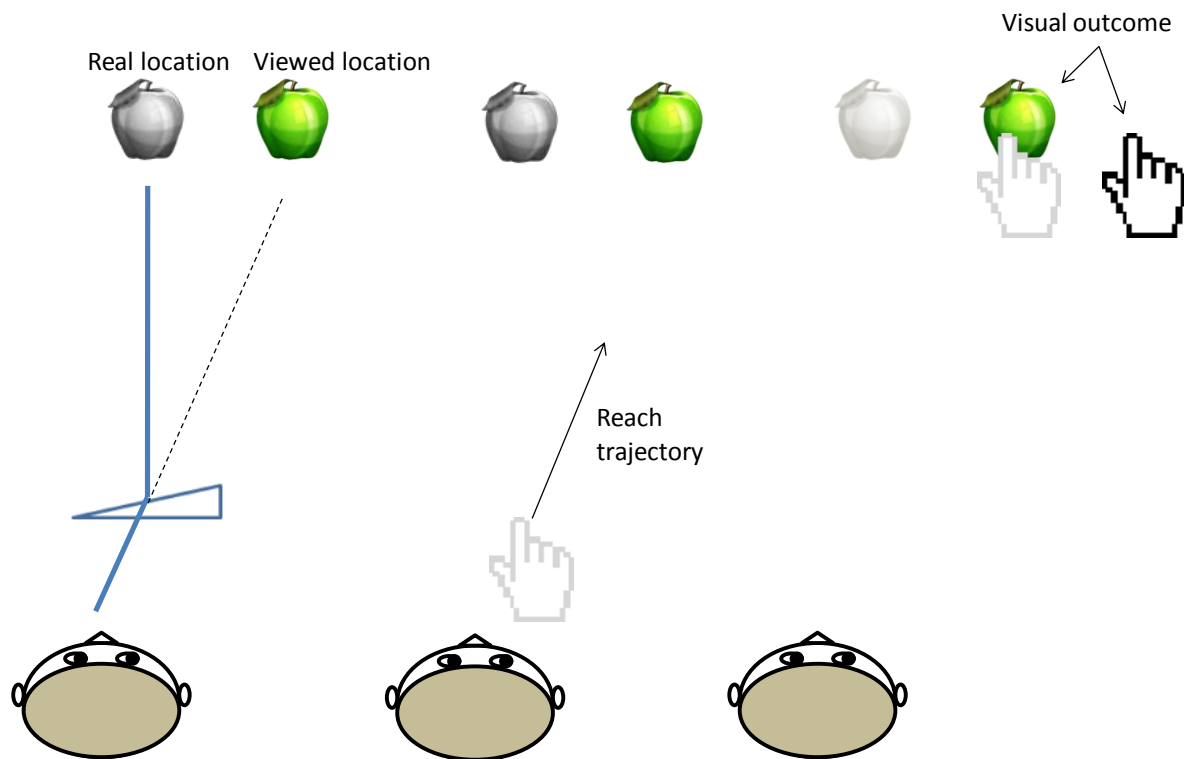


Figure 1.2 Schematic of reaching while viewing a target through displacing prisms.

Notice that the prism perturbation has multiple effects on the movement. The perturbation produces spatial separation between the hand and the target (allocentric error), but the prisms also produce error between the *expected* and *viewed* locations of the limb relative to the body (egocentric error). In other words, even if there had been no reaching target, there would still have been disagreement between the predicted and received visual reafference of the limb. It is also worth

noting that the prisms only perturb visual reafference; proprioception is not directly affected by the prisms, so the prisms have produced conflict between visual and proprioceptive reafferences.

1.4.2 Held's reafference hypothesis and prism adaptation

In an attempt to explain how exposure to a visual perturbation leads to behavioural change, Held and his colleagues, drawing upon Von Holst and Mittelsteadt's reafference principle, proposed that participants build up an association between motor commands and altered reafference. Accordingly, participants must be actively moving for adaptation to occur; mere exposure to the visual perturbation, in the absence of active movement, should not lead to adaptation. To test this hypothesis, Held and Hein (1958) had participants complete a manual target localization task (no hand vision) before and after exposure to a prism perturbation. They employed an apparatus designed by Held and Gottlieb (1958), in which participants would view a mirror reflection of the targets during the pre and posttest phases, a mirror which also occluded vision of the hand while the participants marked each of the target locations. During the exposure phase, the mirror would be replaced by a displacing prism, which would shift vision of the limb as participants either actively moved it or had it passively moved by the experimenter (Held and Hein 1958). Importantly, there was no visual target during the exposure phase (unlike in the apple example I provided earlier), so direct hand-to-target error processing was not a factor in the adaptation. Held and Hein observed a statistically significant negative aftereffect following active exposure to the visual perturbation, but not following passive exposure. They took this as support for their reafference hypothesis, and other prism experiments by Held and others that show greater adaptation for active than for passive exposure (though not necessarily an absence of adaptation from passive exposure) support this view (Held and Schlank 1959; Pick and Hay 1965; Foley and Maynes 1969). However, some prism adaptation studies have shown equivalent adaptation for active and passive exposure, complicating things somewhat (Singer and Day 1966; Fishkin 1969).

I will not attempt, here, to account for the different findings that have arisen from prism studies of active and passive exposure. However, one of the arguments that I will propose over the

course of this document is that adaptive effects of visual perturbations that alter effector feedback produce two, possibly independent, effects: sensory recalibration and error-based learning. The adaptive effects that some researchers have observed following passive exposure are potentially the result of sensory recalibration, while the adaptive effects following active exposure may involve both sensory recalibration and error-based learning. This issue will be taken up again, and in greater depth, in Chapters 5 and 6.

1.4.3 A model for prism adaptation

Shadmehr and Wise (2005) provide a nice model for prism adaptation, one that provides a helpful framework for conceptualizing what processes might be occurring in the sensorimotor system during exposure to such a perturbation. Before describing their model, however, I will briefly go over some of the terminology and concepts that are helpful for understanding it.

Shadmehr and Wise (2005) approach reach control from a perspective that assumes that the sensorimotor system requires knowledge of the end effector location relative to the target location³. The end effector could be anything from the empty hand to a gripped tool to a cursor on a computer screen; however, for simplicity I will simply refer to the hand when discussing the end effector. The system typically relies on vision to acquire an estimate of target location and it relies on proprioception (and often vision, too) to acquire an estimate of initial hand location. In order for the system to estimate hand location from proprioception, it uses a location map, which encodes the relationship between joint angles (e.g., at the shoulder and elbow) and the corresponding location of the hand. This location map, therefore, allows the system to compute hand location, probably in visual coordinates, from sensed joint angles. Once the system has estimates of the hand and the target locations, it computes a difference vector. This difference vector must then be transformed into the requisite changes in joint angle for transporting the hand from its initial location to the target. This

³ Currently, this is a relatively uncontroversial perspective, but it does differ with perspectives that suggest that knowledge of end effector location is not required for reach control, such as the Equilibrium Point model (Polit & Bizzi, 1978).

transformation relies on a displacement map, which encodes the relationship between difference vectors and changes in joint angle.

Each of the transformations discussed so far are kinematic transformations, as they relate joint angle coordinates to end effector location/displacement. Dynamic transformations, which are involved in the conversion between desired changes in joint angle and the requisite torques for achieving those changes, are not thought to be influenced by prism adaptation, as prisms do not alter the dynamic characteristics of the arm. For completeness, however, note that after the difference vector is transformed into changes in joint angles by the kinematic displacement map, a dynamic map would subsequently be engaged to convert these desired joint angle changes into the torques that would need to be applied to the limb to achieve them.

In Shadmehr and Wise's model of prism adaptation it is the location map and the displacement map that are influenced by exposure to the prisms. At the end of an early exposure reach, two things occur: 1) the visual and proprioceptive estimates of final hand location are in disagreement, and 2) the hand fails to reach the target. With respect to the first source of error, the system assumes that the proprioception-based estimate of hand location is in error, and so the location map is subsequently updated. In other words, the location map is brought into alignment with the visual estimate of hand location. This might alternatively be referred to as proprioceptive recalibration. With respect to the second source of error, the system assumes that the target was missed because the difference vector was not correctly transformed into joint angle changes, and so the displacement map is subsequently modified.

The displacement map and the dynamics map that were mentioned in the foregoing paragraphs can also be thought of as internal models that can carry out kinematic or dynamic transformations, respectively. Furthermore, these transformations could be carried out either in a backward (inverse) or forward direction. So far, I have been discussing movement planning, and so have focused on the inverse transformations: difference vector to joint angle changes; joint angle changes to torques. However, when it comes to making predictions about how a motor command will

influence feedback, the transformations would go in the opposite direction: the outgoing motor commands would produce torques that would lead to certain joint angle changes; these joint angle changes would produce a displacement vector that would produce given visual feedback of the hand.

The studies that I carried out, and which are described in the subsequent chapters, involve only visual perturbations, either of the target or of the effector, and so dynamic internal models can be assumed to remain stable during perturbation exposure. Kinematic internal models (or maps) are the sites of interest for the current research.

1.5 Other kinds of perturbations

So far, I have focused on prism perturbations as a way to investigate adaptive mechanisms in the motor system. However, prisms do have some drawbacks, one of which is that they simultaneously create multiple sources of error. As mentioned earlier, prisms create error between the target and the hand, they create error between the expected and received visual feedback of the hand relative to the body, and they create conflict between visual and proprioceptive feedback about hand location. Furthermore, prisms shift the visual location of the target, not just feedback of the effector, and they can lead to changes in eye orientation that may influence motor output (Welch 1986; Redding et al. 2005).

Another type of perturbation that is often used for investigating motor adaptation involves displacing visual feedback of the effector with a projected cursor. In this case, vision of the real effector is occluded, and only vision of the cursor is available. This type of perturbation, which allows for the investigation of rotation, translation, or gain modifications in effector feedback, introduces the same types of error that prisms do; however, this type of perturbation does not alter the location of the target and does not lead to changes in eye orientation. Study 4 of the present document (Chapter 5) applies a cursor perturbation for investigating feedback processing during active and passive movements.

Target perturbations, which have been used extensively for investigating the adaptation of saccadic eye movements (see Pelisson et al., 2009 for a review), have only recently been employed

for investigating the adaptation of reaching movements (Magescas and Prablanc 2006). One of the advantages of target perturbations is that, unlike prism and cursor manipulations, they do not introduce any visual-proprioceptive conflict. Therefore, they allow investigation of error processing contributions to adaptation in isolation. This type of perturbation is employed extensively in the present research (Studies 1, 2, and 3), and will be discussed in greater detail in the following section.

Adaptation can also be investigated with load or force perturbations, in which the dynamics of the effector are altered (e.g., Shadmehr and Mussa-Ivaldi 1994). These types of perturbation are useful for investigating the modification of dynamic internal models. However, such perturbations are not directly relevant to the current research and so will not be discussed in any detail.

1.6 Adapting to target error

One of the aims of this thesis is to understand how the sensorimotor system adapts to error between the effector and the reach target, independent of any visual-proprioceptive conflict. To investigate this type of error, I applied a protocol developed by Magescas and Prablanc (2006), in which the reach target is displaced either during or at the end of the reach. With this protocol there is no perturbation of the limb feedback, so it allows the researcher to investigate how target error, alone, influences adaptive processing.

In Magescas and Prablanc's (2006) study, participants completed pretest, exposure, and posttest phases, and adaptation was indexed by the difference between the pretest and posttest performance. In the pretest and posttest phases, participants looked and pointed to a target that appeared in their right visual periphery. As the eyes began to move, the target disappeared, as did vision of the reaching hand. In the exposure phase, participants executed a similar look and point task; however, when the hand completed its reach, the target re-appeared and vision of the hand was re-introduced, such that participants could see the error between their hand and the target. Importantly, when the target re-appeared, it was shifted to the right of its initial location, but this shift was small enough that participants did not notice that the target had moved. Over the course of the exposure phase, participants generated larger and larger reaching movements, unconsciously

compensating for the target perturbation. Then, when participants performed the posttest phase, during which there was no longer any terminal feedback, they consistently overshoot the target location. These results suggested that reach adaptation could be induced by imperceptibly displacing the reach target. One of the questions that will be addressed in the first study of the present work (Chapter 2) is whether adaptation still occurs when the target perturbation is visible. Does awareness of the perturbation undermine adaptation?

1.6.1 Saccadic adaptation to target error

As mentioned earlier, target perturbations have been used quite extensively to investigate the adaptation of saccadic eye movements. In those studies, the target of the eyes is typically displaced while the eyes are in flight, such that when the primary saccade is complete, there is error between the fovea and the target location. After repeated exposure to such a perturbation, saccades adaptively increase or decrease their gain, depending on the direction of the systematic target perturbation (Pelisson et al. 2009; Hopp and Fuchs 2004). Furthermore, there is evidence to suggest that the eye-control system does not rely on direct foveal-to-target error for adaptation, but rather on the error between the predicted location of the target and the viewed location of the target after saccade completion. Bahcall and Kowler (2000), for instance, showed that saccades adapt to target displacements even when saccades deliberately undershoot the target location. The saccadic control system presumably predicts the visual signal that an undershoot of the target will produce; when a target perturbation causes the visual signal to differ with the predicted one, subsequent saccade programming is adaptively modified. One of the questions that will be addressed in the second study of the present work (Chapter 3) is whether hand movements exhibit similar predictive processing when they adapt to target error.

1.6.2 Adaptation to online target error

Magescas and Prablanc's (2006) reaching study effectively demonstrated that adaptation could be induced in the hand in the same way that it could be induced in the eye. Of course, unlike the eye, which moves too quickly during a saccade to permit much, if any, online control, reaching

movements can be corrected online. Does this capability for online correction alter the way in which reaching movements adapt to target error?

In Magescas and Prablanc's (2006) study, online correction of the limb to target error was precluded by presenting target error only after the hand movement was complete. Recall that in the exposure phase the perturbed target (and the hand) only reappeared once the hand had landed. But what if the target had been displaced while the hand was in flight? Presumably the hand would correct its trajectory and land at the target location. We know that online corrections to target perturbations can occur very rapidly, even without vision of the limb or knowledge that the target has moved (e.g., Goodale et al. 1986; Prablanc and Martin 1992). Would repeated exposure to this type of perturbation induce adaptation in the same way that the terminal error of Magescas and Prablanc's (2006) study did?

Research by Diedrichsen et al. (2005), in which the adaptive effects of a target perturbation were compared to the adaptive effects of other types of perturbations, suggested that people adapt minimally, if at all, to a target jump that occurs during the movement. However, in that study the target perturbation was visible, which probably inhibits the attribution of error to the actor and, accordingly, prevents adaptation.

One might expect, on the other hand, that an *invisible* target perturbation would allow for reach adaptation, for reach error would be attributed to the actor rather than the environment. I tested this hypothesis in a preliminary study (Cameron et al. 2008, outlined in Appendix A of the current document), and the results suggested that movement planning could be influenced by repeated exposure to unseen online target error. However, that study suffered from some problems, among which were a low-sensitivity posttest protocol and a failure to control for the possible transfer of saccadic adaptation to the reaching hand⁴.

⁴ In order to make the online target perturbation invisible, it must be paired to the orienting saccade (Bridgeman et al. 1975); however, repeated exposure to this perturbation may lead to saccadic adaptation. This saccadic adaptation might then transfer to the reaching limb, such that any reach aftereffects from the online target error might actually be a side-effect of saccadic adaptation, rather than reach adaptation in its own right.

A recent study by Magescas et al. (2009) used a more effective design to measure the effects of online target error on reaching; their study controlled for the possible influence of saccadic adaptation by exposing the eyes to forward and backward target jumps, while only exposing the hand to forward target jumps. With this protocol, the eyes should develop a net adaptation of zero, while the hand, if it does adapt, should adapt in the forward direction. The results of their study suggested that online target error, unlike terminal error, does not produce any adaptation in reaching.

As will be discussed in Chapter 4, however, there are some problems with Magescas et al.'s (2009) design that may have led to their failure to see any adaptation to online target error. In the study outlined in Chapter 4, I attempt to address some of those problems and to re-examine the question of whether the reaching limb does adaptively respond to online error.

1.7 Overview of thesis experiments

1.7.1 Study 1: Reach adaptation to explicit versus implicit target error

This study examines the influence of target displacement visibility on reach adaptation. Participants completed an adaptation protocol similar to the one designed by Magescas and Prablanc (2006) in which target error is presented at the end of the reach during the exposure phase. Unlike that study, however, the visibility of the perturbation was manipulated by delaying the offset of the initial target location until either the completion of the saccade or the completion of the reach. The hypothesis was that the more visible the target displacement, the less inclined participants would be to attribute reach error to themselves and, as a consequence, the shorter the duration of the aftereffects would be.

1.7.2 Study 2: Implicit motor learning from target error during explicit reach control

The goal of this study was to determine whether adaptation to target error can occur when the reaching movement is under top-down control. This study, like the first, employed a target error protocol modeled after Magescas and Prablanc (2006). However, instead of aiming directly to the target, participants were instructed to undershoot the target by a given distance. As the size of the target perturbation was increased, so too was the instructed undershoot distance, such that participants

continually aimed to the same location in egocentric space. If adaptation (indexed by aftereffects) were to occur under these conditions, it would suggest not only that explicit control does not inhibit implicit processing of target error, but also that feedback prediction plays a role in the adaptation, the reasoning being that if direct hand-to-target error were the critical signal, adaptation would not occur during successful reach undershooting (Bahcall and Kowler, 2000).

1.7.3 Study 3: Reach adaptation to online target error

This study was designed to test whether target error that occurs during a reaching movement leads to a modification in the way that future movements are planned. In this study, participants looked and pointed to a target that was displaced imperceptibly as the movement unfolded, and the aftereffects of this online target perturbation were examined. The emergence of aftereffects following exposure to online target error would suggest that adaptation can occur even when there is no visual error between the hand and the target. This might, in turn, suggest that the error signal that is generated to correct a reach online (which has been argued to arise from predictive forward modeling) might have an adaptive influence on the motor system.

1.7.4 Study 4: The adaptability of movement perception and movement control when the limb is actively versus passively moved

This study differs from the previous ones in that it focuses on the adaptive effects of effector perturbation instead of a target perturbation. This study deliberately introduced a conflict between visual and proprioceptive reafferences and examined how this conflict influences both how we consciously perceive our movements and how we control them. Participants were exposed to a cursor that represented the movement of their index finger as they made extension-flexion movements about the elbow in the absence of a target. The gain of the cursor was increased, and the influence of this increase on participants' reports of limb movement (perception) and their reaches towards targets (control) were examined. Whether participants were actively moving their limbs or having them passively moved during exposure was also manipulated. With this method, we could determine

whether passive exposure leads to a change in the perceived limb position and whether this sensory recalibration subsequently influences active reaching to targets.

2 Reach adaptation to explicit vs. implicit target error⁵

2.1 Introduction

Our ability to learn new motor skills and to optimize the ones we already have relies on detecting error in our actions and modifying subsequent actions to compensate for that error. Consider, for instance, the actions of a novice astronaut, encountering for the first time the altered limb dynamics created by wearing a spacesuit in a weightless environment. Her first reach will probably miss its target, but over repeated attempts she will reduce and then eliminate reach error. When faced with novel reaching environments, people are very effective at adapting their movements: We adapt quickly to altered limb dynamics, such as when force perturbations are applied to the reaching limb by a robotic arm (e.g., Shadmehr and Mussa Ivaldi 1994), and we adapt quickly to altered visual feedback, such as when prisms rotate our visual field and alter the correspondence between motor commands and visual feedback (Welch 1986; Redding et al. 2005). The speed and ease with which we are able to adapt to these conditions suggests that the human motor system is highly flexible and is constantly primed to detect and eliminate movement error. How we process movement error, however, and the extent to which adaptation persists after a perturbation is removed, may depend greatly on the extent to which we attribute the error to ourselves.

A key determinant of whether we attribute error to ourselves may be the perceived stability of the target of our reach. If, for instance, a target visibly jumps to a new location while we are reaching for it, we might process the reach error differently than if the same amount of error occurred when we reached to a stationary target. In the first case we would, presumably, attribute the error to the behavior of the target (such as when a fly jumps away when we attempt to swat it), while in the latter case we might attribute the error to ourselves – our visuomotor system might conclude that it issued an incorrect command. Diedrichsen et al. (2005) have provided behavioral and neural evidence that these two kinds of error are processed differently. They showed that people adapt less when a target

⁵ A version of this chapter has been published: Cameron BD, Franks IM, Inglis JT, Chua R (2010) Reach adaptation to explicit vs. implicit target error. *Exp Brain Res* 203:367-380

visibly jumps at movement onset relative to when visual feedback of the hand is rotated. Similar amounts of reach error are produced in the two conditions, but participants appear to adapt more when the trajectory of the reach, rather than the position of the target, is perturbed. Diedrichsen et al. also showed that neural activity differed, to some extent, when participants responded to these two types of error; when the target moved, greater activity was observed in the superior parietal lobule and in the striatum.

The results of Diedrichsen et al. (2005) are consistent with the idea that the presence of a visible target jump alters the way we attribute error and, consequently, how we learn from that error. One would predict, therefore, that if a target jump is rendered invisible, reaching movements should adapt to the reach error that the target jump produces. However, the story appears to be somewhat more complicated: Unseen target perturbations seem to produce adaptation if the target error is presented at completion of the movement (Magescas and Prablanc 2006), but not if the target error occurs while the hand is in flight (Magescas et al. 2009).

Magescas and Prablanc (2006) demonstrated adaptation to terminal target error in an experiment where they asked participants to look and point to a target that disappeared with the onset of their eye movement. When the hand landed, the target reappeared at a location slightly to the right of its initial location. Over multiple trials, the size of the shift gradually increased, as did the amplitude of the participants' reaching movements, even though the participants never became aware of the location change. In the posttest phase of the experiment participants exhibited very strong aftereffects (i.e., when visual feedback was removed, they continued to aim far to the right of target locations.) This contrasts with the effect observed when the target was moved *during* the eye and hand movement, allowing participants to correct their reach online. In this case no aftereffects were observed (Magescas et al. 2009), suggesting that an unseen target jump does not produce reach adaptation when it occurs online.⁶ Note that Magescas et al.'s (2009) experiment is effectively the

⁶ However, also see Bekkering, Abrams, and Pratt (1995). These authors show reach adaptation when pointing to an unseen target jump that occurs online, but they do not control for the effects of saccadic adaptation and

‘invisible’ equivalent of Diedrichsen et al.’s (2005) target jump condition, in which participants corrected their movement online to a visible target jump. Taken together, these two studies might indicate that online target error, whether explicit (visible target displacement) or implicit (invisible target displacement), prevents significant adaptation of the reach. The goal of the present study was to examine the role of perceived target stability in reach adaptation without the confounding effects of online error correction.

We attempted to manipulate perceived stability of the reach target in two ways: 1) by varying the timing of the target perturbation with respect to the eye and the hand and 2) by informing participants about the presence of the perturbation. We examined reach adaptation in 4 groups of participants, all of whom were directed to look and point to a target. For the first group (SacStart), we extinguished the target at the onset of the eye movement and re-illuminated it at hand touchdown, a protocol like the one used by Magescas and Prablanc (2006). For the second group (SacEnd), we extinguished the target *after* completion of the orienting eye movement, reasoning that acquisition of the target by the eyes would render its subsequent displacement (when re-illuminated at hand touchdown) more noticeable. For the third group (ReachEnd), we extinguished the target coincident with hand touchdown, immediately re-illuminating it at its shifted location. For the fourth group (Informed) we applied the same stimulus protocol as for the SacStart group, but also explicitly told participants about the presence and size of the target perturbations that they would be encountering. We hypothesized that reach adaptation would be most robust (i.e., show the strongest aftereffects) in the first group, as this is the group for which the target should appear most stable during the acquisition phase (Magescas & Prablanc, 2006).

2.2 Methods

In the present section we describe three experiments. We have divided the report this way to indicate that the ‘SacStart’ and ‘SacEnd’ groups were collected first (Experiment 1) and that a

they argue, in fact, that their results indicate transfer of saccadic adaptation to the hand. The Magescas et al. (2009) study, which deliberately prevented saccadic adaptation, can, therefore, be viewed as a purer test of reach adaptation to an unseen online target perturbation.

preliminary analysis of these data was carried out prior to designing the protocol for the 'ReachEnd' group (Experiment 2). The protocol for the 'Informed' group (Experiment 3) was designed after collection and analysis of the data from Experiments 1 and 2. However, the apparatus and procedures were identical (but for the critical experimental manipulations) across all groups.

2.2.1 Participants

For all experiments, participants were right handed, had normal or corrected-to-normal vision, and were naïve to the aims of the study. Participants were recruited from the University of British Columbia community, and their ages ranged between 18 and 36. All participants provided informed consent prior to participating. The study met the guidelines of the university's research ethics board and was conducted in accordance with the guidelines set by the Declaration of Helsinki

2.2.1.1 Experiment 1.

Twenty-two participants completed this experiment. The data for 3 participants could not be used due to errors in collection. Two participants were excluded for failure to follow instructions. Of the remaining 17 participants, 8 participated in the 'SacStart' condition (3 female, 5 male) and 9 participated in the 'SacEnd' condition (5 female, 4 male).

2.2.1.2 Experiment 2.

Eight participants, none of whom were involved in Experiment 1, completed this experiment. The results for one participant were not analyzed due to a program error that slightly altered stimulus timing relative to the other participants. The remaining 7 participants (3 female, 4 male) all completed the same condition (ReachEnd).

2.2.1.3 Experiment 3

Eight participants (5 female, 3 male), none of whom were involved in Experiments 1 or 2, completed this experiment.

2.2.2 Apparatus

The apparatus was the same for all experiments. An array of red light-emitting diodes (LEDs) was mounted above a half-silvered mirror, which in turn was mounted an equal distance above the

reaching surface (Figure 2.1). The optical geometry of the apparatus created the impression that the targets, reflected by the mirror, were in the same plane as the reaching hand. The half-silvered mirror allowed us to provide or remove vision of the hand by illuminating or extinguishing, respectively, a white light below the mirror. The reaching surface was a featureless white surface but for a circular home position (5 mm diameter) located at the bottom left corner. The surface and the home position were only visible when the light below the mirror was turned on.

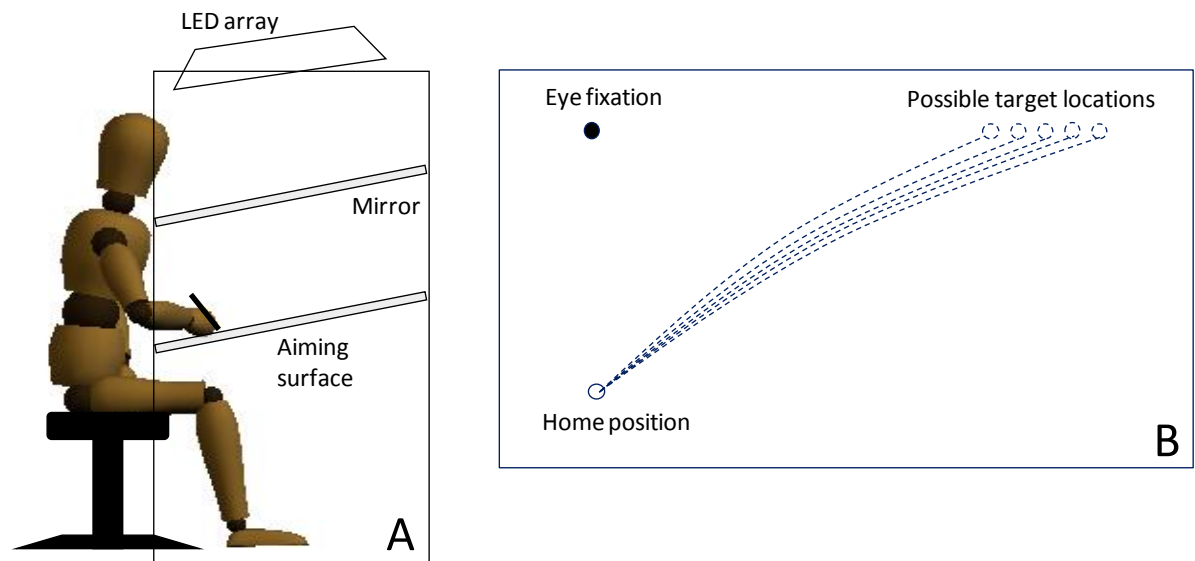


Figure 2.1 A) Schematic of the apparatus. LEDs at the top of the apparatus were reflected by the half-silvered mirror. The reflected stimuli appeared to be in the same plane as the hand. Vision of the hand was manipulated by illuminating/extinguishing white LEDs mounted below the mirror. B) Schematic of the stimulus display. Participants began each trial with the stylus at the home position and their eyes on fixation. A target appeared at one of the possible target locations, coincident with the offset of eye fixation. The dotted lines represent reach trajectories but do not reflect actual data. Reprinted with permission of Springer Science+Business Media.

An eye fixation point (5 mm diameter) was presented 13 cm above the home position at the start of each trial (Figure 2.1). The fixation point was projected from the LED array and could be extinguished simultaneously with the onset of a peripheral target. Target stimuli (5 mm diameter) were also presented by illuminating LEDs in the array. Targets could be presented at 5 locations, each separated by approximately 1.25 cm. The first target position was located 22.5 cm to the right of fixation; the second target position was located 23.75 cm to the right of fixation, and so on. Participants' eyes were located approximately 48 cm from the reaching surface. Accordingly, the distance between adjacent targets was approximately 1.5 degrees of visual angle.

Aiming movements were made with a handheld stylus with an infrared emitting diode attached near the tip. This allowed us to track the position of the stylus with OPTOTRAK (Northern

Digital), which sampled at a rate of 500Hz. The stylus was also equipped with a microswitch tip that allowed us to track movement start and end in real-time. Electrooculography (EOG) was used to monitor horizontal saccades. Disposable Ag-AgCl surface electrodes were placed at the outer canthi of the eyes with a reference electrode placed on the forehead. EOG signals were amplified (5-10K) and band-pass filtered (0.1-30Hz) using an AC preamplifier (Grass Instruments P511) and sampled at a rate of 500Hz. The EOG signal was passed through an analog circuit that enabled online triggering of stimulus events. For each participant we manually set a voltage threshold such that the trigger would occur within the first 3rd of the saccade.

2.2.3 Procedure

2.2.3.1 Experiment 1 (SacStart and SacEnd groups).

Participants began each trial with the stylus at the home position and their eyes at the fixation point. When the experimenter triggered the start of a trial, a warning beep sounded. After a variable fore-period (ranging between 1 and 2 seconds), the fixation point would disappear and a target would simultaneously appear in the visual periphery. The participant was instructed to look and point, smoothly and accurately, to the target. The light below the mirror was on at the start of every trial, such that the participant could view the home position and their hand. Each participant completed 10 practice trials prior to beginning the experiment.

The experiment was divided into 4 phases: a pretest phase, an acquisition phase, and 2 posttest phases. The pretest phase consisted of 50 trials in which a target would randomly appear at one of the 5 possible locations. When the eyes began to move, the target and the light below the mirror were both extinguished and remained off until the end of the trial (i.e., participants had vision of their hand and the target at the start of the trial only) (Figure 2.2). After the trial was over and the participant had begun to return to the home position, the light below the mirror was re-illuminated (750ms after lifting the stylus from its endpoint position) so that the participant could place the stylus at the home position. After completing the pretest, the participant was given a break as well as some additional instructions. Participants were told that the next trials would include visual feedback, such

that they would see their hand and the target at the end of the movement. They were instructed to approach each trial with the intent to minimize any error between their hand and target that they had seen at the end of the previous trial. These instructions were the same for both groups of participants.

The only manipulation that differed between the 'SacStart' and 'SacEnd' groups occurred in the acquisition phase of the experiment. For both groups, the light below the mirror was extinguished at the onset of the orienting saccade (specifically, when the EOG voltage surpassed the trigger threshold). In the 'SacStart' group, the target was extinguished at this point as well. In the 'SacEnd' group, however, the target remained illuminated for 90ms after the saccade trigger, allowing the eyes to acquire the target. The target was then extinguished. For both groups, the target and the hand were re-illuminated for 1 second when the stylus contacted the surface at the end of the reach. The acquisition phase consisted of 50 trials, and the initial (pre-reach) target location was the same for all of these trials (22.5 cm to the right of fixation). During the first 10 trials, the target reappeared at its initial location when the stylus landed (i.e., the target did not move). For the subsequent 10 trials, the target reappeared 1.25 cm to the right of its initial location when the stylus landed. Every 10 trials, the size of the displacement increased by 1.25 cm, such that for the final 10 trials of acquisition, the target was reappearing 5 cm to the right of its initial location. This protocol, except for the 'SacEnd' manipulation, is very similar to that of Magescas and Prablanc (2006).

The first posttest phase was identical to the pretest phase.

The second posttest phase consisted of 20 trials that were identical to the first 10 trials of the acquisition phase. In other words, the hand and the target were visible at the end of the reach, but the target was never displaced. These trials served to washout any residual adaptation that might have been present after the 50 trials of the first posttest phase.

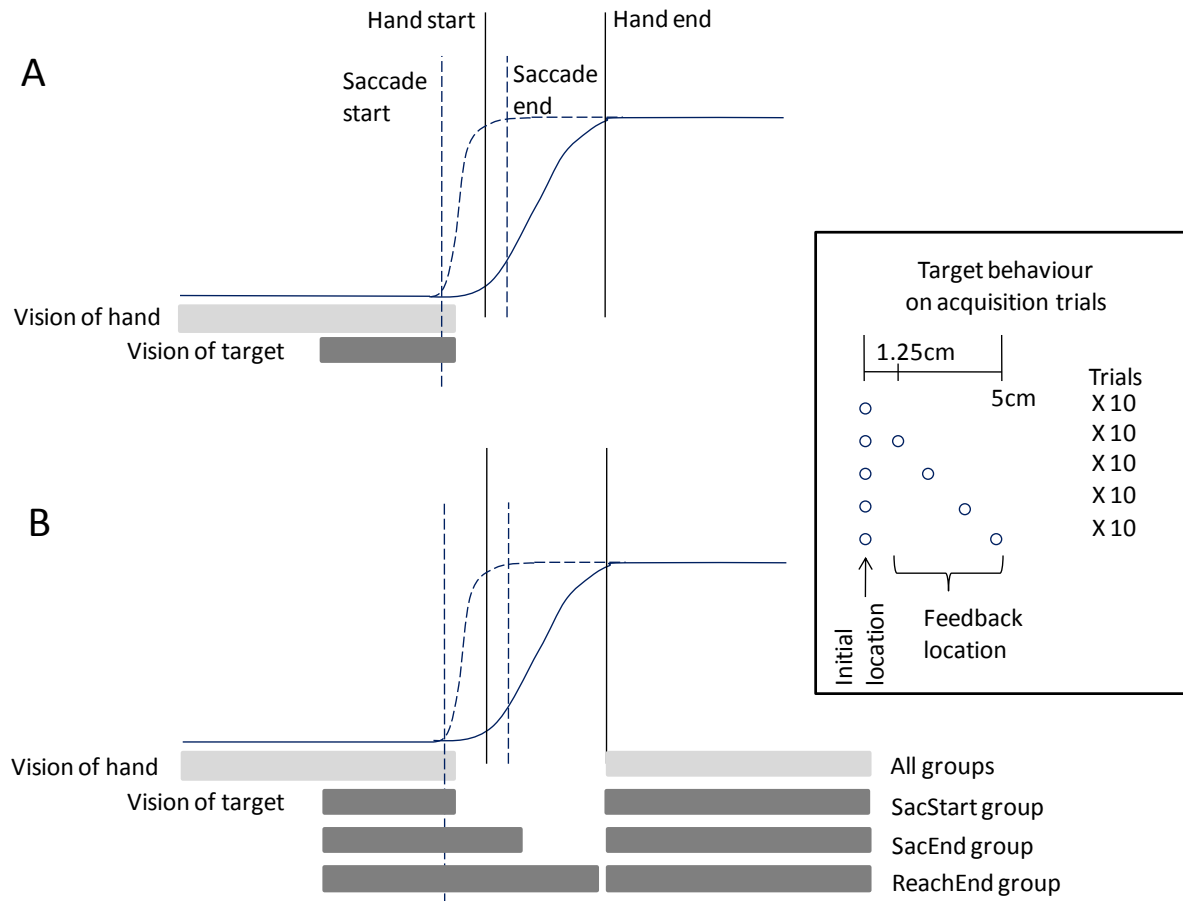


Figure 2.2 A) Sequence of stimulus events during the pre-test and posttest 1 phases of all experiments B) Sequence of events during the acquisition and posttest2 phases of all experiments. *Inset:* Target behaviour during the acquisition phases of all experiments. The initial target location is the same for all acquisition trials, while its second (feedback) location gradually moves to the right. Reprinted with permission of Springer Science+Business Media.

After completion of the experiment, participants were asked about the target displacement in the acquisition phase: whether they noticed it and, if so, how often it occurred and where the target moved to.

2.2.3.2 Experiment 2 (ReachEnd group)

The procedure for this experiment was identical to Experiment 1 but for two differences: 1) in the acquisition phase the target remained illuminated at its initial location until the stylus landed (at which point the light under the mirror was turned on and the target re-appeared at its shifted location, as in the first experiment) (Figure 2.2) and 2) after the first 11 trials of acquisition (i.e., after the

participant had experienced 10 stationary feedback trials and the first of the 40 displacement trials) participants were asked if they noticed anything happen to the target on the last trial. They were then instructed to ensure that on subsequent trials they attempt to aim such that the stylus would land as close to the second target location as possible.

2.2.3.3 Experiment 3 (Informed group)

This group was given an identical stimulus protocol to the SacStart group of Experiment 1. In other words, during the acquisition phase, the target was extinguished at the onset of the orienting saccade and then reappeared at hand touchdown. The critical difference between the Informed group and the SacStart group was that the Informed group was told about the presence of the target perturbation. For the first 10 trials of the acquisition phase (when the target reappeared at the same location from which it disappeared) participants were instructed simply to use the visual feedback to minimize reach error on subsequent trials. After experiencing the first trial on which a perturbation occurred, participants were asked if they noticed anything and then told that on that trial the target had actually moved to the right by 1.25cm and that this would continue to occur for the next several trials. They were also told to continue with attempting to minimize error between their hand and the final location of the target (i.e., to go to the target's second location). After the following 10 trials, the last of which included a 2.5 cm perturbation, participants were again asked if they noticed anything and then told of the increase in the size of the rightward jump. This process of informing the participant about the increased jump magnitude every 10 trials continued until the end of acquisition. After completing the first trial of the posttest, participants were informed that there would no longer be any visual feedback at the end of their movement (like the trial they just completed) and to simply aim to the target that appeared at the start of each trial for the remainder of the trials.

Unlike Experiments 1 and 2, there was no posttest 2 for Experiment 3.

2.2.4 Data reduction and analysis

Because our manipulation systematically induced target error in the lateral dimension, we focused our analysis on this dimension of the reaching movements. Prior to any analysis, movement

endpoints were normalized with respect to the actual target location (normalized lateral endpoint = raw lateral endpoint – lateral position of target for that trial).

We were interested in the robustness of adaptation in each of the four groups, so our analysis focused on the rate of de-adaptation in the first posttest phase for each group. Specifically, we examined the number of posttest trials required for each group to reach baseline (0mm target error) during the posttest phase. We did not use the pretest values as a baseline; as will become evident in the results section, many participants exhibited a large undershoot bias during the pretest, presumably because the absence of visual feedback during this phase prevented them from calibrating to the reach environment. This large undershoot promptly vanished when visual feedback was introduced during the acquisition phase (Figure 2.3), prior to the introduction of the target perturbation. Because we were interested in measuring the influence of the target perturbation (and only the target perturbation), we did not use the pretest as a baseline, as this would have introduced the additional, distorting effects of the un-calibrated movement error.

We carried out two sets of statistical analyses on the Posttest 1 phase to assess de-adaptation across the four groups. For our first analysis, which compares the four groups to each other, we collapsed across every five trials of the posttest (i.e., trials 2-6 of the posttest, trials 7-11 of the posttest, and so on) and submitted these means, along with the first trial of the posttest, to a 4 (group) x 10 (stage of Posttest 1) ANOVA with repeated measures on the second factor. For our second analysis, which examines the rate at which each group reaches baseline in the posttest, we took the same 5-trial means used in the first analysis and compared each mean to 0 with a one-sample t-test. The second analysis involves 9 t-tests for each group, for a total of 36 t-tests. Because this was primarily a way to objectively determine when a group had ceased to significantly overshoot the target (i.e., a search for an absence of a difference), we were not overly concerned about the inflated risk of type-I error and therefore used an alpha of .05 for each comparison (Aivar et al., 2008).

Violations to sphericity on any repeated measures factor were addressed with a Huynh-Feldt correction to degrees of freedom.

Comparisons of endpoint variability between groups were tested with the Bartlett test for homogeneity of variance.

Although we have described Experiments 1, 2 and 3 separately in the methods section, the data from all experiments are considered together in the following results section.

2.3 Results

2.3.1 Eye, hand, and target timings

The average start and end times for the eye and hand are displayed in Table 2.1. Additionally, the table shows the timing of target offset with respect to the eye. These results indicate that, on average, the eyes led the hand by ~61 ms, the target disappeared ~30 ms after the onset of the saccade in the SacStart and Informed groups, and that the target disappeared ~28 ms after completion of the saccade in the SacEnd group.

2.3.2 Motor adaptation to the target perturbation

Figure 2.3 shows the adaptation and de-adaptation to the target displacement across the 4 groups: SacStart, SacEnd, ReachEnd, and Informed. Visual inspection of Figure 2.3 suggests that, while all groups modified their reach endpoints during the acquisition phase in response to the increasing rightward target displacement, the ReachEnd group and the Informed group de-adapted

Table 2.1 Timing of various events (in ms) for each stage of each group. Values represent group means. Reprinted with permission of Springer Science+Business Media.

		Saccade onset	Trigger	Reach onset	Saccade end	T1 off	Reach end	Reach MT
SacStart	Pretest	241.66	270.65	288.78	337.86	270.65	661.33	372.54
	Acquisition	231.37	261.53	290.73	326.99	261.53	677.27	386.54
	Posttest1	233.24	264.08	273.83	339.45	264.08	684.52	410.69
SacEnd	Pretest	217.83	247.51	280.44	309.36	337.51	687.39	406.95
	Acquisition	202.33	230.26	275.24	291.75	320.26	658.41	383.17
	Posttest1	211.47	239.68	261.07	309.37	329.68	678.77	417.70
ReachEnd	Pretest	207.85	236.67	263.84	294.73	670.63	670.63	406.79
	Acquisition	198.32	226.66	266.64	281.81	688.09	688.09	421.45
	Posttest1	200.48	229.86	254.19	292.95	673.17	673.17	418.98
Informed	Pretest	232.03	265.29	309.98	315.63	265.29	839.92	529.94
	Acquisition	237.61	269.95	320.04	319.51	269.95	839.61	519.57
	Posttest1	228.01	262.33	290.45	320.52	262.33	829.06	538.61

(Posttest 1) faster than the other groups. A statistically significant interaction between the stage of Posttest 1 factor and the group factor confirms that not all groups de-adapted at the same rate, $F(12.2, 113.9) = 2.34$, $p = .0098$. Comparisons between the means at each stage of the posttest and a baseline of 0mm error show that the ReachEnd group was fastest to reach baseline, followed by the Informed group, then the SacStart and SacEnd groups (Figure 2.4). The ReachEnd group reached baseline within 6 trials, and the Informed group within 11. The SacStart and SacEnd groups, on the other hand, remained significantly different from baseline until, at least, posttest trials 31 and 46, respectively.

Interestingly, the ReachEnd group appeared to develop a significant target undershoot during the posttest, the possible implications of which are discussed later.

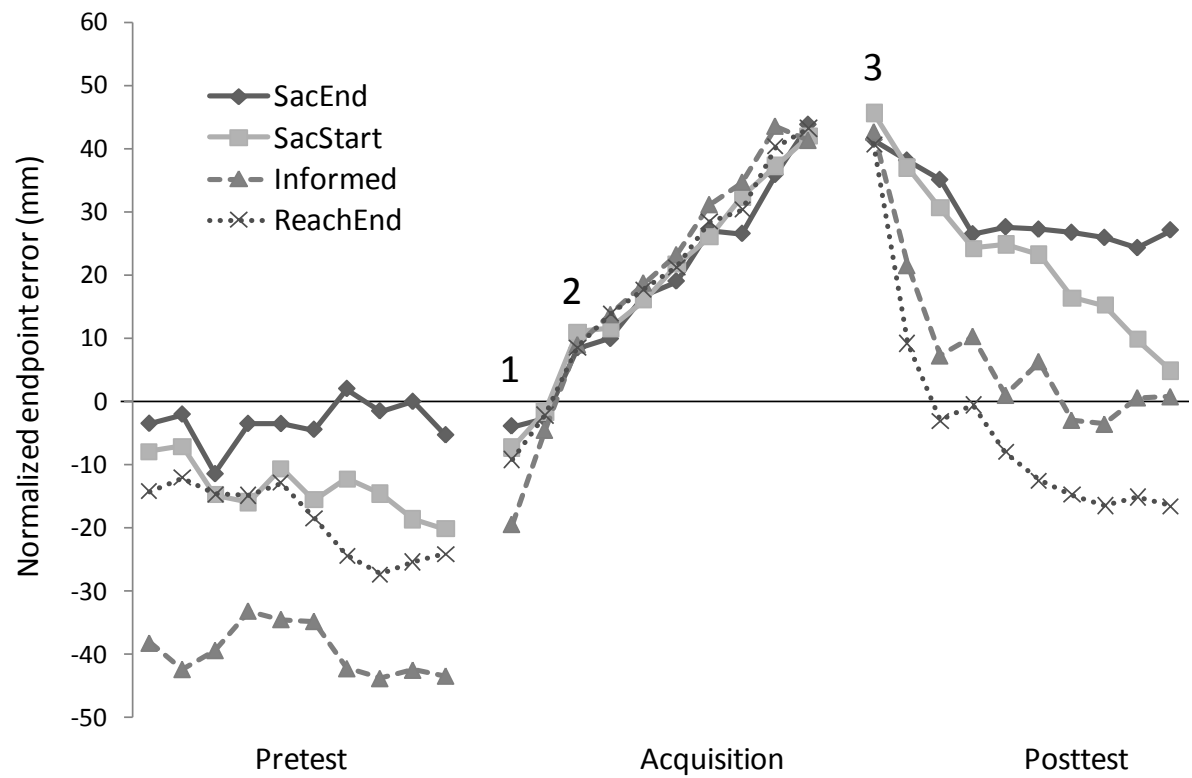


Figure 2.3 Adaptation profile for all 4 groups. All data points, except the first of the posttest phase, are data that have been collapsed across 5 consecutive trials. The first data point in the posttest reflects only the first trial of the posttest. The numbers indicate the onset of visual feedback (1), the onset of the target perturbation (2), and the offset of both the perturbation and visual feedback (3). Endpoint error (on the y-axis) is with respect to the initial target location for each trial. The initial (pre-saccadic) target location was the same for all trials of the acquisition phase. Reprinted with permission of Springer Science+Business Media.

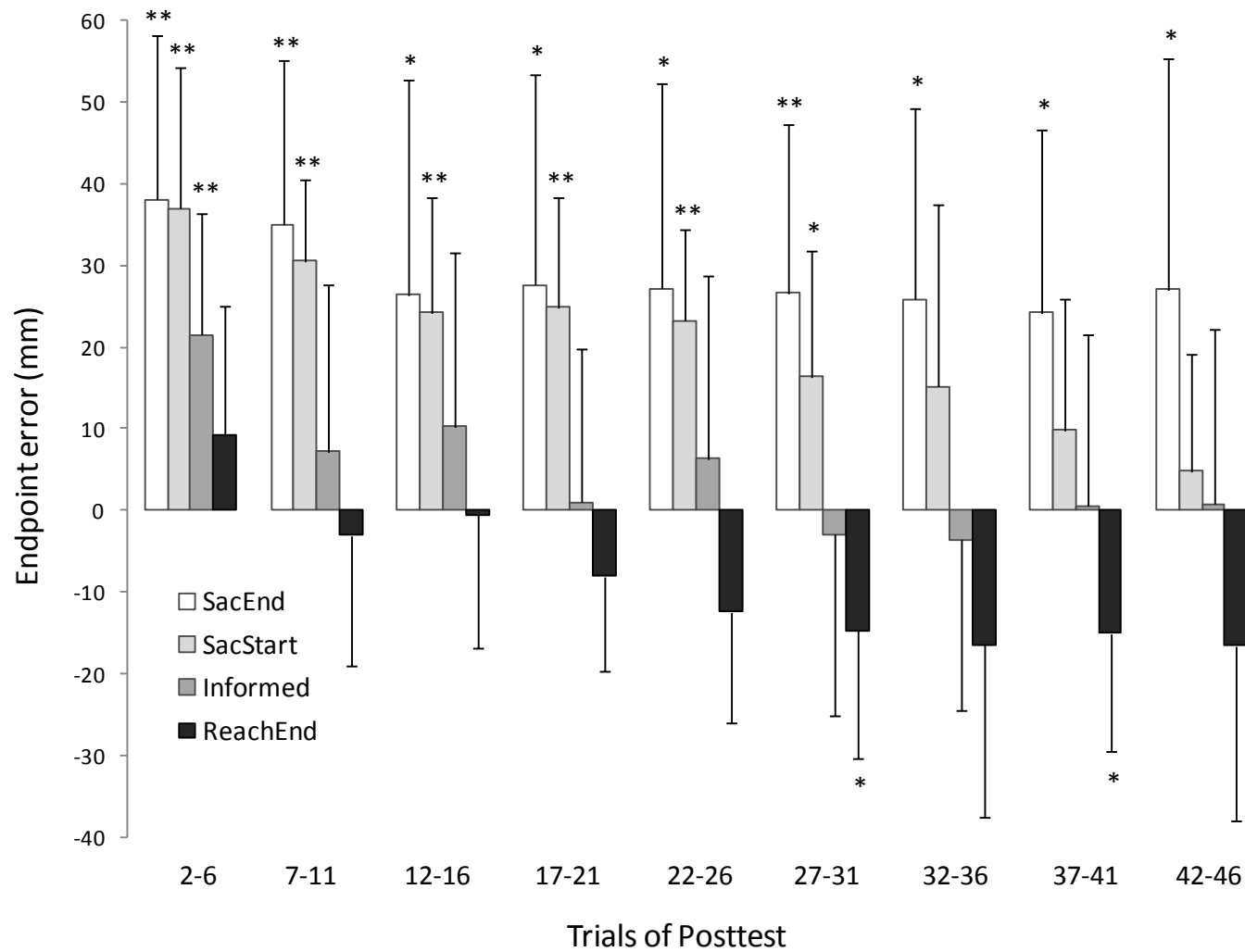


Figure 2.4 De-adaptation during Posttest 1. Group means are plotted for each 5 trials of the posttest, starting with the second trial of the posttest. Error bars represent between-subject standard deviation. The statistical significance of one-sample t-tests comparing each mean to 0mm is indicated with asterisks: ** = $p < .01$; * = $p < .05$. Reprinted with permission of Springer Science+Business Media.

2.3.3 Awareness of the target perturbation

In the 'SacStart' group, 7 of the 8 participants reported no awareness of target displacement. In the 'SacEnd' group, 5 of the 9 participants reported no awareness of target displacement. The two groups did not differ significantly from each other on this measure, $\chi^2 = 2.08$, $p = .149$. This was surprising, as we had expected the delayed offset of the initial target location in the 'SacEnd' group to dramatically increase awareness of the perturbation. Even for those participants who did report awareness of the displacement, awareness appeared to be incomplete. When asked, these participants reported, on average, that the target changed location on about 45% of the acquisition trials (The actual proportion was 80%.) It should be noted that the verbal report was a very rough estimate of awareness, because questioning about the acquisition phase came at the end of testing (after 70 intervening posttest trials) and also because the verbal report only measured what participants thought they detected during testing; it was not a measure of what participants are capable of detecting when they actively search for a perturbation.

In the ReachEnd group, participants were asked if they noticed anything happen after encountering the first trial in which a target displacement occurred. Five of 7 participants reported that the target jumped right. The other 2 participants, surprisingly, did not notice the first jump, but both noticed it on the next trial. All participants were, therefore, aware of the jump to some extent. When questioned at the end of the experiment, 5 of the participants were able to correctly report that the size of the jump had increased during the acquisition period. The other 2 participants thought that jump size was consistent throughout acquisition, and both estimated it to be 'about one inch'.

In the Informed group, participants were asked if they noticed anything happen after the first trial in which a target displacement occurred and then again each time the magnitude of the displacement increased. No participants noticed the first target displacement or the increase in displacement size from 1.25 to 2.5cm. When the displacement increased to 3.5cm and 5cm, several participants successfully indicated that it had moved farther to the right, but it is unclear how much of this report reflects perception of an increased displacement magnitude vs. recognition of the pattern of

target movement reported by the experimenter. Informal questioning of the participants after completion of the experiment suggested that most participants felt like they could see the largest (5cm) displacement, but had difficulty perceiving the displacement at smaller magnitudes.

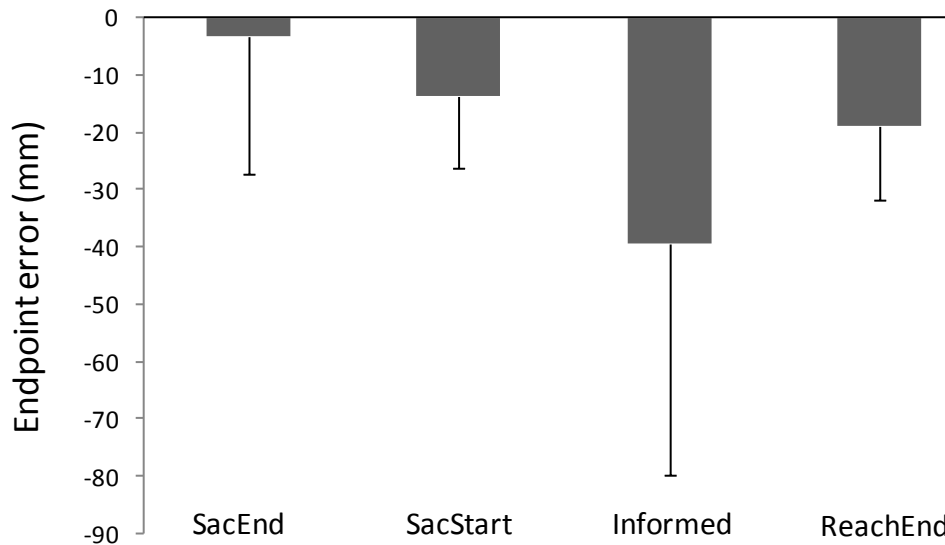


Figure 2.5 Mean lateral endpoint error in the pretest phase for each group. Error bars represent between-subject standard deviation. Reprinted with permission of Springer Science+Business Media.

2.3.4 Endpoint variability in the SacStart and SacEnd groups

Greater inter-subject variability in the posttest for one group relative to another may reflect less robust adaptation. Indeed, the apparently larger standard deviation error bars for the SacEnd group relative to the SacStart group (Figure 2.4) are suggestive of less robust adaptation in the SacEnd group. However, statistical comparison of the variability of the SacStart posttest mean (SD: 12.3) to the variability of the SacEnd posttest mean (SD: 21.7) did not reveal a significant difference, $\chi^2(1) = 2.09$, $p = .148$.

2.3.5 Pretest differences among groups

We do not use the pretest as a baseline for measuring adaptation due to its inclusion of uncalibrated movement error that might distort measurement of target perturbation effects. However, there remains the possibility that differences among groups in the posttest, which we have attributed

to experimental manipulations, might be related to initial differences among groups in the pretest. Comparison of the 4 groups' pretest means (Figure 2.5) suggests that the Informed group's pretest mean may be significantly lower than the SacEnd pretest mean, though not the other groups' pretest means⁷.

In light of this, we examined the performance of the Informed group in greater detail. We asked whether a participant's mean endpoint in the pretest was related to their rate of de-adaptation in the posttest. A significant negative correlation between pretest mean and the amount of decay in the early posttest (i.e., lower pretest value associated with larger decay value) might suggest that differences in rates of de-adaptation between the Informed group and other groups (especially the SacEnd group) should not be attributed to the experimental manipulations alone. However, there was no significant correlation between pretest mean and endpoint decay from posttest trial 1 to posttest trials 2-6, $r = -.03$, $p > .90$, or between pretest mean and endpoint decay from posttest trial 1 to posttest trials 7-11, $r = -.05$, $p > .90$. These near-zero correlations suggest that performance on the pretest in the Informed group is not related to their rate of de-adaptation in the early posttest; it should, therefore, be safe to make comparisons between this group and the other groups despite its potentially lower pretest mean.

2.4 Discussion

Our goal was to examine the influence of perceived target stability on reach adaptation, and we hypothesized that adaptation would decrease with decreased stability. We attempted to manipulate the perceived stability of the target by altering the time at which it disappeared relative to the orienting eye movement, reasoning that the shorter the interval between the offset of the target at its initial location and the onset of the target at its displaced location, the less stable it would appear. We

⁷ Violation of the assumption of homogeneity of variance (HOV) among groups on the pretest (Bartlett, $p = .0075$), along with unequal ns among the groups, dictates that a non-parametric test should be applied. When a Kruskal-Wallis test is applied to the groups, the result is not significant, $H(3, N=32)=6.49$, $p = .09$. However, if one overlooks violation of HOV and applies a one-way ANOVA instead, a significant difference does emerge, $F(3,28)=2.96$, $p = .049$. Subsequent post-hoc testing with Newman-Keuls reveals that the SacEnd and Informed groups do differ significantly in the pretest, $p = .04$. All other pairwise contrasts are not significant ($p > .10$).

hypothesized, therefore, that participants exposed to the earliest offset of the target at its initial location would show the strongest aftereffects. We also investigated the impact of informing participants about the presence of the target perturbation on the robustness of adaptation to the perturbation. In total, we compared adaptation to target error across 4 groups: one in which the target disappeared shortly after the onset of the saccade (SacStart), one in which the target disappeared shortly after the end of the saccade (SacEnd), one in which the target disappeared at the end of the reach (ReachEnd), and one in which participants were informed that the target was being perturbed during their reach (Informed).

Our results failed to show the predicted difference in the aftereffects of the SacStart and SacEnd groups. Both groups exhibited a large and long-lasting rightward shift of reaching movements in the posttest, whereas we had predicted more rapid de-adaptation in the SacEnd group. The ReachEnd and Informed groups, by contrast, exhibited faster rates of de-adaptation in the posttest. The timing of a target perturbation and a participant's knowledge of a target perturbation appear, therefore, to influence aftereffect robustness.

It is important to note that all groups received the same terminal feedback during the acquisition phase: For all groups, the hand was illuminated at the same time that the target appeared at its displaced location. The more rapid aftereffect decay in the ReachEnd group is, therefore, due to some change in the way the terminal error was interpreted by the visuomotor system as a result of the timing of the initial target's offset. This change in timing was designed to make the perturbation more explicit, and so participant awareness of the target perturbation in this group may explain the short-lived aftereffects. (Indeed, the results of the Informed group suggest that awareness of the perturbation can reduce aftereffect duration). However, it is also possible that reach error was processed altogether differently in the ReachEnd group because the initial target remained illuminated throughout the duration of the reach. In the following sections we discuss the possible influences of perturbation awareness and perturbation timing on reach adaptation.

2.4.1 Awareness of the target perturbation

We suggest that a key factor in the decay of the motor aftereffect was participant awareness of the target perturbation. This suggestion rests on the finding that the Informed and the ReachEnd groups (in which participants were aware of the target perturbation) exhibited faster de-adaptation rates than the other 2 groups (in which participants were largely to partially unaware). However, limitations in our measure of awareness as well as changes in the timing of target offset across the groups do present challenges for this explanation, as we discuss below.

In Experiment 1, we had hypothesized that delaying the target's disappearance in the SacEnd group would 1) increase participant awareness of the perturbation and 2) decrease adaptation to the same perturbation relative to the SacStart group. The results of this comparison, however, were inconclusive. The SacEnd group did not show a substantial increase in awareness relative to the SacStart group (as measured by post-experiment verbal report), nor did they exhibit significantly different behavior in the posttest phase relative to the SacStart group. The lack of effect between the SacEnd and SacStart groups, therefore, may simply reflect a failure in our manipulation to increase instability of the target. Without a more sensitive measure of participant awareness, however, we cannot confirm this.

The performance of the ReachEnd group (Experiment 2), on the other hand, is suggestive of a role for awareness in the adaptation to the target perturbation. This group experienced a much later offset of the target and we confirmed, during the experiment, that this perturbation was consciously visible to the participants. Under these conditions, participants exhibited much faster decay of aftereffects relative to the other groups. However, because we were simultaneously manipulating visibility of the target perturbation and the timing of the target's disappearance relative to the reach, it is possible that some effect of the delayed offset other than an increase in awareness was responsible for the rapid de-adaptation in this group.

It may be, for instance, that the longer visual persistence of the target at its initial location in the ReachEnd condition allowed the visuomotor system to process reach error with respect to that

location rather than the post-perturbation location. This might have occurred online or at movement termination. Given the absence of hand vision (recall that the hand was only visible when the perturbed target location was presented), any online error processing would be relying on an internal estimate of hand location for hand-to-target error processing. Such error processing is by no means implausible; online corrections to unseen target perturbations in the absence of limb vision have been well-documented (e.g., Goodale et al. 1986; Pelisson et al. 1986; Desmurget et al. 1999; Bard et al. 1999). However, if such error processing was occurring, it was effectively overridden by the participants during the acquisition phase. Not only did participants terminate their movements at the perturbed location, but they also prepared their movements to the perturbed location during the acquisition phase⁸. In other words, any online error processing with respect to the initial target location either did not occur or, if it did, was countermanded by reach end; more importantly, any offline influence of such error processing did not appear to influence subsequent movement preparation during the acquisition phase.

The other possibility is that *terminal* error processing was influenced by the persistence of the initial target location. The persistence of the initial location in the ReachEnd group may have forced participants into a cognitive mode of control (e.g., ‘reach further right’) that prevented error processing with respect to the post-perturbation location (although, as we discuss later, we believe cognitive control under these circumstances to be more of an effect than a cause of failed adaptation). An interesting side effect of consistently overshooting the initial target location in the ReachEnd group may have been the implicit processing of error with respect to *that* location rather than the final target location. It is possible that upon re-illumination of the hand at movement end, error was processed with respect to the recently extinguished initial target location. This consistent overshoot error during acquisition might then have led to an undershoot error in the posttest, an effect that appeared to emerge in our results for the ReachEnd group. Of course, our experiment was not

⁸ Based on the finding that peak velocity linearly increased as the perturbation size increased across acquisition trials ($r=.86$), $F(1,48)=133.62$, $p<.001$.

designed to test this possibility, and so the occurrence of such error processing remains largely speculative.

An alternative way to consider the ReachEnd results is within the context of different timescales of adaptation. Smith et al. (2006) have suggested that fast-adapting and slow-adapting processes might simultaneously be engaged during motor adaptation, and they have shown that a model that considers multiple timescales closely mimics the behavior of participants engaged in learning and relearning a force-field perturbation task. In their model, any learning that occurs in the fast-adapting system decays rapidly when the perturbation is removed (or a counter-perturbation is introduced), whereas the slow-adapting system retains its learning over an extended period (up to several hundred trials, depending on the duration of the prior exposure). Although Smith et al. do not discuss whether the two processes can be engaged independently, one possibility is that our ReachEnd group only engaged fast-adaptive processing and that this is why the group exhibited such rapid extinction during the posttest. This would still leave the question *why* this group only experienced fast-adaptive processing. It would be tempting to draw parallels between so-called ‘cognitive’ control and fast-adaptive processes (Indeed, initial error reduction during prism exposure has generally been attributed to cognitive control (Redding et al. 2005; Michel et al. 2007)). However, Smith et al. argue that a fast-adaptive system would probably reside in, or at least rely on, the cerebellum, suggesting that cognitive and fast-adaptive processes are not the same thing.

There is also the possibility that two processes were simultaneously occurring for the ReachEnd group: an explicit form of learning about the target perturbation that rapidly decayed in the posttest and an implicit form of error processing with respect to the initial target location that led to the emergence of a negative aftereffect. Again, however, we can only speculate that such implicit processing was occurring, and it is not clear whether such explicit and implicit processes are directly comparable to Smith et al.’s (2006) fast and slow adaptive processes.

Even if we do posit implicit error processing of the initial target location for the ReachEnd group, we are still left trying to understand why these participants failed to implicitly learn from the

perturbed target location. An explanation that eschews any consideration of awareness would have to posit some mechanism by which, at a certain point in the reach (sometime after saccade completion), available target information (i.e., the initial target location in the ReachEnd group) is used to the exclusion of target information presented at the end of the reach (i.e., the perturbed location in the ReachEnd group). Such a mechanism may be operating, but we currently have no theoretical framework from which to judge its plausibility. A more likely explanation, we believe, is that visibility of a perturbation immediately disqualifies the perturbed location of the target as a viable landmark for error processing, thereby opening the possibility of processing reach error with respect to the initial target location.

With Experiment 3 (Informed group) we tested the effect of participant awareness of the perturbation without the confounding effects of a persisting initial target location. This group exhibited a faster rate of de-adaptation than the SacStart and SacEnd groups, suggesting that awareness that a perturbation is occurring can undermine adaptation. This is a result that parallels findings from the prism literature, in which it has been shown that awareness of a perturbation reduces adaptation (Jakobson and Goodale 1989; Michel et al. 2007). Unlike those studies, however, we introduced an unstable target rather than directly altering reafference. It remains unclear whether our result in Experiment 3 is caused by an increased visibility of the target perturbation as a result of being told that it is occurring or the result of cognitive control induced by the instruction.

When people are told that a perturbation is occurring, this might have the effect of increasing the visibility of the perturbation in a top-down manner (somewhat analogous to a person's ability to extract a coherent percept from an ambiguous image only after being told what to look for (Coren et al. 1999)). Thus, a target displacement that might have otherwise gone unperceived might become perceptible as a result of instructions that direct one's attention to it. Although we would not expect top-down processes to dramatically influence the perceptibility of an *intra*-saccadic target displacement, which is subject to strong saccadic suppression effects, the post-saccadic displacement employed here may be more susceptible to detection when it is actively sought (Deubel et al. 1996).

However, participants' post-experiment reports of perceptibility in Experiment 3 do suggest that, even when informed about the presence of the displacement, they had difficulty perceiving it.

In short, there are two possible awareness-related explanations for the reduced adaptation in the ReachEnd and Informed groups. In what we will term the 'bottom-up' explanation, visibility of a target displacement might undermine the motor system's assumption of a stable environment, causing it to attribute reach error to the environment rather than an incorrect motor command⁹. Alternatively, in what we will term the 'top-down' explanation, awareness that a perturbation is occurring might prompt a cognitive, or explicit, mode of reach control that potentially inhibits implicit motor adaptation. It is possible that both explanations apply, and they may even apply differently to the ReachEnd and Informed groups. In the following section we discuss previous research on explicit and implicit processes in motor adaptation, research that suggests displacement visibility may be a more important determinant of motor adaptation than cognitive control.

2.4.2 Implicit vs. explicit processes in motor adaptation

Previous research suggests that a person's awareness of a perturbation impacts how they learn from it, at least when it comes to prism adaptation. Michel et al. (2007), for instance, showed that awareness of a prismatic displacement decreases the magnitude and robustness of aftereffects. They also found that awareness of the perturbation decreased inter-limb transfer of the adaptation. In their study, Michel et al. compared a group that received immediate onset of a consciously detectable prismatic perturbation of 10 degrees (aware group) to a group that received an incremental, and undetectable, increase in prismatic perturbation from 2 to 10 degrees (unaware group). Overall, participants in the aware group exhibited 40% adaptation to the distortion compared to 56% for the unaware group. Other research has also shown that when participants are told about the presence of a 5 degree prism distortion, they adapt less than participants who are not told about the presence of the same distortion (Jakobson and Goodale 1989).

⁹ This 'bottom-up' explanation does not preclude the possibility that top-down factors (such as instruction in the Informed group) may initially induce visibility of a target displacement. If visibility were being induced in this way, we would still consider the bottom-up explanation to account for the reduced adaptation.

Such findings are partially consistent with our suggestion that awareness played a role in the rapid de-adaptation of our ReachEnd and Informed groups. We say ‘partially consistent’, because there is reason to believe that a detectable target perturbation undermines adaptation *more* than a detectable prism shift or cursor rotation. For instance, Diedrichsen et al. (2005) (described in the Introduction) showed that people adapt more to a 12 degree cursor rotation than they do to a comparable online target jump. Although Diedrichsen et al. did not measure awareness of perturbations in their study, it is safe to assume that the 12 degree cursor rotation and the non-saccadically-suppressed target jump were easily detected by participants. Moreover, an important feature of the Diedrichsen et al. (2005) study is that they employed a randomized perturbation procedure, such that participants could not anticipate the upcoming jump/rotation direction. The effects that they observed, therefore, would not likely be due to cognitive (i.e., top-down) control of reaching. Any adaptation (or lack thereof) that they observed would, rather, be due to lower-level processing. Their results, therefore, are consistent with the idea that visibility of a target displacement can dramatically influence motor adaptation, independent of the presence/absence of cognitive control. We do not mean to imply, however, that cognitive control of the reach was absent in our ReachEnd and Informed groups; it was very likely required, at least in the ReachEnd group, for successfully hitting the perturbed target during the acquisition phase. Rather, we are suggesting that cognitive control likely emerged as an *effect* of the failure to learn implicitly, instead of being the cause of the failure.

Work by Mazzoni and Krakauer (2006) provides further evidence that cognitive control per se does not prevent motor adaptation. In their study, participants who were given an explicit strategy by which they could successfully guide a rotated cursor to a target still exhibited robust implicit adaptation to the rotation. In other words, participants who were cognitively engaged in aiming to one target (reach target) so that the rotated cursor would hit an adjacent target (cursor target) gradually worsened at hitting the cursor target, effectively adapting to the cursor error around the intended reach target. These participants also exhibited long lasting aftereffects, suggesting that implicit motor

learning is not undermined by cognitive control of the reach. Rather, implicit processes override explicit control under these conditions.

The foregoing evidence suggests that the short-lived aftereffects in our ReachEnd group, and possibly the Informed group, are the result of low-level registration of an unstable reaching environment, rather than the result of the cognitive control that may have been occurring simultaneously.

2.4.3 Relevance of reach error

Why would the motor system fail to adapt to a visible target displacement? The simple answer is that learning from such error would be counterproductive. If the error can be attributed to the environment rather than the motor system, modifying the motor system should normally serve little purpose. Wei and Kording (2009) have recently shown that the amount that reach error is weighted during motor learning depends on the size of the error. Larger errors receive less weighting, apparently because the likelihood that they are due to planning error (as opposed to the environment) is lower than for smaller errors. In other words, large errors seem to be less relevant for learning than small errors.

Unlike Wei and Kording's (2009) study, our study manipulated visibility of a target perturbation, rather than the size of the hand-to-target error. Accordingly, a potentially important difference between our study and that of Wei and Kording is the basis upon which error relevance is being assessed by the participant. In Wei and Kording's study, relevance was based on a post-reach comparison of target and reach endpoint. In our study, by contrast, visibility of a target perturbation may have reduced relevance *prior* to any comparison of the reach endpoint to the target. In fact, hand-to-target comparisons in our study would have been roughly equivalent across the 4 groups. Furthermore, the incremental nature of the target error in our study (increments of 1.25cm) was such that the size of the error on any given trial would have been well within a range that would allow it to be self-attributed. Thus, while we consider our findings to be consistent with the error-relevance perspective of Wei and Kording, the visibility of a target perturbation in the ReachEnd group may

have reduced the likelihood that reach error was due to planning error to a very low (perhaps near-zero) level. If, however, visibility of a target perturbation could be manipulated in a graded fashion (analogous to the graded spatial error used by Wei and Kording) we would predict an inverse relationship between a person's confidence that a perturbation had occurred and the amount of motor adaptation resulting from that trial.

2.4.4 The mechanisms of motor adaptation to target error

A prominent theory of motor adaptation suggests that adaptation relies on a comparison of predicted sensory feedback of the movement to actual sensory feedback (e.g. Wolpert et al. 2001; Tseng et al. 2007). This theory proposes that a copy of the outgoing motor command is fed through a forward model (an internal representation of an effector system), which generates a prediction of the sensory consequences of the motor command. Any difference between this prediction and the actual outcome can then be used as a training signal for an internal model (Wolpert and Miall 1996; Ramnani 2006).

However, in the case of a target perturbation (Magescas and Prablanc 2006) there is seemingly no conflict between predicted and actual feedback of the hand because vision of the hand is not distorted (unlike what occurs with prisms or a cursor rotation). On this basis, Magescas et al. (2009) have challenged the notion that motor adaptation relies on a comparison of prediction and feedback.

Another way to view the target, however, is as an environmental reference point, especially when it is the primary visual feature of the reach environment (as it is in Magescas and Prablanc (2006) and the present study). If we reach towards that point (while simultaneously predicting that our reach will land somewhere near that point), only to find that our hand did not land as near to the point as we had predicted, we would experience conflict between predicted and actual feedback. Although *egocentrically* there would be no conflict between predicted and actual feedback, *allocentrically* there would be. In other words, an imperceptible target displacement could plausibly introduce disagreement between predicted and viewed feedback of the hand. If we consider the results

of the present study in this context, the visible target perturbation that occurred for the ReachEnd group would undermine the visual system's assumption of environmental stability and, accordingly, prevent the visuomotor system from registering a mismatch between predicted and viewed feedback. This would, in turn, prevent any internal model updating.

2.4.5 Neural correlates of reach adaptation

Both the posterior parietal cortex (PPC) and the cerebellum have been implicated in the adaptation of reaching movements to laterally-displacing prisms, and it has been suggested that different adaptive processes are served by the different areas. The strategic component of adaptation might rely more on the PPC, while the spatial realignment component might rely more on the cerebellum (Pisella et al. 2004). The importance of the cerebellum in spatial realignment is supported by work showing that cerebellar lesions can produce reduced aftereffects in both humans (Weiner et al. 1983) and macaques (Baizer et al. 1999). Tseng et al. (2007) have also shown that cerebellar patients exhibit not only reduced aftereffects, but also impaired error correction during the exposure phase. Bilateral lesions of the PPC, on the other hand, do not appear to impair the development of aftereffects (Pisella et al. 2004). Neuroimaging studies, meanwhile, have implicated the PPC alone (Clower et al. 1996) or both the PPC and cerebellum (Dankert et al. 2008) in the early stages of prism exposure, while a recent study by Luaute et al. (2009) that examined extended prism exposure has implicated the PPC in the early stages of adaptation and the cerebellum in the later stages of adaptation. Taken together, the foregoing evidence suggests that the cerebellum is critical for post-exposure aftereffects but may also be involved in error reduction during the exposure phase, while the PPC is mostly involved in the early, possibly strategic, component of error reduction.

Although our study did not employ prisms, it is likely that some of the processes involved in prism adaptation are also involved in target-error adaptation. Thus, it is reasonable to speculate that our SacStart and SacEnd groups, which both exhibited robust aftereffects, developed cerebellum-based internal model adjustment over the course of the acquisition phase. The ReachEnd and Informed groups, however, which were both aware of the perturbation and which exhibited rapid

extinction in the posttest, probably relied on strategic, PPC-based processes throughout the acquisition phase. The absence of aftereffects in these two groups may indicate less involvement of cerebellum-based learning.

The study by Diedrichsen et al. (2005) may also be informative in this context, as it examined the neural correlates of target errors (target jump) vs. execution errors (cursor rotation) and showed greater activation in the PPC for target errors than for execution errors. The target errors in that study were created with visible target jumps, making them comparable to the explicit target errors experienced by our ReachEnd and (possibly) Informed groups. This lends further support to the speculation that PPC-based processes dominated in these two groups.

2.5 Conclusion

We manipulated the timing of target offset and observed the adaptation to post-reach error as a function of this timing. We also informed some participants about the presence of a target perturbation. Our results show that 1) participants who experienced the latest offset (reach end) exhibited the least amount of adaptation and 2) participants who were informed about the target perturbation also exhibited reduced adaptation. We suggest that the later the offset of the target, the more unstable the target appeared, causing the motor system to attribute error to the environment rather than itself. In future experiments we will examine whether it is top-down control or bottom-up registration of more than one target location that is directly responsible for the rapid de-adaptation we observed in these groups.

2.6 Bridging summary

The data presented in Study 1 suggest that the perceptibility of a target perturbation undermines motor adaptation, and I have suggested that adaptation fails because of a breakdown in the assumption of environmental stability. That is, when the reach environment is unstable, the participant no longer attributes reach error to his or herself, and so implicit motor learning does not occur. However, an alternative hypothesis might be that adaptation broke down in the ReachEnd group not because of a bottom-up registration of an unstable environment, but rather because of the top-down (or explicit) control of the reaching that occurred as a result of the visible target perturbation. This hypothesis presumes that implicit motor learning could have occurred in the ReachEnd group had the participants not consciously attempted to compensate for the visible perturbation by imposing explicit control over their reaching. A key difference between hypotheses, then, is *when* adaptation is thought to break down. The stability (or ‘bottom-up’) hypothesis suggests that it fails immediately and that the subsequent explicit control is simply a way to accomplish the targeting task when implicit control fails. The explicit control (or ‘top-down’) hypothesis suggests that adaptation fails once explicit control is imposed (i.e. explicit control is a causal factor rather than a side-effect).

The next study tests the influence of explicit control on motor learning. Can people implicitly learn from targeting error when they exert top-down control over their reaching? Study 2 employs a similar target perturbation protocol to the one used for the SacStart group in Study 1; however, in Study 2, participants are given an explicit reach task that requires them to aim away from the visible target during the exposure phase. The influence of the target perturbation is then measured in the post-test phase, in which participants are asked to aim directly to the target. A positive aftereffect in the post-test would suggest that explicit reach control does not, by itself, prevent adaptation to a target perturbation.

3 Implicit motor learning from target error during explicit reach control¹⁰

3.1 Introduction

When movement error occurs, our motor system learns from it, adjusting subsequent motor commands to eliminate, or at least reduce, the error. This happens even when we are consciously unaware that any systematic error is present; in fact, it appears that the *less* aware we are and the *smaller* the error, the more enduring the learning (Magescas and Prablanc 2006; Jakobson and Goodale 1989; Michel et al. 2007; Cameron et al. 2010; Wei and Kording 2009). By contrast, when error is large and unexpected, we can compensate very quickly for it (even on the very next trial), but this type of compensation seems to involve a different kind of processing – a cognitively-driven adjustment to the motor commands – that is not thought to produce true adaptation (Redding and Wallace 1996; 2002; Welch 1986; Michel et al. 2007; Richter et al. 2002). Thus, how we learn from our movements may depend on whether or not they are under implicit or explicit control.

It can be difficult, however, to determine from traditional adaptation paradigms what is learned when movements are under explicit control. Learning is usually measured with aftereffects, but these reflect the combined effects of all exposure phase movements, the majority of which are likely to be under implicit control. Any motor learning that might have occurred during the early part of the exposure phase (when movements may have been explicitly guided) cannot be detected. Recent work by Mazzoni and Krakauer (2006), however, was able to test directly the interaction of explicit and implicit processes by dissociating an explicit task from implicit learning. In Mazzoni and Krakauer's study, participants were given an explicit strategy by which they could successfully guide a rotated cursor to a target. The strategy was to execute their actual movement to one target (reach target) so that the rotated cursor would hit an adjacent target (cursor target). In this way, the explicit task (hitting the cursor target by aiming for the reach target) was put in conflict with implicit learning (realigning expected and actual visual feedback). Initially, participants were successful at the task, but

¹⁰ A version of this chapter has been published: Cameron BD, Franks IM, Inglis JT, Chua R (2010b) Implicit motor learning from target error during explicit reach control. *Exp Brain Res*, 206:99-104

over the course of exposure performance worsened. The cursor began to migrate away from the cursor target and towards the reach target, suggesting that participants were adapting to cursor error around the reach target. These participants also exhibited aftereffects (i.e., when the rotation was removed, participants misreached in the direction opposite to the rotation), suggesting that implicit motor learning is not undermined by explicit control of the reach. In fact, implicit processes appear to override explicit control under such conditions.

Our aim with the present study was to further investigate the interaction of explicit control and implicit learning and to potentially shed light on the mechanisms by which our motor system learns from targeting error. Unlike Mazzoni and Krakauer (2006), we perturbed the location of the reach target rather than visual feedback of the effector. We employed an adaptation protocol developed by Magescas and Prablanc (2006) in which a target imperceptibly moves farther to the right over the course of the exposure phase. In their protocol, a reach target appears in the visual periphery, and participants are tasked with looking and pointing to it. As the eyes and hand begin to move, the target disappears, reappearing at a shifted location when the hand lands. Magescas and Prablanc showed that people gradually adjust the gain of their reach in response to the perturbation – much like saccadic adaptation – and they exhibit robust aftereffects when the perturbation is removed. (I.e., they misreach in the direction of the perturbation even after the perturbation is removed). Unlike that study, however, the present study deliberately prevented participants from modifying their reaches in the direction of the perturbation during exposure. We instructed participants to undershoot the target by a specific amount and provided verbal feedback about their performance on this explicit task. While the target gradually moved farther to the right during the exposure phase, participants were simultaneously instructed to undershoot farther to the left. Adherence to the explicit task would maintain the endpoint of the reach at a constant location throughout the exposure phase.

This design allows for several things. It allows us to see whether implicit learning occurs when explicit control is maintained (and direct error correction inhibited) throughout the entire exposure phase. This contrasts with Mazzoni and Krakauer's study (2006), in which implicit

processes took over reach control as the exposure phase progressed. Importantly, our design also allows us to investigate pure error-based learning, avoiding as it does the visual-proprioceptive conflict that occurs with protocols that perturb vision of the effector. Furthermore, our design potentially allows for insight into the mechanisms governing the error-based learning. If participants exhibit aftereffects of the target perturbation in our study, it would suggest that indirect error processing is occurring and some form of remapping is being employed by the visuomotor system (Bays and Husain 2007). In other words, rather than relying on direct hand-to-target error, the visuomotor system would be anticipating a gap between the hand and the target of a certain magnitude, and then assessing error based on the level of agreement between the anticipated and ultimate gap size.

3.2 Methods

3.2.1 Participants

Sixteen participants (8 female, 8 male; ages 18-31) completed the study after providing consent. All participants were self-described right-handed, had normal or corrected-to-normal vision, and were naïve to the aims of the study. Participants were assigned to either an experimental or a control group (4 male and 4 female in each). The study was conducted according to the guidelines of the local research ethics board. Participants received \$10 for participation.

3.2.2 Apparatus

An array of red light-emitting diodes (LEDs) was mounted above a half-silvered mirror, which in turn was mounted an equal distance above the reaching surface. The optical geometry of the apparatus created the impression that the targets, reflected by the mirror, were in the same plane as the reaching hand. The half-silvered mirror allowed us to provide or remove vision of the hand by illuminating or extinguishing, respectively, a white light below the mirror. The reaching surface was a featureless white surface but for a circular home position (5 mm diameter) located at the bottom left corner. The surface and the home position were only visible when the light below the mirror was turned on.

An eye fixation point (5 mm diameter) was presented 13cm above the home position at the start of each trial. The fixation point was projected from the LED array and could be extinguished simultaneously with the onset of a peripheral target. Target stimuli (5 mm diameter) were also presented by illuminating LEDs in the array. Targets could be presented at 5 locations, each separated by approximately 1.25 cm. The first target position was located 22.5 cm to the right of fixation; the second target position was located 23.75 cm to the right of fixation, and so on. Participants' eyes were located approximately 48cm from the reaching surface. Accordingly, the distance between adjacent targets was approximately 1.5 degrees of visual angle.

Aiming movements were made with a handheld stylus with an infrared emitting diode attached near the tip. This allowed us to track the position of the stylus with OPTOTRAK (Northern Digital), which sampled at 500Hz. The stylus was also equipped with a microswitch tip that allowed us to track movement start and end in real-time. Electrooculography (EOG) was used to monitor horizontal saccades. Disposable Ag-AgCl surface electrodes were placed at the outer canthi of the eyes with a reference electrode placed on the forehead. EOG signals were amplified (5-10K) and band-pass filtered (0.1-30Hz) using an AC preamplifier (Grass Instruments P511) and sampled at 500Hz. The EOG signal was passed through an analog circuit that enabled online triggering of stimulus events. For each participant we manually set a voltage threshold such that the triggering would occur within the first 3rd of the saccade.

3.2.3 Procedure

3.2.3.1 Experimental group

Participants began each trial with the stylus at the home position and their eyes at the fixation point. When the experimenter triggered the start of a trial, a warning beep sounded. After a variable fore-period (ranging between 1 and 2 seconds), the fixation point would disappear and a target would simultaneously appear in the visual periphery. The participant was instructed to look and point, smoothly and accurately, to the target. The light below the mirror was on at the start of every trial, such that the participant could view the home position and their hand. Each participant completed 10

practice trials prior to beginning the experiment. These practice trials (like the pretest trials) permitted no online or terminal vision of the limb.

The experiment was divided into 3 phases: a pretest phase, an exposure phase, and a posttest phase. The pretest phase consisted of 50 trials in which a target would randomly appear at one of the 5 possible locations. At saccade onset, the target and the light below the mirror were both extinguished and remained off until the end of the trial (i.e., participants had vision of their hand and the target at the start of the trial only). After the trial was over and the participant had begun to return to the home position, the light below the mirror was re-illuminated (750ms after lifting the stylus from its endpoint position) so that the participant could place the stylus at the home position.

The exposure phase consisted of 50 trials, and the initial (pre-reach) target location was the same for all of these trials (22.5 cm to the right of fixation). During the first 10 trials, the target reappeared at its initial location when the stylus landed (i.e., the target did not move). For the subsequent 10 trials, the target reappeared 1.25 cm to the right of its initial location when the stylus landed. Every 10 trials, the size of the displacement increased by 1.25 cm, such that for the final 10 trials of exposure, the target was reappearing 5 cm to the right of its initial location. At the start of the exposure phase, participants were told that the next trials would include visual feedback, such that they would see their hand and the target at the end of the movement. They were instructed to approach the next 10 trials with the intent to minimize any error between the stylus and the target (i.e., to land as close to the target as possible). After those 10 trials, participants were told to undershoot the target by 1.25cm, such that when they viewed the stylus at the end of their reach it should be 1.25cm to the left of the target. This instructed undershoot distance was increased every 10 trials by 1.25cm (while the shift between pre-saccadic and post-reach target location was increased rightward by the same amount). After every trial, participants were given verbal feedback, in cm, about the position of the stylus relative to the post-reach target location.

The posttest phase consisted of 50 trials. These trials were identical to those of the pretest phase. At the start of this phase, participants were told that they would no longer receive visual feedback and that they should aim directly to the target that appeared at the start of each trial.

3.2.3.2 Control group

The procedure for this group was identical to the experimental group in all ways but one. For this group, there was no target perturbation during the exposure phase. Rather than having a pre-saccadic target location of 22.5cm to the right of fixation for every trial of the exposure phase, the pre-saccadic target location was the same as the post-reach target location (22.5cm for the first ten trials, 23.75cm for the next ten trials, 25cm for the next ten trials, and so on). The post-reach locations during exposure were the same as for the experimental group, as were the instructions to participants. In other words, participants were engaged in the same undershoot task as the experimental group, but without any target perturbation. The control group was included in the design so that, by comparing it to the experimental group, the adaptive effect of the target perturbation could be isolated. Previous research with a similar protocol (Cameron et al. 2010) had suggested that post-test effects can, in part, be due to calibration to the reach environment during the exposure phase, and we wanted to control for this effect.

3.2.4 Analysis

Because our manipulation systematically induced target error in the lateral dimension, we focused our analysis on this dimension of the reaching movements. Prior to any analysis, movement endpoints were converted to lateral displacement error values. (I.e., lateral target location was subtracted from the lateral endpoint of the reach.)

For each phase of the experiment, we compared the experimental and control groups to each other at 3 time points: early, middle, and late. That is, we collapsed across the 1st set of 15 trials, the 2nd set of 15 trials, and the 3rd set of 15 trials in the pre- and post-tests and examined the difference between groups for each of these blocks of 15 trials. This type of analysis allows us to test for differences that exist early in the post-test phase, but potentially decay as the phase progresses.

Analysis of the exposure phase required a slightly different partitioning, as the first 10 trials did not include an undershoot task, whereas the last 40 trials involved target undershooting. Accordingly, we treated the first 10 trials as the ‘early’ block, the next 20 trials as the ‘middle’ block, and the last 20 trials as the ‘late’ block. To compare the experimental and control groups, we applied independent-samples t-tests to the lateral error values at each time point in each phase.

For analysis of adherence to the explicit task in the exposure phase, single sample t-tests were used to compare lateral error to a value of 0 mm error.

3.3 Results

3.3.1 Adherence to the explicit task

Participants in both groups tended to point slightly to the left of the instructed location during the undershoot task (the middle and late blocks of exposure). This bias was statistically significant in the experimental group’s middle ($t(7)=4.45$, $p=.003$) and late ($t(7)=6.13$, $p<.001$) blocks of exposure. The bias was also significant in the control group’s middle ($t(7)=3.97$, $p=.005$) and late ($t(7)=4.28$, $p=.004$) blocks of exposure. Furthermore, the experimental group was significantly more to the left of the instructed location than the control group in the late block of exposure ($t(14)=2.99$, $p=.01$) but not in the middle ($t(14)=1.44$, $p=.17$) or early ($t(14)=.51$, $p=.62$) blocks of that phase. It is important to note that the ‘extra’ undershooting that occurred in both groups reflects over-adherence to the explicit task. Failing to adhere to the task and succumbing to direct error processing would emerge as a positive error (i.e., a rightward overshoot of the instructed location). Neither group displayed rightward error during exposure, so both groups can be considered to have adhered to the explicit task. The fact that the experimental group was landing slightly more leftward during the late block of exposure may not be particularly surprising. Recall that for this group, the initial (i.e., pre-saccadic) target location was farther to the left than for the control group.

3.3.2 Aftereffects of the perturbation

The most important comparison for testing for the emergence of implicit motor learning during explicit control is the one between the control and experimental groups in the post-test. As

shown in Figure 3.1, there is a significantly larger overshoot of the target by the experimental group in the early post-test ($t(14)=2.64$, $p=.02$). This effect is in the direction that one would predict if the target perturbation was implicitly influencing learning during exposure. The mean difference between groups (15.35 mm) reflects 31% of the total perturbation size in the experimental group, which is comparable to the approximately 40% adjustment that tends to occur with prisms (Redding et al. 2005). Note, however, that the effect decays after the first block of 15 trials, such that the two groups do not differ in the middle ($t(14)=0.81$, $p=.43$) or late ($t(14)=.52$, $p=.61$) posttest.

The pattern of results in the posttest differs from the one in the pre-test, where the experimental and control groups did not differ from each other in the early ($t(14)=.39$, $p=.70$), middle ($t(14)=.37$, $p=.72$), or late ($t(14)=.68$, $p=.51$) blocks. In other words, the difference between groups that we observed in the early posttest was not present in the pretest, suggesting that the experimental group learned something from exposure that the control group did not.

3.3.3 Awareness of the perturbation

When questioned about the target perturbation after completion of the experiment, all participants in the experimental group reported no awareness that the target was being displaced during the exposure phase.

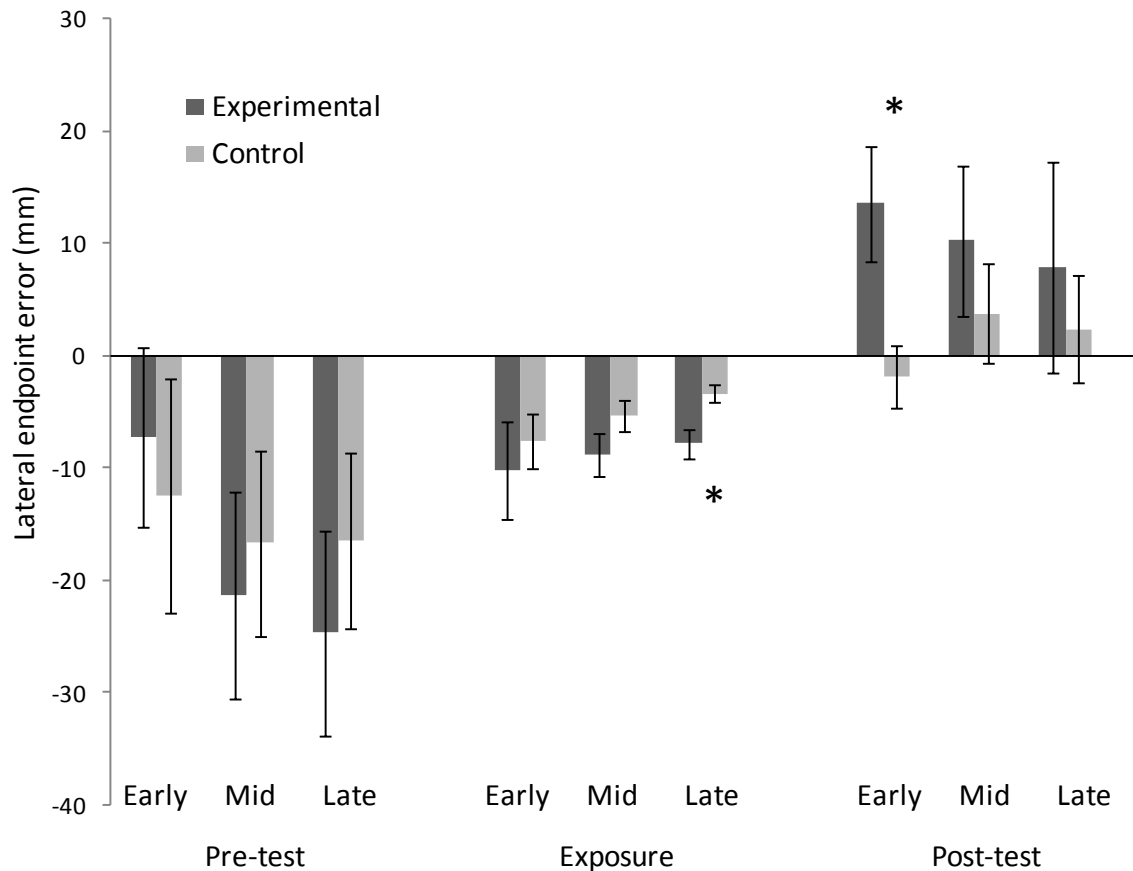


Figure 3.1 Reach performance in the experimental and control groups. Means are for blocks of consecutive trials. In the pre- and post-test phases these blocks consisted of 15 trials each. For the exposure phase, the early block represents the first 10 trials, during which there was no explicit task. The middle and late blocks of the exposure phase consist of 20 trials each, trials during which participants were engaged in the explicit task. Y-axis: for the pre- and post-test phases, negative values represent reach endpoints left of the target, positive values reach endpoints right of the target, and zero represents actual target location. In the exposure phase, negative values represent reach endpoints to the left of the instructed undershoot location, positive values reach endpoints to the right of the undershoot location, and zero represents perfect performance of the explicit task. Error bars represent standard error of the mean. Asterisks represent statistically significant differences between groups. Reprinted with permission of Springer Science+Business Media.

3.4 Discussion

Our study examined whether explicit reach control, successfully maintained throughout exposure to a perturbation, would prevent implicit motor learning. Our results show that participants in the experimental group developed significant reach aftereffects (a sign of implicit motor learning) despite their successful adherence to an explicit undershoot task that maintained reach endpoint at a constant location throughout exposure. This result confirms the findings of Mazzoni and Krakauer

(2006), who previously showed that implicit learning occurs despite an explicit reach strategy. Our study extends their findings to show that such learning is not dependent on perturbed visual feedback of the effector, but can occur when the target of the reach is perturbed instead.

In the absence of undershoot instructions, a participant's natural tendency is to minimize reach error with respect to the target during the exposure phase, and we know that participants develop persistent reach aftereffects under such conditions (Magescas and Prablanc 2006). The presence of aftereffects in our study suggests that the reach does not need to directly respond to the target error during exposure; rather, direct adaptation to target error can be inhibited during exposure and error can be processed indirectly. What mechanisms might underlie adaptation under these conditions?

One possible cause of aftereffects that we can confidently rule out is the realignment of vision and proprioception. The use of a target perturbation rather than a visually-displaced effector (as occurs for prism and cursor rotation protocols) ensures that the perturbation does not introduce any conflict between visual and proprioceptive feedback from the hand. Indeed, this is one of the strengths of the protocol (Magescas and Prablanc 2006). The adaptation we observed must, therefore, arise through some other mechanism.

Our results do serve to highlight some of the similarity between saccadic and reach adaptation, and our understanding of the former may provide insight into the mechanisms of the latter. Magescas and Prablanc (2006), in developing the target error protocol for reach adaptation that we employed here, have already shown that reaches adapt to target error in a fashion similar to saccades. Here we have shown that reach adaptation still occurs when a deliberate target undershoot is performed. In the saccadic system, adaptation has, likewise, been shown for saccades that deliberately undershoot the target (Bahcall and Kowler 2000). The fact that adaptation can occur for saccades that deliberately undershoot a target has been taken as evidence that visual remapping, rather than simply fovea-to-target error processing, may be a critical component of saccadic adaptation (Bahcall and Kowler 2000; Bays and Husain 2007). With remapping, predicted retinal feedback and

actual retinal feedback can be compared, and an error signal generated. We suggest that a similar process underlies the reach adaptation that we observed here: The participant generates a prediction about hand-to-target distance from a motor command that has been explicitly generated and then compares this prediction to the visual outcome. The reader should note that this proposed mechanism differs somewhat from the one suggested by Magescas and colleagues, who argue that direct hand-to-target error is the critical signal for reach adaptation, rather than a predicted-to-actual-feedback comparison (Magescas et al. 2009). However, a direct error mechanism would have difficulty accounting for the adaptation effects we observed here for the same reason that direct foveal-to-target error processing has difficulty accounting for saccadic adaptation during deliberate saccade undershoot (Bahcall and Kowler, 2000).

We should note, however, that the adaptive effects we observed in the experimental group were smaller, and also appeared to decay faster than those that have been observed previously (Magescas and Prablanc, 2006). Thus, while implicit processing occurred during explicit control in our study, there remains the possibility that this processing was impaired by the concurrent explicit task and the lack of direct error correction.

3.5 Conclusion

We have demonstrated that successful explicit control of a reach does not prevent the development of reach aftereffects during exposure to a target perturbation. Furthermore, participants are able to adapt their movements without directly responding to hand-to-target error. We suggest that these findings argue against a direct hand-to-target error processing mechanism for reach adaptation and in favor of a prediction-based mechanism.

3.6 Bridging summary

Study 1 showed that perceptibility of a target perturbation undermines reach adaptation, and Study 2 has now shown that adaptation can occur when the limb is under explicit control. This latter finding suggests that the failed adaptation that occurs when a target perturbation is visible is probably not due to explicit control but rather to the instability of the reach environment created by the perturbation. The results of Study 2 also suggest that terminal error processing does not necessarily rely on computations of direct hand-to-target error. Rather, the visuomotor system appears to predict what feedback will be generated by a motor command and then compares the actual feedback to this prediction.

The foregoing two studies have investigated how the visuomotor system processes error that occurs at the end of a movement. (Recall that in both Studies 1 and 2, the target only reappeared after the hand had landed.) The next study (Study 3) investigates how the visuomotor system processes error that occurs while a movement is underway. That is, if error is introduced prior to completion of a reach, such that the reach can be corrected online, will the visuomotor system still adapt to the error?

4 Reach adaptation to online target error¹¹

4.1 Introduction

Error in reach trajectories can be overcome in different ways. If we have real-time feedback and sufficient time, we can correct a reach online, successfully acquiring a target despite initial error in the reach trajectory. If online corrections are not possible, we can modify subsequent reaches such that we improve our accuracy over the course of multiple reaches. Previous work has shown that error correction processes occurring in the second case (terminal error-based correction) lead to reach adaptation (Magescas and Prablanc 2006; Cameron et al. 2010). Participants in those studies were exposed to target perturbations in which the target disappeared at the start of the saccade and then reappeared, imperceptibly displaced, at the end of the reach. Participants exhibited robust aftereffects as a result of this exposure. The central question of the current study is whether the error correction processes in the first case (online error) also lead to adaptation. In other words, if a target error is introduced during a movement, rather than at the end, does this lead to a persistent change in the way participants plan their reaches?

Recent work by Magescas et al. (2009) suggests that online error does not produce adaptation. The authors examined the reach aftereffects that were induced by exposure to a recurring rightward target jump that was tied to the orienting saccade, eliminating awareness of the target displacement (Bridgeman et al. 1975). In the online error condition of Magescas et al.'s study, the jump occurred at the onset of the orienting saccade and the target was present throughout the reach, such that participants were able to correct their reach online. To ensure that they measured pure reach adaptation, rather than possible transfer of saccadic adaptation to the reach, the authors interspersed an equal number of look-only trials (in which the target always jumped leftward) with the look-and-point trials. The look-only trials were designed to negate any rightward saccadic adaptation that might normally accumulate during repeated exposure to the rightward target jump that occurred on look-and-point trials (Hopp and Fuchs 2004; Bekkering et al. 1995; Pelisson et al. 2009).

¹¹ A version of this chapter is currently under review

Magescas et al. (2009) showed that their online error protocol did not produce any reach aftereffects, which was in stark contrast to the robust aftereffects that occurred in their terminal error condition, a condition in which the target was extinguished at saccade onset and then re-illuminated when the hand landed (Magescas and Prablanc 2006).

The difference in aftereffects that Magescas et al. (2009) observed for online versus terminal error contrasts with the findings of studies that manipulate vision of the limb rather than the target location. Cursor rotation and prism adaptation studies have shown that adaptation occurs regardless of whether online corrections are permitted or prevented (Tseng et al. 2007; Diedrichsen et al. 2005; Hinder et al. 2009; Shabbott and Sainburg 2010; Jakobson and Goodale 1989). The reason for this discrepancy is not yet clear. It may be that target error is processed altogether differently from effector-based error. Indeed, Diedrichsen et al. (2005) have shown that larger adaptive effects are induced by a cursor rotation, which introduces effector-based error, than by an online target jump, which introduces target error. However, a crucial feature of Diedrichsen et al.'s design was that the target jump in that study was visible to the participant (it was not paired to a saccade), such that movement error could be attributed to a change in the environment rather than to a flaw in the actor's motor command.

An *invisible* target jump, in contrast, should lead the actor to attribute the reach error to a flawed motor command and (theoretically) lead to motor learning. Magescas et al.'s (2009) finding of no aftereffects with such a perturbation is, from this perspective, somewhat unexpected. Alternatively, however, one might argue that, because online correction allows achievement of the movement goal (i.e., acquiring the target), there is no real need for adaptation to occur. This second perspective, though, would have difficulty accounting for the adaptation to cursor and prism perturbations that still arises when online corrections are permitted (Tseng et al. 2007; Diedrichsen et al. 2005; Hinder et al. 2009; Shabbott and Sainburg 2009; Jakobson and Goodale 1989).

In short, Magescas et al.'s (2009) findings suggest that online target perturbations do not produce adaptation, and, when considered together with the findings from cursor and prism

perturbation studies, their results further suggest that what is learned from online error critically depends on whether or not the target or the effector is being perturbed. However, there is reason to revisit adaptation to online target error before accepting this conclusion. There are several features of Magescas et al.'s (2009) design that may account for the failed adaptation to online error that are independent of the presence of an online correction. First among these is the size of the target jump (7.7 cm). Although none of the participants in the study reported awareness of the jump, it was a large enough perturbation that the visuomotor system may have been less inclined to attribute that amount of reach error to itself. Wei and Kording (2009), for instance, have shown that as the error between an effector and its target is increased, the adaptive weighting of that error signal is reduced. Furthermore, the immediate onset of the 7.7 cm jump in the online error condition of Magescas et al.'s study differed dramatically from their terminal error condition, in which incremental displacements of 1.28 cm were used to build up to a 7.7 cm displacement over the course of the exposure phase. Thus, the hand-to-target error introduced in their terminal error condition was considerably more likely to be attributed to planning error than in the online error condition, where the error was large and instant.

A second feature of their design that may have undermined adaptation in the online error condition was the presence of limb vision throughout the entire reach. The congruency between the expected and actual visual feedback that this would have permitted may have counteracted any possible adaptive effects of the online error created by the displaced target. Their terminal error condition, by contrast, eliminated limb vision during the reach.

A third feature of their design that may have led to adaptation differences between the two conditions was the presence of look-only trials in only the online error condition. The inclusion of these trials in only the online condition is certainly understandable, given that only in this condition would it be necessary to counteract potential rightward saccadic adaptation and, further, given that including the same trials in the terminal error condition would have produced an unwanted net leftward saccadic adaptation in that condition. However, the presence of an intervening saccade-only

task in only the online error group may have somehow inhibited the accumulation of reach adaptation from the look-and-point trials. Though such a deleterious effect of intervening saccade trials seems unlikely, a similar intervening task should also be included in the terminal error group to ensure that the task switching or temporal delay produced by the saccade task is not the reason for the absence of adaptation in the online error condition.

The goal of the present study was to re-examine online versus terminal error with a design that provides favorable conditions for online error-based learning (if, that is, such learning is possible), while keeping as many design features as possible constant across the online and terminal error groups. For instance, we used a smaller target displacement (3.75 cm) than Magescas et al. (2009) and we used the same displacement size for both online and terminal error groups. We also ensured that vision of the limb was consistent across groups; both groups received visual information at the start and end, but not during, the reach. We also included look-only trials in both groups, though we did have to modify these trials for the terminal error group (we delayed the reappearance of the target) in order to prevent any leftward saccadic adaptation. In short, we tried to make both conditions as similar as possible, with the only important difference between them being the presence/absence of the target during the reach.

This design should allow us to determine whether adaptation can develop as a result of recurring online error correction or whether, as argued by Magescas et al. (2009), adaptation is only induced by terminal reach error.

4.2 Methods

4.2.1 Participants

Twenty four volunteers from the university community (11 male, 13 female; ages 20-34) participated in the study. All participants were self-described right-handed, had normal or corrected-to-normal vision, and were naïve to the aims of the study. Participants were assigned to one of three groups: the terminal error group, the online error group, or the control group. The experiment took approximately 45 minutes to complete, and participants received \$10 for their participation. All

participants provided informed consent prior to the experiment, and the study was conducted in accordance with the ethical guidelines of the university's research ethics board and in accordance with the Declaration of Helsinki.

4.2.2 Apparatus

Participants were seated with their head in a chinrest at the apparatus depicted in Figure 4.1. Participants' eyes were approximately 48cm from the reaching surface. An array of red light-emitting diodes (LEDs) was mounted above a half-silvered mirror, which in turn was mounted an equal distance above the reaching surface. The optical geometry of the apparatus created the impression that the targets, reflected by the mirror, were in the same plane as the reaching hand. The half-silvered mirror allowed us to provide or remove vision of the hand by illuminating or extinguishing, respectively, a white light below the mirror. The reaching surface was a featureless white surface but for a circular home position (5 mm diameter) located at the bottom left corner. The surface and the home position were only visible when the light below the mirror was turned on.

An eye fixation point (5 mm diameter) was presented 15 cm above the home position at the start of each trial (Figure 4.1). The fixation point was projected from the LED array and could be extinguished at the same time as the onset of a peripheral target. Target stimuli (5 mm diameter) were also presented by illuminating LEDs in the array. Reach targets could be presented at 5 locations, each of which was horizontally aligned with the fixation point and separated from its neighbor by approximately 1.25 cm. The nearest target location (location #1) was 22 cm to the right of the fixation point, the next target location (location #2) was 23.25 cm from the fixation point, and so on. The target could appear at any one of these 5 locations in the pre- and post-test phases of the experiment. Another location (location E) was used only on look-only trials of the exposure phase (i.e., it was never a reach target). This location was 3.75 cm to the left of location #2, or 19.5 cm to the right of the fixation point (Figure 4.1).

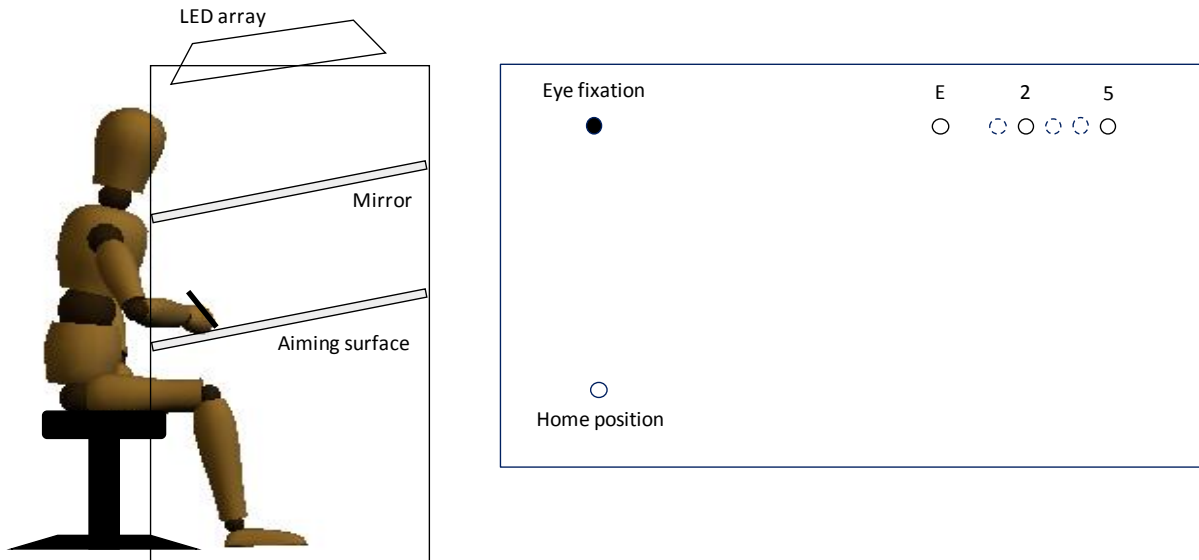


Figure 4.1 On the left, a schematic of the apparatus. LEDs at the top of the apparatus are reflected by the half-silvered mirror. The reflected stimuli appear to be in the same plane as the hand. Vision of the hand is manipulated by illuminating/extinguishing white LEDs mounted below the mirror. On the right, a schematic of the stimulus display. Participants began each trial with the stylus at the home position and their eyes on fixation. A target would appear at one of the possible target locations, concurrent with the offset of the eye fixation LED. Note that target locations 1 through 5 were employed during the pre and posttests, while targets E, 2, and 5 were employed during the exposure phases.

Aiming movements were made with a handheld stylus with an infrared emitting diode attached near the tip. This allowed us to track the position of the stylus with OPTOTRAK (Northern Digital), which sampled at a rate of 500Hz. The stylus was also equipped with a microswitch tip that allowed us to track movement start and end in real-time. Electrooculography (EOG) was used to monitor horizontal saccades. Disposable Ag-AgCl surface electrodes were placed at the outer canthi of the eyes with a reference electrode placed on the forehead. EOG signals were amplified (5-10K) and band-pass filtered (0.1-30Hz) using an AC preamplifier (Grass Instruments P511) and sampled at a rate of 500Hz. The EOG signal was passed through an analog circuit that enabled online triggering of stimulus events. For each participant we manually set a voltage threshold such that the trigger would occur within roughly the first 3rd of the saccade.

4.2.3 Procedure

Participants began each trial with the stylus at the home position and their eyes at the fixation point. When the experimenter triggered the start of a trial, a warning beep sounded. After a variable fore-period (ranging between 1 and 2 seconds), the fixation point would disappear and a target would simultaneously appear in the visual periphery. The participant was instructed to look and point, smoothly and accurately, to the target, but a movement time criterion was not provided or enforced, other than encouraging the participant to slow down or speed up if their movement time on a trial was less than 250 ms or more than 650 ms, respectively. The light below the mirror was on at the start of every trial, such that the participant could view the home position and their hand. Each participant completed 15 practice trials prior to beginning the experiment. On practice trials the target and the light remained on throughout the reach.

The experiment was divided into 3 phases: a pretest phase, an exposure phase, and a posttest phase. The pretest phase (which was identical to the posttest phase) consisted of 50 trials in which a target would randomly appear at one of the 5 possible locations. When the eyes began to move (i.e., when the saccade trigger threshold was surpassed), the target and the light below the mirror were both extinguished and remained off until the end of the trial (i.e., participants had vision of their hand and the target at the start of the trial only) (Figure 4.2D). After the trial was over and the participant had begun to return to the home position, the light below the mirror was re-illuminated (750ms after lifting the stylus from its endpoint position) so that the participant could place the stylus at the home position. All 3 groups received identical pretest and posttest phases.

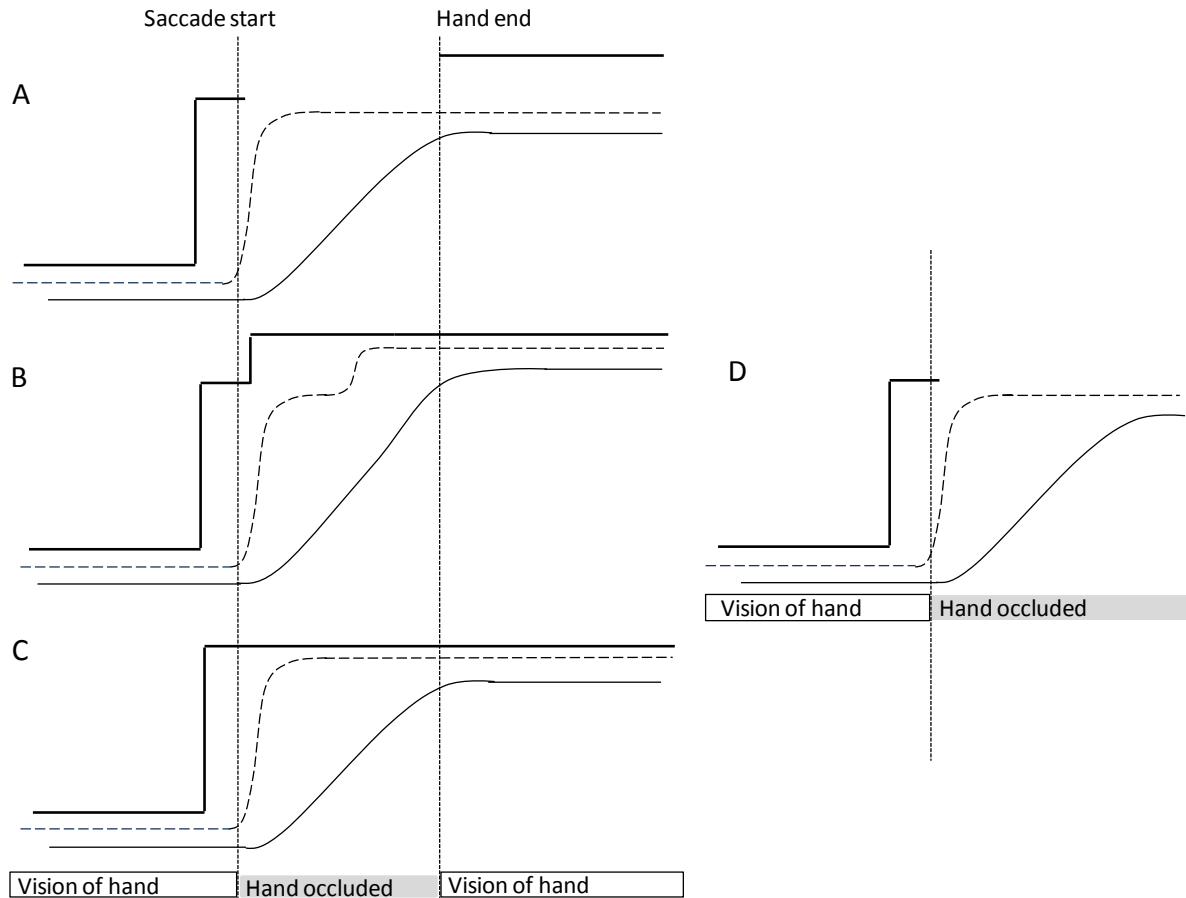


Figure 4.2 Sequence of events on the look-and-point trials of the exposure phase for the terminal (A), online (B), and control (C) groups. Stimulus events in the pre- and post-test phases (D) were the same for all groups. The solid bold line represents target position over time. The dashed line represents eye position over time. The solid (non-bold) line represents hand position over time. Note that on the look-only trials of the exposure phase (not shown here), target displacements would be in the opposite direction to the displacements that occurred on look-and-point trials.

After completing the pretest, the participant was given a break as well as some additional instructions. Participants were told that the next trials (the trials of the exposure phase) would include visual feedback, such that they would see their hand and the target at the end of the movement. They were instructed to approach each trial with the intent to minimize any error between their hand and target that they had seen at the end of the previous trial. These instructions were the same for all groups. (Indeed, all instructions were identical for all groups.) Participants were also told that they would encounter two kinds of trial: look-and-point and look-only trials. Look-and-point trials were cued with a red fixation point at the start of the trial. On these trials, participants were to look and

point, smoothly and accurately, to the target. Look-only trials were cued with a green fixation point at the start of the trial. For these trials, participants were to keep their hand at the home position and to only move their eyes to the target. The exposure phase of each group consisted of 60 trials, 30 of which were look-and-point and 30 of which were look-only trials. These trials alternated, such that participants would complete a look-and-point trial then a look-only trial then a look-and-point trial, and so on.

On exposure trials, the white light that provided vision of the hand was always extinguished at the onset of the eye or hand movement (whichever occurred first) and was always re-illuminated coincident with the completion of the reaching movement. This was the same for all groups (conditions). The behaviour of the target during the exposure phase was the only thing that differed between conditions, and we describe each of these below. The key differences are also depicted in Figure 4.2.

4.2.3.1 Online error condition

For the first 20 trials of the exposure phase the target appeared at location #2, and it remained at that location until the end of the trial. In other words, the target was at its initial location throughout the saccade and reach (look-and-point trials) or throughout the entire saccade (look-only trials). For the next 40 trials, the target initially appeared at location #2 and then either jumped rightward to location #5 (look-and-point trials) or jumped leftward to location E (look-only trials). These target jumps were always paired with the saccade. Note that in the Online Error condition the target always reappeared at its shifted location immediately after its offset at its initial location.

4.2.3.2 Terminal error condition

For the first 20 trials of the exposure phase the target appeared at location #2, disappeared at the onset of the saccade, and then reappeared at location #2 when the hand landed (look-and-point trials) or reappeared at location #2 after a 450 ms delay (look-only trials). For the next 40 trials, the target appeared at location #2, disappeared at the onset of the saccade, and then reappeared at location #5 when the hand landed (look-and-point trials) or reappeared at location E after a 450 ms delay

(look-only trials). In choosing the delay for the look-only trials, we wanted a duration that would be roughly equivalent to the delay between target offset and reappearance that would occur on look-and-point trials. We chose a 450 ms delay because this was approximately the amount of time between target offset and reappearance that we found in a previous study with a look-and-point terminal error condition (Cameron et al. 2010). Furthermore, 450 ms should be long enough to avoid the development of significant saccadic adaptation (Bahcall and Kowler, 2000; Fujita et al. 2002). The most important thing to note about the Terminal Error condition is that the target was absent during the reaching movement, unlike the Online Error condition.

4.2.3.3 Control condition

For the first 20 trials of the exposure phase the target appeared at location #2, and it remained at that location until the end of the trial for both look-and-point and look-only trials. For the next 40 trials, the target either appeared at location #5 (look-and-point trials) or appeared at location E (look-only trials). In both cases the target remained at its initial location throughout the trial. In other words, the control condition included no target perturbations during the exposure phase, unlike the other conditions.

4.2.4 Data analysis

Because our manipulation systematically induced target error in the lateral dimension, we focused our analysis on this dimension of the reaching movements. Prior to analysis of movement endpoints, endpoints were normalized with respect to the actual target location (normalized lateral endpoint = raw lateral endpoint – lateral position of target for that trial). After normalization, endpoint data for each participant was collapsed across every consecutive 5 trials, such that each participant had 10 values from the 50 trial pretest, 6 values from the exposure phase, and 10 values from the 50 trial posttest.

For analysis of saccadic eye movements, eye displacement was quantified by calculating the EOG voltage change between saccade onset and saccade end. Saccade end and onset were specified

offline by locating the peak voltage (saccade end) and then working backward from that point to find the first local minimum (saccade onset).

All statistical tests applied an alpha of .05.

4.3 Results

4.3.1 Motor adaptation from terminal and online error

We were particularly interested in whether exposure to the target perturbations produced aftereffects in the posttest phase. If participants were adapting to the error induced by the target displacement, we should see a positive aftereffect (i.e., a target overshoot) in the posttest. Figure 4.3, which shows the endpoint performance for each group over the course of all 3 phases, suggests that both the terminal error and online error groups developed positive aftereffects as a result of exposure, unlike the control group, which appears to have quickly returned to its pretest baseline. To statistically assess differences between the groups, we first subtracted pretest values from posttest values at each 5 trial time point for each participant. We then submitted these difference values to a 3 (group) x 10 (time point) ANOVA, with repeated measures on the second factor. The absence of an interaction between group and time point ($F(18,189)=.61, p>.80$) suggests that the stability of the aftereffects over time was not influenced by group membership. The absence of a main effect for time point ($F(9,189)=.89, p>.50$) further suggests that the strength of the aftereffects did not diminish over time. Finally, and most importantly, a significant effect for group ($F(2, 21)=17.04, p<.0001$) indicates that the magnitude of the aftereffects was not equivalent across groups. Post-hoc analysis of this effect (Tukey's HSD) reveals that both the terminal error group ($p=.0002$) and the online error group ($p=.002$) differed from the control group, but did not differ significantly from each other ($p=.19$).

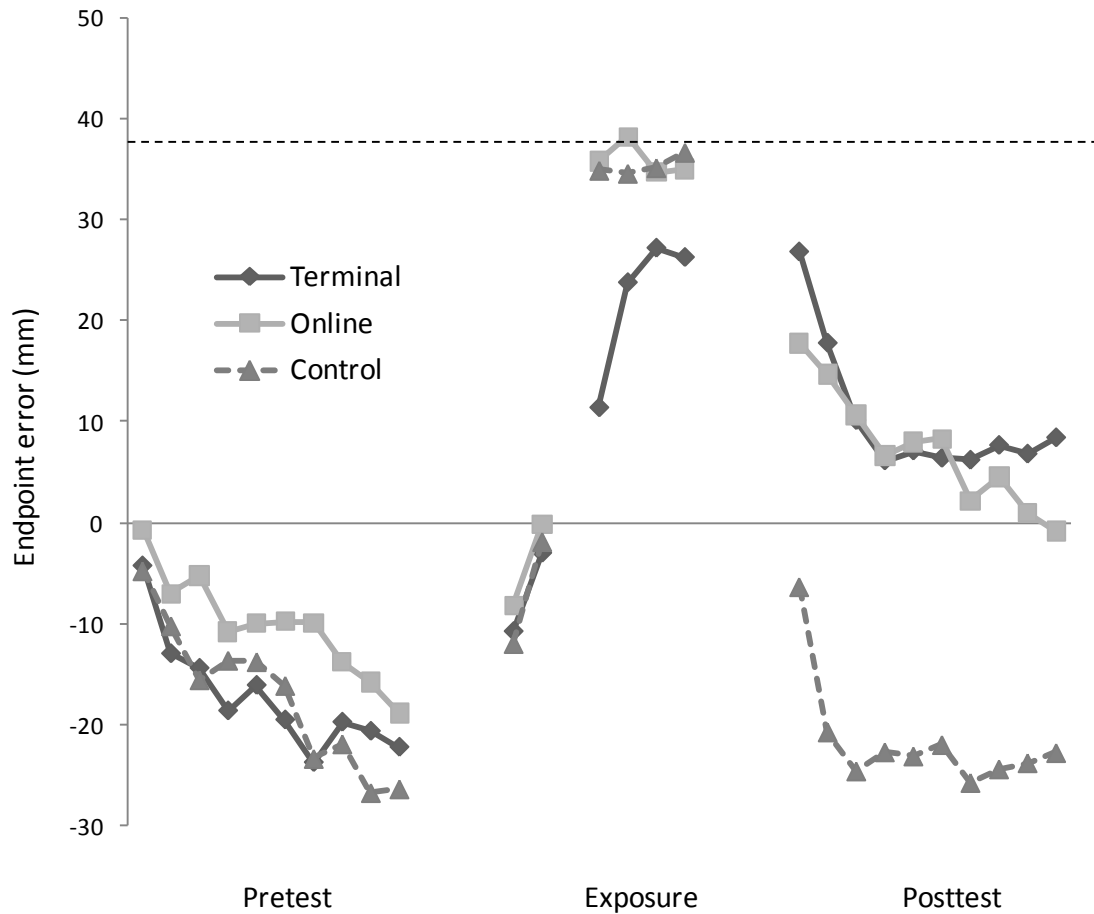


Figure 4.3 Time-course of reach endpoint performance for all 3 groups. All data points are data that have been collapsed across 5 consecutive trials and across participants. Endpoint error (on the y-axis) is with respect to the pre-saccadic target location. The horizontal dashed line at the top of the figure depicts the perturbed, post-saccadic location of the target (location #5) on the look-and-point trials of the exposure phase. Note that for all groups, the first 10 trials of exposure were non-perturbed trials: on these trials, the target had the same pre- and post-saccadic location (location #2). For the remaining 30 trials of exposure, the target was perturbed for the experimental groups. That is, the target appeared at its pre-saccadic location (#2) at the start of each trial and then reappeared at its post-saccadic location (#5), either coincident with the saccade (online error group) or at the end of the reach (terminal error group). For the control group, however, the target never jumped. It simply appeared at location #5 and remained there throughout the reach on each of the last 30 trials of the exposure phase.

4.3.2 Transfer of saccadic adaptation is not responsible for the reach aftereffects

It is important, particularly with the online error group, to rule out the possibility that reach aftereffects are the result of saccadic adaptation that transferred to the reaching movements, and it was for this reason that we included the de-adaptive look-only trials in the exposure phase. To

confirm that the reach adaptation that we observed was not the result of saccadic adaptation, we examined the change in saccade magnitude from pretest to posttest for each group. For each participant, we subtracted their average pretest saccade magnitude from their average posttest saccade magnitude. We then compared the difference scores across the 3 groups with a one-way ANOVA. There was no evidence of a difference between groups, $F(2,21)=.114$, $p>.80$. Thus, the reach aftereffects that occurred in the terminal and online error groups, but not in the control group, cannot be attributed to a transfer of saccadic adaptation to the limb.

There is, of course, the possibility that EOG (which, admittedly, provides only a rough measure of saccade magnitude) was not sensitive enough to pick up potential saccade differences between groups. To confirm that our EOG method was sensitive to saccade amplitude for the target distances we employed, we took each participant's average eye amplitude for each of the 5 target distances and submitted the data to a one-way repeated measures ANOVA. Target distance clearly influenced the EOG signal magnitude, $F(4, 92)=118.23$, $p<.0001$, suggesting that we can be confident in the EOG measure and, therefore, confident in our prior claim that reach aftereffects were not attributable to saccadic adaptation.

4.3.3 Awareness of the target perturbation

When participants were questioned at the end of the experiment about the presence of the target jump, none of the participants in either the terminal or online error groups reported noticing the target move during the look-and-point exposure trials.

4.4 Discussion

Our goal with the present study was to determine whether online error correction leads to a persistent modification in the way that subsequent movements are prepared. We employed a target error protocol (Magescas and Prablanc 2006; Magescas et al. 2009) in which error was created by the unseen displacement of a reach target rather than by the perturbation of limb feedback. Our results show that people adapt their reaches whether error is introduced at reach end (terminal error) or while the limb is in flight (online error). This finding does not necessarily imply that the same learning

processes are occurring for terminal and online error, but it does imply that persistent motor learning can result from either type of error.

As we mentioned in the Introduction, reach adaptation has been previously shown in studies that perturb visual feedback of the limb but also allow the participant to correct their reach online (Tseng et al. 2007; Diedrichsen et al. 2005; Hinder et al. 2009; Shabbott and Sainburg 2009; Jakobson and Goodale 1989). Those studies clearly suggest that terminal reach error is not required for adaptation; however, those studies include two sources of potentially relevant error that the present study does not. First, when vision of the hand is perturbed, visual hand-to-target error is available throughout the reach. Second, when visual feedback is perturbed, there is a discrepancy between anticipated visual feedback of the hand and the actual visual feedback. In the present study, visual feedback was not available during the reach so there was never any online visual hand-to-target error. (And, because movements were corrected online by the participants in the online error group, there was never any systematic terminal visual hand-to-target error.) Furthermore, because we never distorted visual feedback of the limb, there was never any discrepancy between anticipated visual feedback and actual visual feedback at the end of the reach. The results of our online error group suggest, therefore, that in the absence of each of these sources of error, some form of learning is still possible.

There are at least two remaining candidate error sources for the online error group: 1) online hand-to-target error based on a proprioceptive estimate of hand position and a visual estimate of target location and 2) online error between the predicted location of the limb (derived from efference copy) and the visual target location. Our study does not allow us to comment on which of these is the most likely contributor to the learning that we observed; however, in light of evidence that online error corrections can be driven by efference copy-based error signals (Bard et al. 1999; Desmurget and Grafton 2000), it is intriguing to consider that these same error signals might lead to modifications in movement planning.

We consider, next, three previous studies that have examined what is learned from online reach corrections to pure target error. The first of these, by Bekkering et al. (1995), had participants look and point, simultaneously, to a target that jumped during the saccade. Participants were exposed to repeated leftward target jumps, and the researchers examined the adaptive effects of the jumps on both eye and hand movements. Participants in their study received no online or terminal feedback of the limb during the exposure phase. Bekkering et al. observed that the amplitude of the eye movements and the reaching movements were shortened by the exposure to the target jump. They argued that this was evidence for the transfer of saccadic adaptation to the limb. They dismissed the alternative explanation that reach adaptation had transferred to the eye (or that the two systems had adapted independently) based on the not unreasonable assumption that because no visual error signals were present for the limb, there was no way for it to learn from the target jump. However, as we have shown in the present study, adaptation of reaching movements can occur in the absence of both a visual error signal and saccadic adaptation. Thus, the shortening of reach amplitudes that Bekkering et al. observed may, in fact, reflect adaptation of the limb to online error, independent of any concurrent saccadic adaptation.

The second study, by Diedrichsen et al. (2005), compared the learning effects of target jumps to the learning effects of cursor and force-field perturbations. In their target-jump condition, in which participants would correct their movement online to a visible target jump, they observed little to no learning. As we mentioned in the Introduction, the visibility of the target jump was a key factor in that experiment; it presumably allowed the participants to attribute the reach error to the environment rather than to themselves. We believe, therefore, that the difference in outcomes between Diedrichsen et al.'s target error condition and our online error condition can largely be accounted for by the visibility/invisibility of the target jump and the resulting differences in error attribution. Indeed, previous research from our lab has shown that a visible target jump in a terminal error protocol dramatically reduces the persistence of motor learning compared to the effects of an invisible jump (Cameron et al., 2010).

The third study, of course, is the one by Magescas et al. (2009), which employed a similar protocol to the one we used here. Like the present study, Magescas et al.'s study used an invisible target jump to induce error during the reach. Unlike the present study, however, that study found that participants did not adapt to online target error. There are some important differences between the studies, any one of which may account for the different outcomes. As mentioned in the Introduction, Magescas et al.'s study used a target perturbation (7.7 cm) that was considerably larger than the one used here (3.75 cm), such that error may have been less likely to have been attributed to programming and more likely to have been attributed to the environment. Their study also permitted vision of the limb throughout the reach, a feature that may have undermined adaptation by reinforcing the congruence between intended and actual visual outcome of the reach. Alternatively, the full vision may have created a large enough contextual difference between exposure and test phases that the learning did not transfer to the posttest phase (although such differences do not normally undermine adaptation in cursor perturbation protocols).

Another difference between our study and that of Magescas et al. (2009) was the arrangement of the limb and targets during the test phases. Magescas et al. (2009) applied a much stronger test than we did of the generalizability of the learning throughout the workspace and across limb configurations. In both their terminal and online error conditions, the pre- and post-tests involved a different hand start position and different target locations than the exposure phase. Our experiment, on the other hand, applied the same hand start position for all phases and, although we measured some generalizability by using several target locations in the test phases that were different from the locations used in the exposure phase, the locations we used were not distributed very widely throughout the workspace. It is possible, therefore, that our experiment simply revealed a local learning effect of online error that Magescas et al.'s study did not detect due to their more generalized testing method. In other words, it may be that learning occurs from both terminal and online error, but learning from the former generalizes considerably more than learning from the latter. Further experimentation would be required to isolate the critical difference between studies that led to the

different outcomes and to determine whether terminal and online error processing produce different kinds of motor learning. At the very least, however, our study allows us to conclude that both types of error processing can produce some form of persistent learning.

4.5 Bridging summary

Studies 1 and 2 investigated adaptation to terminal reach error, and the results of Study 2 suggested that predictive processing may be involved in such error processing. Study 3 has now shown that the visuomotor system adapts to online error, not just terminal error, and the study may also implicate predictive processing in this adaptation. The error signal that is generated during online control has been suggested to involve forward model predictions of limb position (Desmurget and Grafton 2000), and I have speculated, in the present chapter, that this online error signal may also act as a training signal for internal models, based on the observation that participants exhibit adaptation to online error. My research does not, however, provide direct evidence for predictive processing in adaptation to either terminal or online error; results from Studies 2 and 3 are merely consistent with the idea that sensory prediction is involved in motor adaptation.

The next study, Study 4, departs somewhat from the previous studies in that it does not investigate adaptation to target perturbations. Instead, it addresses adaptation to visual perturbation of the effector. Like the target perturbation studies, though, it indirectly investigates how expectations about movement feedback might influence learning. Study 4 examines the ways in which perception and motor control are influenced by active and passive exposure to a visual perturbation. Active exposure, in which participants control their movements themselves, theoretically involves the production of an efference copy and a sensory prediction, while passive exposure, in which the participant has their movement controlled by the experimenter, involves no efference-based predictions. By examining these conditions, we can make inferences about what kinds of information are necessary for adaptation of our perceptual sense of limb position and adaptation of movement control.

5 The adaptability of movement perception and movement control when the limb is actively versus passively moved¹²

5.1 Introduction

For most of our daily actions we spend little time consciously thinking about the locations of our various body parts or how to make these body parts do the things we want them to do. Our sensorimotor system seems to effortlessly draw upon visual, proprioceptive, and vestibular feedback, and probably even upon knowledge of its foregoing commands, to update its estimates of limb and body position and then to fluidly guide our actions. The system is also highly flexible, for it can adapt motor output when we encounter novel environments. If the dynamics of a limb are altered or if visual feedback is distorted, accurate performance can be reacquired after repeated exposure to the distortion (e.g., Shadmehr and Mussa-Ivaldi 1994; Krakauer et al. 2000; Welch, 1986). What processes drive this motor adaptation and what is the relationship between motor adaptation and our perceptual sense of limb position?

One influential model for motor adaptation suggests that the sensorimotor system uses a copy of an outgoing motor command (an efference copy) to make a prediction about forthcoming sensory feedback, a process called forward modeling (Tseng et al. 2007; Wolpert and Gharahmani 2000). To the extent that the prediction fails to match the actual sensory outcome, motor updating and forward model updating are required. A similar mechanism is thought to underlie our attribution of agency to our actions (Cullen 2004): If a comparison of predicted sensory feedback to actual sensory feedback produces a match, we attribute the action to ourselves, while a mismatch suggests that an external force has generated, or at least influenced, the sensory feedback¹³.

However, forward modeling for adaptation and forward modeling for agency attribution appear to be operating at cross-purposes. For motor adaptation, the greater the discordance between

¹² A version of this chapter is currently under review

¹³ The notion that an efference copy might be involved in differentiating self-generated from external feedback was originally developed by Von Holst and Mittelstaedt (1950) and subsequently elaborated to incorporate the concept of a forward model and a broader sense of action agency by Frith and colleagues (Frith et al. 2000).

predicted and actual feedback, the greater the error signal should be and the larger the adaptive response. For agency attribution, on the other hand, the greater the sensory mismatch, the less agency should be attributed, and the less relevant the error signal should be for action modification. (Why modify motor commands when the error is not self-generated?) Research on credit assignment during error correction may resolve this apparent conflict by suggesting that agency attribution comes before motor adaptation. Wei and Kording (2009), for instance, have shown that the larger the error between the target and the reach endpoint, the smaller the weighting of the subsequent adaptive response. It has also been shown that gradual introduction of prismatic displacements produces more robust aftereffects than the sudden onset of a large displacement (Michel et al. 2007) and, further, that people who are informed about a prismatic shift adapt less than those who are not (Jakobson and Goodale 1989). These prism studies suggest that the less aware people are of an external perturbation, and, accordingly, the more confident they are in their agency over the action, the stronger the adaptive response.

If the mechanisms for motor adaptation and sense of agency described in the foregoing paragraphs are correct, and if one further allows that a sense of agency over an action is required for motor adaptation to occur, then at least two claims should follow: 1) motor adaptation should only occur for actively generated movements, for only in these cases will an efference copy-based sensory prediction be produced, and 2) one's sensory expectations about self-generated movement should adapt in tandem with one's motor output. This second claim follows from the idea that sense of agency (i.e., one's sense of having caused a movement) relies on congruency between sensory expectation and sensory outcome; if sensory expectation did not adapt, we would not claim agency for the perturbed feedback, and motor adaptation would stall. Thus, if visual feedback is altered during active movement, we should see a modification in both our motor output and our perceptual expectations about the visual feedback.

With respect to the first claim, the necessity of active movement for motor adaptation has not been definitively shown, although the position has been strongly argued and empirically supported by

Held and colleagues (Held and Hein 1958; Held and Schlank 1959; Held 1965). It certainly appears that active exposure to a prismatically-induced perturbation *increases* the amount of adaptation relative to passive exposure (Pick and Hay 1965), although whether this is due to the presence of efference copy-based predictions or simply to enhanced proprioceptive feedback during active movement is not entirely clear (Welch 1986). The ability of a patient with proprioceptive loss to adapt to a cursor rotation (Bernier et al. 2006), however, does weigh in favor of the notion that efference copy plays a significant role in adaptation during active movement. Still, prism exposure experiments do appear to show that at least some adaptive response can be generated when participants are passively moved during exposure (Pick and Hay 1965; Singer and Day 1966; and see Welch 1986 for a review), suggesting that some form of motor adaptation can occur without efference copy. Such adaptation would presumably be the result of proprioceptive recalibration (i.e., a shift in proprioceptively-perceived limb position), which in turn results in modified active movement control.

As for the relationship between one's perceptual expectations and motor adaptation, only one study, to our knowledge, has directly investigated it. Synofzik et al. (2006) showed that people's perception of their own actions and their motor output were modified as a result of exposure to rotated visual feedback of their hand during active movement. The researchers probed changes in perceptual expectations by having people report the outcome of an active movement in the absence of visual feedback. They probed motor adaptation by examining changes in goal-directed action in the absence of visual feedback. They argued that the changed perceptual expectations were a pre-requisite for the changed motor output, for, although they sometimes observed perceptual adaptation without accompanying motor adaptation, the researchers never observed motor adaptation without perceptual adaptation.

In short, Synofzik et al. (2006) have suggested that motor adaptation develops as a result of modification of an adaptable sensory prediction, a sensory prediction that is generated as a result of active movement. In other words, the sensory consequences of movements for which we claim agency are updated, and this updating leads to motor updating. With the present study we wanted to

test whether similar sensory updating and motor adaptation might occur for movements over which we *do not* claim agency. Can sensory updating of active movements occur when visual exposure is constrained to passive movements? And if it can, does this also lead to motor adaptation? To address these questions, we occluded vision of the hand and forearm and projected a cursor over the location of the index finger. We gradually changed the gain between the finger's motion and the motion of the cursor and then examined how this perturbed visual feedback influenced subsequent perception and control of the limb. In the passive case, we exposed participants to the cursor perturbation while their limb was moved by a motor and then we probed active movement perception and control on trials in which there was no vision of the cursor or the limb. The absence of the cursor on probe trials was important for assessing adaptive influences that were independent of the effects of visual capture. Visual capture, a phenomenon whereby one perceives the limb to be at the same location as a perturbed representation of it, would be expected to occur when the cursor is visible (Hay et al. 1965).

We also investigated a secondary question, one that pertains to actively-guided movements: Might some of the perceptual updating observed by Synofzik et al. (2006) reflect recalibration of proprioception rather than an updated sensory prediction? There is some evidence that exposure to altered visual feedback during active movement recalibrates proprioception (Cressman and Henriques 2009; Malfait et al. 2008, cf. Wong and Henriques 2009; Smeets et al. 2006). To address this question we exposed participants to a cursor perturbation during active movements and then probed not only perception and control of active movements but also perception of passive movements. For the sake of completeness and clarity, we lay out below each of the questions that our experiment was designed to address:

Does exposure to visual feedback during **passive** movement of the limb influence perception of the passively moved limb? Does it influence perception of an actively moved limb? Does it influence goal-directed action?

Does exposure to visual feedback during **active** movement of the limb influence perception of the passively moved limb? Does it influence perception of an actively moved limb? Does it influence goal-directed action?

5.2 Materials and methods

5.2.1 Participants

Seven participants (3 female, 4 male) recruited from the university community took part in the study. All participants were self-reported right handed and had normal or corrected-to-normal vision. Ages ranged from 21-30. All participants provided informed consent prior to participation, and the study was conducted according to the guidelines of the University of British Columbia research ethics board.

5.2.2 Apparatus

Participants were seated at the apparatus depicted in Figure 5.1, their left and right arms positioned in manipulanda that allowed planar movement of each arm about the elbow joint. A computer mouse was fixed to the end of each manipulandum, such that the participant's index finger of each hand rested on a mouse button that could be used for perceptual report (see Procedure below). A half-silvered mirror located above the right arm prevented any vision of the limb when light below the mirror was extinguished, which was the case for the duration of the study. An inverted computer monitor was placed over the mirror at a distance equal to the distance between the right hand and the mirror, such that stimuli projected from the monitor onto the mirror appeared to be in the same plane as the hand. Vision of the left arm was occluded with a black cloth.

Display: A circular cursor (3.1 mm diameter) was projected over the location of the participant's right index finger. The distance from elbow to the tip of the index finger was measured for each participant so that the position of the mouse button and the projected cursor could be adjusted to coincide with the position of the tip of the right index finger. Each trial began with the cursor at the home position (a hollow circle, 12 mm in diameter). The home position was located at a position 25 deg counterclockwise from vertical, with the origin defined as the pivot point of the

manipulandum (the location of the participant's elbow). At the start of each trial, words appeared above the home position, indicating what type of movement and feedback would occur. On trials where the cursor was visible during the movement (exposure trials) vision of the cursor was occluded for the first 10 deg of the movement, reappearing once the 10 deg occlusion window was passed. The distance between the participant's eyes and their index finger was approximately 50cm at the home position; however, this did vary slightly between participants, depending on the length of the arm.

Stimuli were presented on a Viewsonic G220 flatscreen CRT monitor with image reversed left-right to compensate for the mirror reflection.

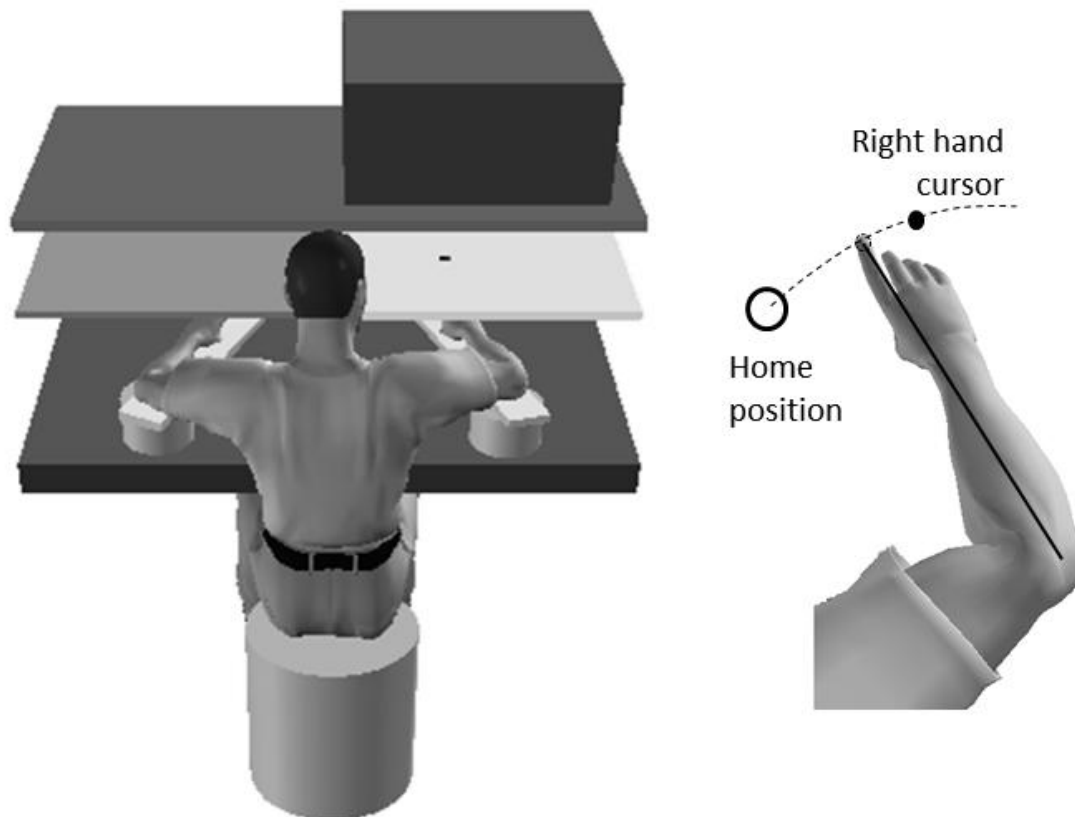


Figure 5.1 Schematic of the apparatus. Vision of both arms was occluded for the duration of the experiment. Cursor feedback was projected from the monitor onto the mirror above the participant's right hand. On the right is a schematic of the right hand and its cursor. Shown here is an exposure trial in which the cursor is at its maximum gain. Note that the active and passive reversal movements all occurred with the right arm. The perceptual report of right hand reversal point was accomplished by moving a second cursor (not shown here) with the left hand.

Manipulanda: The manipulanda were controlled by a Tech 80 three axis motion control card in a Pentium 233 MHz computer running Microsoft Windows '98 in DOS mode. Movement was executed by Infranor SMVEN 2410 servo amplifiers and Mavilor MT 220 DC servo motors (3.4 Nm, 135 Volts, 3.6 Amps). In the passive exposure and passive perception trials of the study, the right arm manipulandum accelerated at 200 deg/s^2 until the manipulandum was half-way to the reversal point (reversal points were 20, 22.5, 25, or 27.5 deg, depending on the trial), at which point it decelerated at -200 deg/s^2 until the reversal point was reached, then returned to the home position with a reciprocal velocity profile. Peak velocities were, accordingly, 63.2, 67.0, 70.7, and 73.48 deg/s for the movements to the 4 possible reversal points. On passive *target* trials, the manipulandum accelerated at 200 deg/s^2 until it reached a maximum velocity of 75 deg/s at 14 deg from the home position. It maintained this velocity until it reached 26 deg from the home position, at which point it decelerated at -200 deg/s^2 until it reached a final reversal point at 40 deg from home. This pattern would occur only if the participant failed to press the mouse button. As soon as the right hand's mouse button was pressed on these trials, the manipulandum immediately reversed its motion and returned to the home position. The movement profiles for the passive conditions were selected so as to roughly mimic a smooth reaching action. These profiles were chosen prior to data collection and were constant across participants; they did not, consequently, perfectly match the active movement profiles produced by the participants (Table 5.1).

The position of each manipulandum was measured with an optical encoder located at the manipulandum's axis of rotation. The encoders had a resolution of 60, 000 counts per revolution, and the position was sampled at 1, 000Hz as a 32 bit value that was subsequently converted to degrees.

Muscle activity: Electromyography (EMG) was used to monitor muscle activity in the biceps and triceps of the right arm. This was done to ensure that participants were relaxing their arm during the passive trials, allowing the servo motors to carry out the movement. EMG was collected with Ag-AgCl surface electrodes placed on the biceps and triceps of the right arm. The signal was amplified (10K) with a Grass Telefactor P55 A.C. Pre-amplifier. After each trial, the EMG signal was displayed

on screen to the experimenter, who could instruct the participant to relax their arm if significant muscle activity was observed on passive trials. This generally wasn't an issue, as participants had little difficulty allowing the motor to move their arm on passive trials. The EMG data were also stored for off-line analysis.

Table 5.1 Time to peak velocity and peak velocity for each trial type. PV = peak velocity. Exposure trials were either passive or active, depending on the session.

		Passive Session				Active Session			
Trial Type	Phase	Time to PV (ms)		PV (deg/s)		Time to PV (ms)		PV (deg/s)	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Exposure	Pre	352.79	15.63	68.48	0.20	342.43	57.04	119.34	34.40
	Post	352.77	7.11	68.36	0.15	289.16	65.86	96.54	27.97
Passive Target	Pre	423.46	22.01	77.37	0.94	408.74	27.69	76.32	1.56
	Post	410.00	31.10	75.57	2.73	395.88	37.33	75.04	3.54
Passive Perception	Pre	349.06	5.97	68.57	0.27	348.73	4.06	68.54	0.22
	Post	351.48	11.62	68.36	0.20	347.14	1.92	68.52	0.12
Active Target	Pre	311.01	74.77	121.16	26.89	326.28	57.67	115.09	35.19
	Post	317.91	67.38	115.75	27.26	299.10	62.40	99.98	31.72
Active Perception	Pre	308.31	69.66	123.73	29.43	349.98	88.35	121.25	34.84
	Post	305.90	63.46	122.27	25.25	298.09	64.97	95.98	30.22

5.2.3 Procedure

Each participant participated in two sessions, one of which involved exposure to visual feedback during passive movement only (passive exposure session), and one of which involved exposure to visual feedback during active movement only (active exposure session). These sessions occurred on separate days, and the order of the sessions was counterbalanced across participants. Each session included an entire 4-phase adaptation protocol: preadaptation phase, build-up phase, post-adaptation phase, and de-adaptation phase. The distribution of trial types within each session is shown in Table 5.2. Each of these trial types is described in more detail below. One's understanding

of the protocol may be aided by noting that we essentially applied two types of ‘training’ trials (passive exposure trials or active exposure trials) in which visual feedback of the fingertip was altered¹⁴. We then examined how each type of ‘training’ transferred to passive or active test trials (probe trials) in which no visual feedback was available.

5.2.3.1 Exposure trials

Exposure trials made up the bulk of trials in each session. During the pre-adaptation phase, the cursor was directly overlaid and mapped 1:1 with the motion of the participant’s index finger. In other words, there was no distortion of visual feedback on the exposure trials of the pre-adaptation phase: the gain of the cursor was 100%. During the build-up phase, the gain of the cursor was gradually increased from 100 to 150% over the course of 20 trials; each trial, the gain of the cursor was increased by 2.5%. During the post-adaptation phase, the cursor remained at 150% gain. During the de-adaptation phase, the cursor was at 100% gain for all trials. The relationship of the cursor with respect to the motion of the hand was the same for active exposure and passive exposure trials. No target was present on any exposure trials.

5.2.3.1.1 Active exposure trials (Active session only)

On these trials, the participant was instructed to make an out-and-back reaching movement to a self-chosen distance anywhere within a 20 deg arc that flashed on screen prior to the go tone.

5.2.3.1.2 Passive exposure trials (Passive session only)

On these trials, the participant was instructed to relax their right arm and allow the motor to move it for them. The motor would move the participant’s right arm, in an out-and-back motion, to one of four reversal-point distances (20, 22.5, 25, or 27.5 deg).

¹⁴ However, the term ‘training’ is slightly misleading, as there was no performance criterion that participants were aiming to achieve. There was no task other than moving the arm (or having it moved for you) and there was no error feedback at any point during the experiment.

Table 5.2 Distribution of trial types. The nature of exposure trials (active or passive movement) differed between sessions. All other trial types were the same for both sessions. Trial types were randomized in the pre- and post-adaptation phases.

Pre-adaptation phase	Build-up phase	Post-adaptation phase	De-adaptation phase
20% Exposure (cursor gain at 1.0)	100% Exposure (cursor gain increases from 1.0 to 1.5)	65% Exposure (cursor gain at 1.5)	100% Exposure (cursor gain at 1.0)
20% Active perception		9% Active perception	
20% Passive perception		9% Passive perception	
20% Active target		9% Active target	
20% Passive target		9% Passive target	

5.2.3.2 Probe trials

The experiment included four types of probe trials, none of which involved any visual feedback during movement. All probe trial types were present in the pre-adaptation and post-adaptation phases of each session. There were no probe trials in the build-up and de-adaptation phases of either session.

5.2.3.2.1 Active perception trials

These probe trials were used to assess the transfer of learning to the participant's perception of their own active limb movement. On these trials, the participant was instructed to make a fast out-and-back movement with their right arm to a self-chosen location within a 20 deg arc that was flashed prior to the onset of the movement. Perception of reversal point was assessed with a left-hand response. After completion of the right hand movement, the participant positioned a cursor, using the left manipulandum, at the point where they believed their right index finger reversed its movement.

5.2.3.2.2 Passive perception trials

These probe trials were used to assess the transfer of learning to the participant's perception of their passively moved limb. On these trials, the participant was instructed to relax their right arm while the motor moved it, out-and-back, with a reversal point at one of four distances (20, 22.5, 25, or 27.5 deg). Perception of reversal point was assessed with a left-hand response. After completion of

the right hand movement, the participant positioned a cursor, using the left manipulandum, at the point where they believed their right index finger reversed its movement.

5.2.3.2.3 Active target trials

These probe trials were used to assess the transfer of learning to goal-directed action. On these trials, a target would briefly flash at one of four locations (20, 22.5, 25, or 27.5 deg), disappearing prior to the go tone. The participant was instructed to make a fast and accurate out-and-back movement to the target location.

5.2.3.2.4 Passive target trials

These probe trials served a similar purpose to the passive perception trials in that they assessed the participant's perception of limb position during passive movement. In this case, however, a target was presented at the start of the trial. Participants were instructed to relax their right arm, allow the motor to move their arm, and then to press the mouse button with their right index finger when they felt that their right index finger was below the location at which the target had appeared. As soon as the button was pressed, the motor reversed its movement and returned the arm to the home position.

5.2.3.3 Left hand perceptual response

Every trial, both exposure and probe, consisted of two components: a right arm movement followed by a left hand response. Participants were not allowed to make the left hand response until the right arm had returned to the home position. The left hand response was made by moving the left manipulandum left or right, which caused a cursor to simultaneously move left or right along the same arc that the right index finger had recently traversed. The cursor gain for the left-hand response was constant throughout the experiment. Participants were permitted as much time as needed to place the left-hand-guided cursor as precisely as possible at the location where they believed their right hand had reversed its movement; once the participant had reached a decision, they pressed the mouse button under the left index finger. We stress that this was an un-speeded perceptual positioning task in which participants were able to move the cursor back and forth until a desired position had been

acquired. Left-hand responses were, therefore, unlikely to have been confounded by any potential inter-manual transfer of adaptation from the right hand¹⁵.

Although the left hand response was included for every trial type, its analysis was of particular interest for trials that were aimed at assessing perceptual adaptation (active perception and passive perception probe trials).

The participant was told that cursor feedback of the right hand, which only occurred on exposure trials, might be incorrect on some trials, so they should not rely solely on visual information to make their perceptual report, but should also rely on internal information about where they think their right hand went (Synofzik et al. 2006).

5.2.3.4 Experiment phases

As mentioned earlier, each session included several phases, as well as some initial practice. These phases are described here in greater detail. The only difference between active and passive sessions was the nature of the exposure trials. In all other ways the phases for each session were the same.

5.2.3.4.1 Pre-practice

This phase was not part of any analysis, and was simply administered to introduce the participant to the testing environment and to washout any lingering effects of the previous session. Ambient lighting was turned on, allowing participants to view their hand beneath the mirror. The cursor was projected over the tip of the right index finger, and 4 targets were visible to the right of the home position. Participants were instructed to make 5 out-and-back movements to each of the 4 targets.

¹⁵ Consider, as a similar case, trying to place one's finger at a desired location immediately after removing displacing prisms to which one had adapted. Although one's initial trajectory would likely be in error, online corrections would easily permit acquisition of the target on the first trial. Thus, even if the right-hand's adaptation was transferring to the left hand in our study, we are not particularly concerned about this influencing the accuracy of the left-hand perceptual report. Furthermore, even if inter-manual transfer were influencing the left-hand report, this would produce an undershoot bias with the left hand; i.e., it would lead to an *underestimate* of the magnitude of perceptual adaptation. Accordingly, any perceptual effects that we show would be *in spite* of such transfer rather than because of it.

5.2.3.4.2 Practice

After receiving the instructions describing all 5 types of trial that would occur during the session, lights were extinguished (removing all vision of the right hand), and participants were given 20 trials of practice, in which 4 repetitions of each trial type were encountered. All ambient light remained extinguished for the rest of the session.

5.2.3.4.3 Pre-adaptation phase

In this phase, participants completed 80 trials. Each of the 5 trial types made up 20% of trials, such that there were 16 repetitions of each trial type, and these were randomly intermingled. On exposure trials the cursor was directly over the right index finger tip (i.e., unperturbed).

5.2.3.4.4 Build-up phase

In this phase, participants completed 20 trials, all of which were exposure trials. Over the course of the 20 trials, the cursor gain was increased from 100% (cursor distance from home matched the hand's distance from home) to 150% (cursor distance was 1.5 times the hand's distance from home) in increments of 2.5% each trial.

5.2.3.4.5 Post-adaptation phase

In this phase, participants completed 184 trials. Roughly 65% (120 trials) were exposure trials, all of which were at 150% cursor gain. The 4 types of probe trial (Active perception, Passive perception, Active target, and Passive target) each occurred 8.7% of the time (16 trials). Trial types were randomly intermingled.

5.2.3.4.6 De-adaptation phase

In this phase, participants completed 20 trials, all of which were exposure trials. Cursor gain was at 100% for all trials. These trials were designed to eliminate adaptation to the cursor distortion, minimizing any potential carry-over of adaptation to the second day of testing.

5.2.4 Data analysis

5.2.4.1 EMG analysis

EMG data were analyzed for the active target trials and the passive exposure trials of the pre-adaptation phase of the passive exposure session. The passive exposure trials were chosen for analysis because they are the critical trials on which recalibration to the visual stimulus would be occurring during the passive session. Active target trials were chosen for comparison for two reasons: 1) because they occur on the same day as the passive exposure trials, unlike the active exposure trials, and this reduces differences in the EMG signal that might arise from electrode placement on different days, and 2) it allows for averaging across trials for a specific target distance that is not possible with the active exposure trials. For each trial type, EMG traces were averaged across 5 trials of the same distance (25 degrees).

5.2.4.2 Adaptation analysis

We quantified adaptation effects by calculating an error score for each type of response and then comparing pre-adaptation and post-adaptation error scores. For movement endpoint on target trials, error was equal to the distance between the target location and the right hand's endpoint (reversal point). These error values were normalized to the distance of the target. For perceptual report of endpoint, error was equal to the distance between the reported location (i.e., left-hand report) of the right hand's endpoint and the right hand's actual endpoint. These error values were normalized to the amplitude of the right hand reach, which was the target for the perceptual report.

Our analysis focused on two main questions. First, did the cursor manipulation produce adaptation for each trial type? Second, did the amount of adaptation for each trial type depend on the type of exposure? To address the first question, we compared pre-adaptation error values to post-adaptation error values with one-tailed paired-sample t-tests. We employed directional tests because of our expectation that the positive cursor gain, if it was to have an effect, would produce a positive change on perception probe trials and a negative change on target probe trials (Synofzik et al., 2006; Krakauer et al., 2000). For these planned comparisons, an alpha level of .05 was used for each test.

To address the second question, we first calculated adaptation scores for each trial type by subtracting the pre-adaptation error from the post-adaptation error. We then submitted these adaptation scores to two-tailed paired-sample t-tests, comparing the amount of adaptation for a given trial type across exposure types. Non-directional tests were employed here because we did not have strong predictions about the direction of these differences. A Bonferroni correction was applied to these comparisons, resulting in a corrected alpha level of .01 for each test.

To aid interpretation of the adaptation effects, we have also included adaptation effects expressed as percent adaptation. This was done by dividing the adaptation score (post-adaptation error – pre-adaptation error) by the difference that would be expected from complete adaptation to the 1.5 cursor gain. To get this expected difference, we first added the normalized error in the pre-adaptation phase to 1, which provided the proportion of the target distance that was travelled prior to the perturbation. If, for instance, mean normalized error was -0.10 in the pre-adaptation phase, the proportion of target distance travelled would be 0.9. We then multiplied this proportion by 1.5 to obtain the distance that would have been travelled in the case of complete adaptation to the perturbation (1.35 in this example). The difference between the pre-adaptation value and the ‘complete adaptation’ value constituted the expected difference (0.45 in this example). The ratio of the actual adaptation score to this expected difference was the percent adaptation.

5.3 Results

5.3.1 Muscle activity on active and passive trials

Figure 5.2 shows agonist (triceps) and antagonist (bicep) activity for each participant on the active target trials and passive exposure trials of the passive session. Each participant’s EMG trace exhibits an agonist burst followed by an antagonist (braking) burst on the active target trials. Importantly, the agonist burst always precedes the onset of displacement of the manipulandum in the active target trials. This contrasts with the muscle activity on passive exposure trials, where there is never any burst preceding the onset of the movement. Some participants exhibit a small amount of muscle activity on these trials, but where this does occur, it is always as a response (probably

reflexive) to the motion of the manipulandum. It is reasonable to infer, therefore, that participants were not generating goal-directed actions on the passive trials and did not experience agency over the movements, which were guided entirely by the motor.

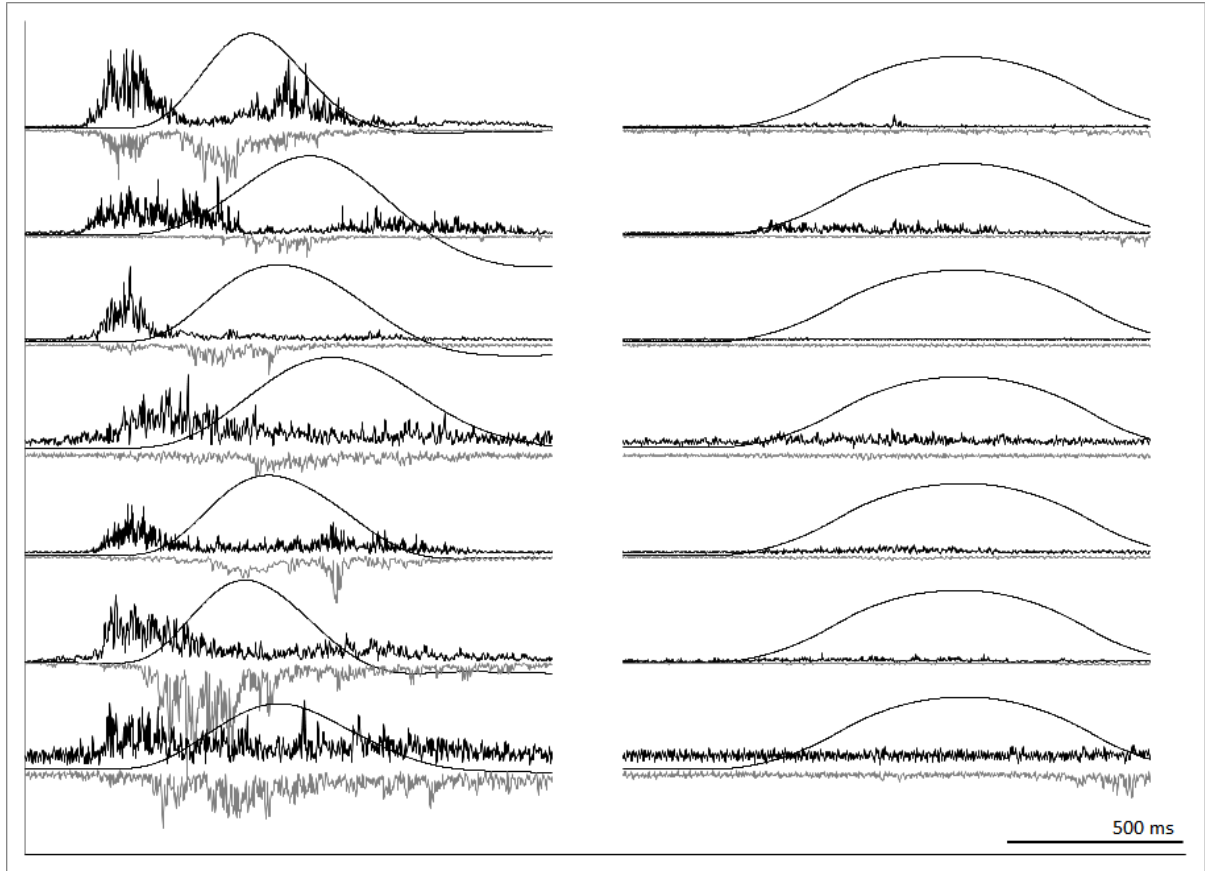


Figure 5.2 Average EMG traces for active target trials (left) and passive exposure trials (right). Each row contains the data for a single participant. The upper EMG trace in each profile represents the activity of the triceps (agonist), while the lower trace represents the activity of the bicep (antagonist). Corresponding average displacement profiles of the right arm (smooth black lines) are also displayed.

5.3.2 Passive exposure influences passive movement perception

In the passive exposure session participants viewed the cursor only when their limb was being passively moved. What impact did this have on participants' reports of their limb's reversal point? On exposure trials themselves, participants reported that their right hand was moving farther rightward in the post-adaptation phase than in the pre-adaptation phase, $t(6) = 12.13$, $p < .0001$ (Figure 5.3A). This outcome is not particularly surprising, but it does suggest that the cursor manipulation

was producing a ‘visual capture’ of sorts, in which participants perceived their limb to be nearer a concurrent visual stimulus than it actually was (Hay, Pick, & Ikeda, 1965). Note that this occurred despite participants’ explicit knowledge that the cursor feedback may be incorrect.

Passive probe trials provide a better measure of a true modification in participants’ perception of their passively moved limb as a result of the visual manipulation. Recall that probe trials involved no visual feedback and thus, in this case, forced participants to rely on proprioception. On passive perception trials, participants generally indicated that their right hand had traveled farther on post-adaptation trials than on pre-adaptation trials, $t(6) = 5.35$, $p = .0009$ (Figure 5.3B). On passive target trials (trials on which participants depressed the right mouse button when they perceived the right index finger to be at a flashed target) participants generally depressed the button sooner in the post-adaptation phase than in the pre-adaptation phase, $t(6) = 6.46$, $p = .0003$ (Figure 5.3C). Both sets of probe trial results imply that participants’ perception of their passively moved right limb was shifted rightward by the cursor manipulation.

5.3.3 Passive exposure influences active perception and control

Did the effects of passive exposure transfer to active movement perception and active movement control? These effects were assessed with active perception and active target trials, respectively. On active perception trials, participants generally perceived their movement reversals to be farther to the right in the post-adaptation phase than in the pre-adaptation phase, $t(6) = 2.96$, $p = .013$ (Figure 5.3D). On active target trials, participants generally made shorter movements on post-adaptation trials than on pre-adaptation trials, $t(6) = 4.43$, $p = .0003$ (Figure 5.3E). These results suggest that both active movement perception and targeted movement control were influenced by the passive cursor manipulation.

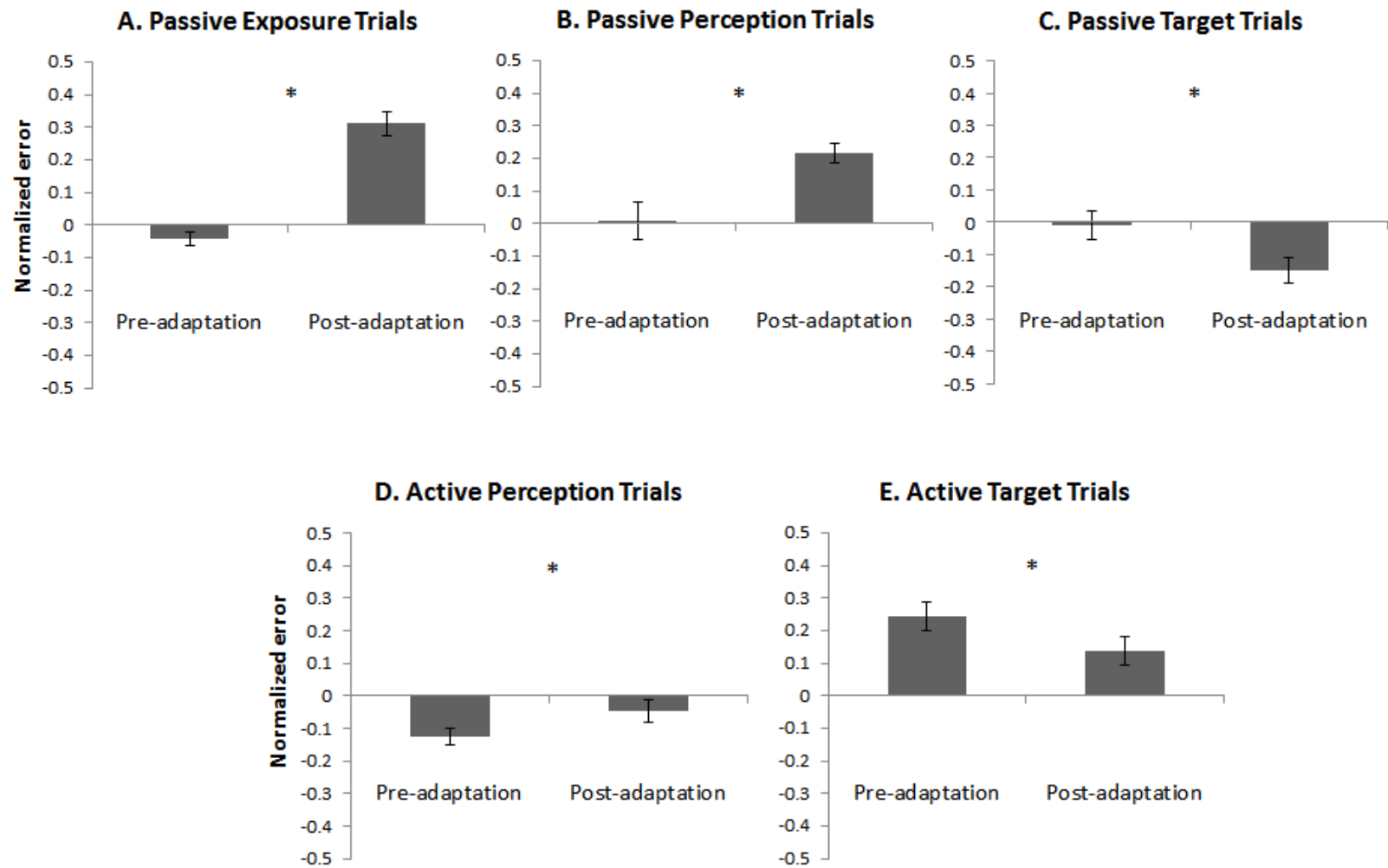


Figure 5.3 Adaptation in the **passive exposure** session. Error on perception trials reflects the difference between reported reversal point and actual reversal point, whereas error on target trials reflects the difference between the right hand's reversal point and target location. Error bars represent standard error of the mean.

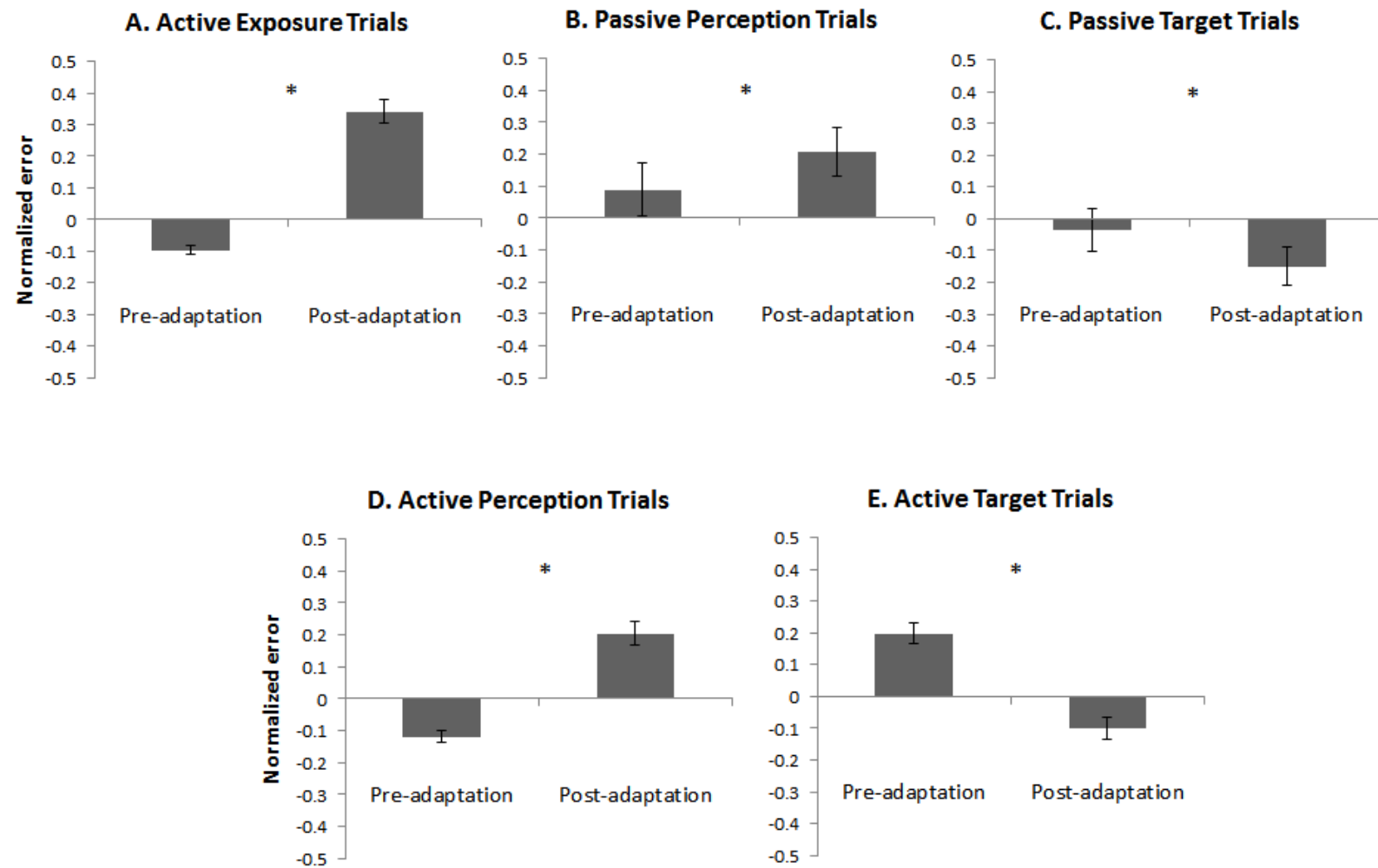


Figure 5.4 Adaptation in the **active exposure** session. Error on perception trials reflects the difference between reported reversal point and actual reversal point, whereas error on target trials reflects the difference between the right hand's reversal point and target location. Error bars represent standard error of the mean.

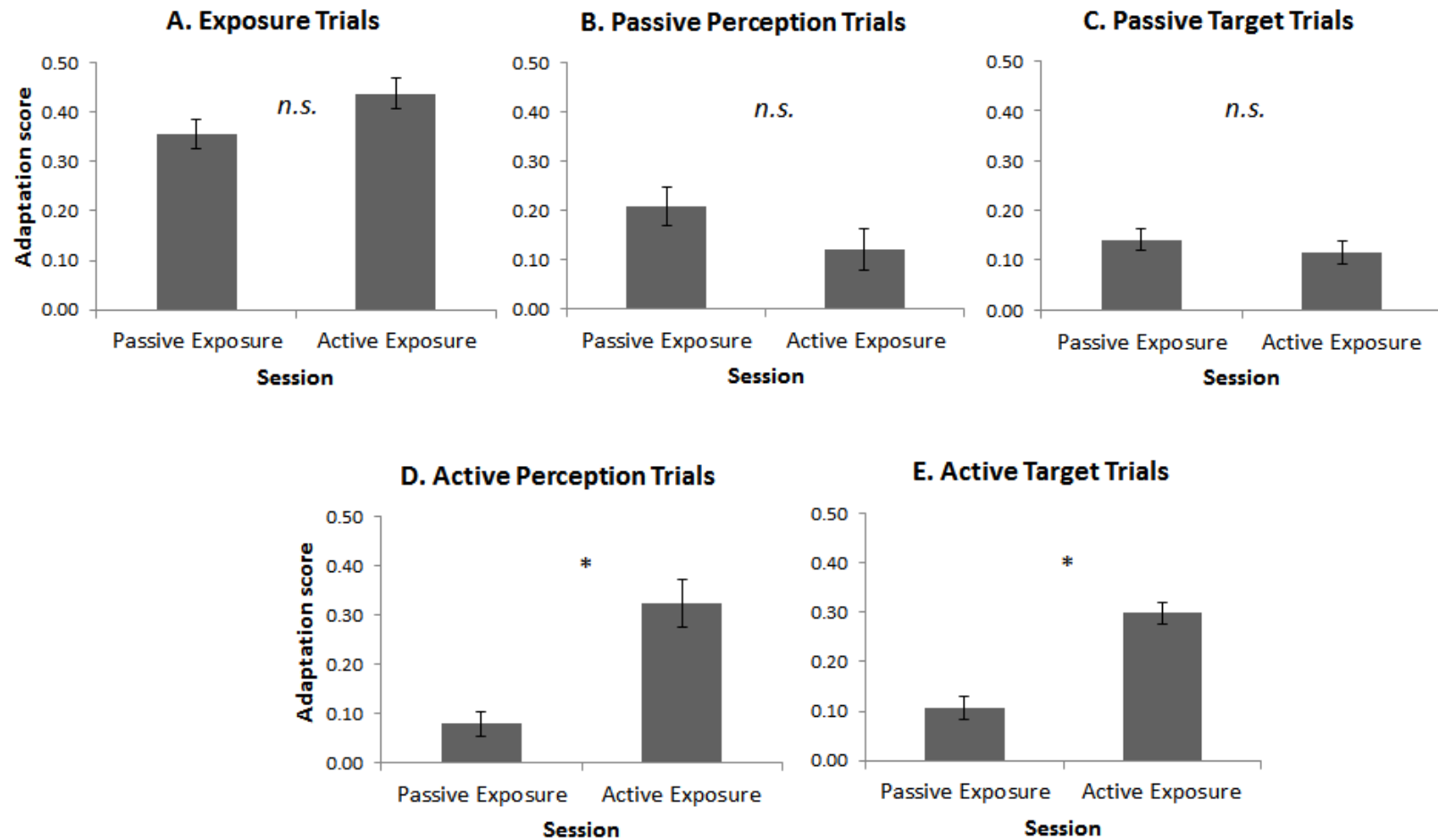


Figure 5.5 Relative amounts of adaptation after passive versus active exposure. Adaptation score is the difference between the normalized post-adaptation error and the normalized pre-adaptation error. Error bars represent standard error of the mean.

5.3.4 Active exposure influences active perception and control

In the active exposure session participants viewed the cursor only when they actively moved their right arm. On active exposure trials themselves, participants' reports of their right hand's reversal point were strongly affected by the cursor manipulation; participants reported that their right hand moved farther rightward in the post-adaptation phase than in the pre-adaptation phase, $t(6)=13.98$, $p<.0001$ (Figure 5.4A).

The cursor manipulation also influenced how participants perceived their active movements when no visual feedback was available. On active perception trials, participants reported that they moved their right hand farther on post-adaptation trials than on pre-adaptation trials, $t(6)=6.78$, $p=.0003$ (Figure 5.4D). Participants also changed their targeted reaching as a result of the cursor manipulation. On active target trials, participants made shorter reaches in the post-adaptation phase than in the pre-adaptation phase, $t(6)=13.66$, $p<.0001$ (Figure 5.4E). Thus, both perception and control of active movements were affected by active exposure to the cursor manipulation.

5.3.5 Active exposure influences perception of passive movements

To assess the impact of active exposure on perception of the passively moved limb we examined passive perception trials and passive target trials. Participants generally reported that their limb moved farther rightward in the post-adaptation phase than in the pre-adaptation phase on passive perception trials, $t(6)=2.78$, $p=.016$ (Figure 5.4B). Participants also tended to stop their movements earlier on passive target trials in the post-adaptation phase, $t(6)=4.85$, $p=.003$ (Figure 5.4C). Both effects suggest that active exposure to the cursor perturbation produced some degree of proprioceptive recalibration in the participants.

5.3.6 Active exposure produces more adaptation on active test trials than passive exposure does

For each trial type we compared the adaptation score (post-adaptation – pre-adaptation) from the passive exposure session and the active exposure session. This comparison allowed us to examine the amount of adaptation on exposure trials themselves as well as the amount of transfer from each

exposure type to each trial type (Figure 5.5). For exposure trials, we did not find a statistically significant difference between passive and active sessions, though there was a trend towards greater adaptation for the active (97%) than for the passive (74%) session, $t(6)=2.06$, $p=.085$. For passive perception trials, we did not find a significant difference between active (22%) and passive (41%) sessions, $t(6)=1.80$, $p=.12$. For passive target trials, there also was no difference between active (35%) and passive (42%) sessions, $t(6)=-.97$, $p=.37$. On active perception trials, however, we observed significantly greater adaptation for the active (73%) than for the passive (18%) session, $t(6)=3.88$, $p=.008$. On active target trials, we also observed significantly greater adaptation for the active (75%) than for the passive (26%) session, $t(6)=7.09$, $p=.0004$.

5.4 Discussion

Our goal was to assess the impact of passive and active exposure on the perception and control of reaching movements. Synofzik et al. (2006) have already shown that people's perception of their limb movements adapts in tandem with, and may even be a pre-requisite for, adaptation of goal-directed action. Their study, however, restricted visual feedback exposure to active movements. In the present study we introduced passive movements, movements to which we would not expect people to attribute self-agency¹⁶. We used these passive trials to assess, first, whether proprioceptive recalibration occurs in the absence of self-agency. We then examined whether such recalibration, if it occurs, impacts participants' perception and control of active movements. We were also interested in whether proprioceptive recalibration occurs during active movement exposure.

Our main findings are that 1) passive exposure to a perturbed visual stimulus can produce proprioceptive recalibration, which, in turn, can influence not only the perceived outcome of active movements, but also their control, and 2) active exposure to a perturbed visual stimulus can also

¹⁶ We did not ask participants about their sense of agency over the movements. We are, therefore, relying on the assumption that participants did not perceive passive movements as self-generated. Our own experience with the apparatus strongly suggests that this is a safe assumption; the perception is that one's arm is being transported entirely by the motors.

produce proprioceptive recalibration, though this change appears to account for only a fraction of the modification in active movement perception and control that results from active exposure.

5.4.1 Adaptation from passive exposure

When participants in our study were exposed to an increased cursor gain during passive movements, they tended to report (immediately after exposure) that their limb had moved quite a bit farther than it really had (Figure 5.2A). On average, participants changed their report of the right hand's displacement by about 74% of the perturbation magnitude. This large and immediate effect that occurred on exposure trials is probably driven largely by 'visual capture', in which people perceive their limb to be at or near the same location as a visually-perturbed representation of it. Visual capture is thought to decay fairly rapidly (Hay et al. 1965), and it has been argued that it is a separate process from true proprioceptive recalibration (Welch et al. 1979). Our passive perception and passive target trials, during which participants received no visual feedback, are, therefore, better measures of actual proprioceptive recalibration. The results from these no-vision trials suggest that some degree of proprioceptive recalibration had occurred (Figure 5.3). Perceptual reports on passive perception trials were shifted by about 41% of the perturbation magnitude.

Actively controlled movements were also influenced by the passive exposure. Participants reported that they were moving their limb farther in the post-adaptation phase and they made shorter reaches on trials in which they had to hit a target. Thus, the proprioceptive recalibration that occurred from passive exposure to the cursor appeared to impact how participants perceived and controlled their active movements.

Ours is not the first study to show that passive exposure to a visual perturbation can influence active movement control to a target. Indeed, several prism adaptation studies have shown that passive exposure can produce motor aftereffects (e.g., Pick and Hay 1965; Singer and Day 1966; Fishkin 1969). Whether these effects argue against a role for actively generated feedback (reafference) in motor adaptation, however, is not clear. Although Pick and Hay (1965), Held and colleagues (Held and Hein 1958; Held and Schlank 1959), and Foley and Maynes (1969) found stronger aftereffects

from active exposure than from passive exposure, suggesting that reafference is important, Singer and Day (1966) and Fishkin (1969) found that active and passive exposure did not produce significantly different effects.

Our results tend to support the view that reafference plays an important role in motor adaptation. Although we observed some influence of passive exposure on active targeted movements, it was a relatively small effect (approximately 26% of total perturbation magnitude) compared to the impact of active exposure on active targeted movements (approximately 75% of total perturbation magnitude). This might indicate that efference copy-based sensory predictions play a significant role in motor adaptation. However, given possible contextual differences between active and passive movements in our study, such as movement kinematics that were not perfectly equated between movement types, that are independent of the presence/absence of efference copy, we recognize that our finding of greater active-to-active transfer than passive-to-active transfer can only be offered as weak support for efference copy-mediated adaptation. There is also the possibility that proprioceptive feedback is enhanced during active movements relative to passive movements, allowing for stronger adaptation during active movements, independent of any putative efference copy-based sensory prediction. Notably, however, direct measurements of spindle activity do not support the hypothesis that active movement enhances spindle tuning relative to passive movement (Jones et al. 2001).

Let us return, though, to the effect of passive exposure on active reaching. Although this was a relatively small effect, it does suggest that proprioceptive recalibration, which presumably occurred without any sense of agency over the movement apart from a sense of ownership over the limb, can transfer to active limb movements. The shorter movements that occurred on active target trials following passive exposure to the cursor may be the result of a change in the visuomotor system's estimate of limb starting position. If the estimate of the reaching limb's starting position was farther to the right after adaptation, this would lead to the shorter movements that we observed in the post-adaptation phase. We are assuming, here, that visual and proprioceptive estimates of initial starting position are combined and then used in the preparation of a motor command (Rossetti et al., 1995;

Sarlegna & Sainburg, 2009). In our design, visual information about the hand's start position was present and veridical on every trial. Consequently, any shift in the estimate of the hand's start position that might have occurred on active target trials would have resulted from a bias in the proprioceptive estimate. The transfer of passive exposure to active reaching in our study is consistent with recent work by Cressman and Henriques (2010), which showed that passive exposure to a visually rotated cursor influences subsequent active reaching. It appears, therefore, that transfer of passive exposure to active reaching occurs for both visual rotations and gain manipulations.

However, our findings contrast somewhat with the findings of a recent study by Kammers et al. (2009). In their study, Kammers et al. investigated the impact of the rubber hand illusion (RHI) on action. Briefly, the RHI is the perceptual illusion that one's hand is at the same location as a fake hand, and the effect is often enhanced by simultaneously stroking the real and fake hands. The effect is, presumably, similar in nature to the visual capture that occurs with prisms (Hay et al. 1965). Kammers et al. found that, while perception of hand position was influenced by the fake hand, active movements with the hand were not affected. Kammers et al. interpreted this outcome as evidence for dissociation between perception and action (Milner and Goodale 1995). However, other studies of visual capture and reaching (Rossetti et al. 1995; Holmes et al. 2004; Holmes et al. 2006) have shown an impact of the visual manipulation on subsequent reaching movements. Rossetti et al. (1995) used prisms to shift vision of the hand's initial position; Holmes et al. (2004) used a mirror to shift vision of the hand's initial position; and Holmes et al. (2006) used a fake limb, like Kammers et al. (2009). It is possible that some of the difference in outcome between these studies, which all showed strong effects of the visual manipulation, and that of Kammers et al., which did not, is due to the timing of the perturbation relative to movement onset. Unlike the other studies, Kammers et al.'s study included a delay of approximately a minute between visual exposure and movement onset (a delay during which the perceptual report was made). It may be that the effects of visual capture had decayed by the time the motor response was made in the Kammers et al. study, as there is some evidence, with prisms at least, that the effect decays within a matter of seconds (Hay et al. 1965). This issue of

timing does not necessarily undermine Kammers et al.'s claim that perception and action are impacted differently by the RHI, for they did show that the perceptual effect persisted even after the motor task was completed, implying that the perceptual effect had not disappeared over time. However, it does leave the possibility that the effects of visual capture impacting motor control, which may operate on a different timescale than the perceptual effects, had decayed during the period of no vision. Consequently, their claim that the RHI does not impact action is still open to debate.

Of course, an important difference between our study and the foregoing visual capture studies is the dynamic versus static nature of the perturbation. In our study, the arm and cursor moved together through the reaching space, whereas in the other studies the perturbation was only applied to the static limb prior to movement. A second important difference between our study and the other studies is that ours presented unperturbed visual feedback, at the home position, at the start of every trial. Thus, the potential visual capture by the cursor at the start of each active target trial would have actually been working *against* any recalibration of proprioception that had been built up during the exposure trials.

Another difference between our study and those that apply the RHI is the visual stimulus itself. A rubber hand is considerably less abstract than a cursor, and the RHI can induce the conscious sensation that the rubber hand *is* the real hand (Botvinick and Cohen 1998), whereas a cursor – even in cases where one might believe that it is directly above one's hand – is unlikely to have such a visceral effect. Indeed, merely placing the rubber hand in an unnatural position or replacing it with a block of wood can significantly reduce the impact of the stimulus on reaching movements (Holmes et al. 2006), suggesting that a lack of morphological similarity between the hand and the object can diminish visual capture. There is also evidence from the adaptation literature that reach aftereffects are smaller with a cursor than with vision of the hand (Clower and Boussaoud 2000). These considerations raise an important question: What do cursor perturbation protocols tell us about real-world sensory integration?

With the present study, we are working under the assumption that the cognitive processes that underlie sensory recalibration in real-world settings are the same ones that operate during exposure to a cursor perturbation, even though the strength of the recalibration may be weaker in the latter case. This potentially weaker recalibration by a cursor may imply that the present study underestimates the amount of proprioceptive recalibration that would occur had we used a more hand-like stimulus. However, the recalibration induced by a cursor may not be as relatively weak as what one might expect from the RHI literature; although a stationary block of wood induces less visual capture than a rubber hand, the block of wood, unlike the cursor in the present design, does not move with the hand, so there is potentially less basis for proprioceptive recalibration with a block of wood than with a moving cursor.

5.4.2 Perception versus action

An important feature of our study was that it measured both participants' perceptions of their movements and participants' control over their movements. When participants were exposed to visual feedback on active movements, we found that both perception and action were updated. These results are consistent with those of Synofzik et al. (2006), who similarly showed that perceptual reports were updated in tandem with the control of targeted reaches. We further showed that perception of active movements was updated following passive movement exposure and, importantly, that this perceptual updating influenced active movement as well. Both outcomes imply a perception-action link, particularly the passive exposure effect, for in this case (where there was never any conflict between action and feedback, i.e., no motor training) pure perceptual updating did have an influence, albeit small, on motor performance.

Our intent is not to challenge models of visual processing that suggest a perception-action dissociation (e.g., Milner and Goodale 1995), and, indeed, our experiment was not designed as a strong test of such models. However, our results, as well as those of Synofzik et al. (2006) do suggest that there is an intimate link, at some stage of visuomotor processing, between what we consciously perceive and how action adapts to a visual perturbation.

Although we have stressed that perceptual modification from passive exposure affected motor performance in our study, there remains the possibility that the effects we observed from passive exposure reflect a very different mode of learning from that which occurs during active movement. Even if one could find equivalent amounts of motor adaptation following passive exposure and active exposure, as some prism studies have done (e.g., Singer and Day 1966; Fishman 1969), this would not necessarily imply that learning during *active* movement is solely, or even partly, due to the perceptual changes that occur during passive exposure.

5.4.3 Proprioceptive recalibration from active exposure

There is currently some debate as to whether proprioception is recalibrated in the presence of visual feedback. Smeets et al. (2006), for instance, argued that it is not. Employing a design that alternated blocks of no vision with blocks of veridical visual feedback, they showed that position sense quickly drifts back to its pre-exposure level once vision is removed. Consistent with those findings, Wong and Henriques (2009) showed that proprioceptive sense of hand path was not altered after participants were exposed to altered visual feedback. However, studies by Malfait et al. (2008) and by Cressman and Henriques (2009) have provided evidence that people *do* recalibrate proprioception after exposure to altered visual feedback. The latter study, for instance, in which participants were exposed to a cursor perturbation during active targeted reaching, showed a resulting shift in perceived hand location that was equivalent to approximately 25% of the perturbation magnitude.

Our results tend to support the view that proprioception does undergo some recalibration, however modest, after active exposure to a visual perturbation. We found that, on passive perception trials, participants reported their limbs to have moved farther in the posttest than in the pretest by an amount that was equivalent to approximately 22% of the perturbation (compared to 73% on active perception trials and 75% on active target trials). These results are remarkably similar to those of Cressman and Henriques (2009), despite major differences in protocol. They employed translation and rotation perturbations, whereas we used a gain perturbation. Furthermore they had participants

report static limb position with respect to reference markers, whereas we had participants report the remembered reversal point of the limb's movement.

5.4.4 The relationship between proprioceptive recalibration and motor adaptation

Visual distortion protocols such as ours clearly create conflict between proprioceptive and visual feedback, and some researchers (e.g., Redding and Wallace 2002) have suggested that this conflict, and subsequent realignment between visual and proprioceptive reference frames, is critical for 'true' adaptation. However, two lines of evidence suggest that sensory realignment may not be a critical process for adaptation. First, there is evidence from studies of deafferented patients that adaptation to altered visual feedback is possible in the absence of proprioception (e.g., Bernier et al. 2006; Ingram et al. 2000). Second, robust aftereffects have been shown in studies that only manipulate target location during the reach, rather than feedback of the limb (Magescas and Prablanc 2006; Cameron et al. 2010). It appears, therefore, that aftereffects can occur when there is no sensory conflict; yet we also know from the passive exposure results of the present study and from passive prism exposure studies that aftereffects can occur when there is *only* sensory conflict.

Thus, it appears that at least two processes – sensory recalibration and error-based learning (possibly forward-model mediated) – can contribute to aftereffects. The relative contributions of each process will, of course, depend on the nature of the perturbation and the task. Target perturbations (e.g., Magescas and Prablanc 2006) will produce purely error-driven adaptation, whereas active exposure to a cursor perturbation may involve a combination of proprioceptive recalibration and error-based learning, where error is the difference between the intended and actual visual outcome. The presence of a target during such visually-perturbed reaching may amplify the amount of error-based learning by providing a stable reference point for error assessment. Indeed, there is evidence that adaptation to prisms is more robust when a target is present (Welch 1986), though whether this enhancement is due to an increase in error-based learning has not been shown; we are only speculating.

5.5 Conclusion

Our results show that passive exposure to a cursor gain perturbation produces proprioceptive recalibration and that this recalibration can influence not only the perception of active movements, but also their control. Thus, sensory conflict in the absence of efference-based sensory prediction does appear to affect perceptual and motor performance, though the effect is relatively small. Our results also suggest that active exposure to a cursor gain perturbation can lead to some proprioceptive recalibration; however, this effect was also small, suggesting that it is not an integral part of motor adaptation.

6 General discussion

The research outlined in the foregoing chapters was aimed at understanding some of the principles that govern the adaptation of reaching movements in humans. More specifically, the research investigated the ways in which adaptation is influenced by 1) an agent's awareness of the source of reach error, 2) an agent's explicit control over their reach, 3) whether target error occurs *during* a movement or at its end, and 4) sensory recalibration from exposure to a visual perturbation. Overall, the research paints a picture of a visuomotor system that learns most effectively by anticipating movement feedback from self-generated movements and then assessing error based on the difference between anticipated error and movement outcome. However, the research also suggests that more than one process may contribute to reach adaptation, one of which (sensory recalibration) may not rely on active control. In the following discussion I will first summarize the key outcomes of each study. I will then address what my research and relevant literature suggest about specific principles of error-based processing. I will then address some of the implications that my results have for our understanding of sensory recalibration, why we may want to consider it as operating independently of error corrective processes during adaptation, and why reafference may only be relevant to error-based processing. Finally, I will provide some speculations about how my findings inform a current model of reach control and motor learning.

6.1 Summary of research findings

6.1.1 The visibility of a target perturbation undermines reach adaptation

The first study of the thesis tested the hypothesis that, in order to adapt to target error, the error must be attributable to the agent rather than the environment. I manipulated the visibility of a target perturbation and showed that when the perturbation was most visible, aftereffects were the least robust. This was despite the fact that participants in all groups adjusted their movements, during exposure, so as to compensate for the error induced by the target perturbation. These results suggest that awareness of the perturbation prevented the accumulation of implicit learning. That is, participants who were *unaware* that the target was being displaced came to implicitly associate a

target at a given distance with a motor command of a larger magnitude than prior to exposure, such that they over-reached the targets in the posttest, whereas participants who saw that the target was being moved during exposure developed no such implicit association. However, it was not clear from this study whether it was the explicitness of the perturbation or the explicitness of the resulting control (i.e., a top-down control of the movement during the exposure phase so as to contact the target) that was directly responsible for the absence of aftereffects in the explicit error group. The next study was informative in this regard.

6.1.2 Explicit control of reaching does not undermine adaptation to target error

The second study of the thesis had two goals: first, to determine whether explicit control, when rigidly maintained, would prohibit the development of implicit motor learning and, second, to determine whether error-based learning in a target perturbation protocol is driven by direct error processing or indirect, prediction-based, error processing. This study employed the same type of target perturbation that was used for the SacStart group in the first study of the thesis (for which a target disappeared at the onset of the saccade and then reappeared, displaced, at reach completion). However, in this study, participants were given an explicit undershoot task in which they were instructed to miss the target, to the left, by a specific distance. Our results showed that participants still implicitly learned from the invisible target perturbation, for they demonstrated aftereffects in the posttest, reaching too far to the right when they were instructed to aim directly to the target. This outcome demonstrated that implicit motor learning can occur while participants are engaged in an explicit reach task. This result supported previous research by Mazzoni and Krakauer (2006), but also extended it by showing that neither visual perturbation of the effector nor direct error correction over the course of the exposure phase is required for the emergence of reach aftereffects. Furthermore, this study suggested that, during reaching movements, the visuomotor system makes a prediction about hand-to-target distance and compares this prediction to the actual outcome. This mechanism contrasts with the one proposed by Magescas and Prablanc (2006) and Magescas et al. (2009), who suggest that direct hand-to-target error, not feedback prediction, is what drives motor adaptation.

6.1.3 Online and terminal error can both produce reach aftereffects

The third study of the thesis investigated the impact of online error correction on reach adaptation. Online correction, which eliminates hand-to-target error at the end of a reach, might eliminate the need for adaptation. On the other hand, an error signal is being generated when a target jumps during a movement and it is not unreasonable to assume that the system might want to eliminate such error during future reaches, perhaps for greater movement efficiency. Previous research had suggested that online error correction does not produce aftereffects (Magescas et al. 2009), but there were features of that study, such as large target jumps and concurrent vision of the limb that may have undermined the development of reach aftereffects. We examined a terminal error condition (where the displaced target appeared at the end of the reach) and an online error condition (where the target displacement occurred during the reach) and found significant aftereffects in both conditions. These results suggest that the error signal that occurs while the limb is in flight can have a lasting impact on subsequent movement planning. Furthermore, this study suggests that visual hand-to-target error is not a necessary component for the adaptation of reaching movements.

6.1.4 Passive exposure to a visual perturbation of the effector influences movement perception and control

The fourth study of the thesis contrasts with the other studies in that it investigated adaptation to a visual perturbation of limb feedback, rather than adaptation to a target perturbation. Whereas the previous studies expressly avoided creating conflict between vision and proprioception, the fourth study focused on such a conflict. Furthermore, the study prevented target-based adaptation by not presenting a target on exposure trials. In short, the fourth study served as a complement to the other studies, focusing as it did on the adaptive effects of perturbed limb feedback, rather than targeting error.

The main findings of the study were that 1) passive exposure to a visual perturbation influences how we perceive such movements (proprioceptive recalibration), 2) passive exposure to a visual perturbation can influence how subsequent active movements are controlled, suggesting that

proprioceptive recalibration from passive exposure influences the control of active movements, and 3) active exposure to a visual perturbation influences how we perceive our passive movements, which suggests that proprioception is also recalibrated from active exposure to a visual perturbation. However, the study also suggested that the proprioceptive recalibration that occurs during active exposure accounts for only a small amount of the total adaptive effect that arises from active exposure. This implies that a major component of adaptation is the error signal between expected and received visual feedback, even when no target is present.

6.2 Principles of error-based processing

This section of the discussion focuses specifically on error-processing contributions to adaptation, as opposed to sensory recalibration contributions. Because Studies 1 through 3 employed a target perturbation protocol, which precludes adaptive influences from sensory recalibration, this section draws mainly on those studies to inform our understanding of error processing in the visuomotor system.

6.2.1 Error attribution during motor learning

Prior research on visual perception suggests that our visual system tends to assume that the environment is stable. If, for instance, an object moves at the same time as our eyes do, pre-saccadic estimates of target location will typically be ignored in favor of the assumption of environment stability (Deubel et al. 1998). One of the hypotheses of the current research was that the adaptation of reaching movements relies on the integrity of this assumption. We hypothesized that if the assumption of stability was violated by, for instance, visibly moving the target of a reach, then adaptation would be undermined. The results from Study 1 (Chapter 2) support this hypothesis. The rapid aftereffect decay for a visible target perturbation suggests that participants in that group did not develop an implicit association between the pre-reach target location and the requisite motor commands for transporting the hand to its perturbed location. That is, despite repeated successful acquisition of the perturbed target in that group, it did not produce the same kind of motor learning as when the target was presumed to be stable.

The visible target perturbation in Study 1 presents an extreme example of environment instability, one that presumably permits nearly complete attribution of error to an external source. Under normal reaching conditions, however, error attribution is probably rarely so clear-cut. Rather, the visuomotor system is likely continually faced with uncertainty about how much error in movement is due to internal sources and how much is due to external perturbations of the limb or the target. Recent work by Wei and Kording (2009; 2010) suggests that the visuomotor system may use a Bayesian approach to attributing error, in which the system's estimate of the probability that movement error resulted from a given source influences the extent and locus of the adaptive response.

A discussion of Bayesian processes in motor learning is beyond the scope of the present document. However, investigations of error attribution may benefit from a consideration, in the future, of possible differences in error attribution tendencies when people are exposed to target versus effector perturbations. Although I did not make a direct comparison, within a single study, between adaptation to target perturbation and adaptation to effector perturbation, there are hints from the present research, as well as from research by others (e.g., Diedrichsen et al. 2005), that we adapt differently to each type of perturbation. This may be especially true when the perturbations are noticeable. That is, even when a very large and easily detectable visual perturbation of the effector is applied, people still exhibit aftereffects, though they may be smaller and shorter-lived than when the perturbation goes undetected (Michel et al. 2007). However, when a target perturbation is made visible (Study 1), aftereffects are virtually non-existent.

The difference between noticeable target displacements and noticeable effector displacements may, in fact, be due to inherent uncertainty about the actual location of the limb in effector perturbation protocols. In such protocols there is no visual information about the veridical location of the effector; there is only proprioceptive information about its location. However, this proprioceptive estimate comes with uncertainty about the location of the limb relative to other objects in the reach environment, and even some uncertainty about the actual location of the effector may not allow for complete cancellation of the adaptive influence of the effector perturbation in such a scenario. This

contrasts with a visible target jump like the one used in Study 1, where there is little ambiguity about the presence or size of the target perturbation, which occurs entirely within the visual domain.

Perhaps a better comparison of the adaptive effects of visible target and visible effector perturbations could be achieved by presenting the effector's veridical location alongside the perturbed effector feedback. Such a protocol would allow the visuomotor system a more accurate, and entirely visual, assessment of the amount of reach error resulting from the effector perturbation, making it more comparable to a visible target perturbation.

6.2.2 'Top-down' versus 'bottom-up' control of reaching

One of the questions that arose from Study 1 was whether the explicit control of reaching, by which participants in the ReachEnd group would deliberately reach farther than the target's initial location so as to hit the perturbed location, was responsible for the absence of aftereffects. In other words, does explicit, or 'top-down', reach control inhibit adaptive processing? This type of reaching is comparable to 'anti-pointing', in which participants point away from a target location. This contrasts with more 'bottom-up' reaching, in which the visual stimulus is permitted to directly guide the movement.

As already described, Study 2 showed that implicit motor learning could emerge despite not only explicit control, but also prevention of direct corrections to target error. This study was in accord, therefore, with previous work by Mazzoni and Krakauer (2006) (previously described in Chapter 3) that showed that implicit learning could proceed during explicit control when an effector perturbation was applied. One of the novel contributions of Study 2 was to show that similar principles applied when the target was perturbed, rather than visual feedback of the effector.

These target error-based results reveal some of the similarity between reach adaptation and saccadic adaptation (Bahcall and Kowler 2000) and, more importantly, allow us to make inferences about the role that feedback prediction plays in the adaptation of reaching movements. These are topics that are explored in the next section.

6.2.3 Adapting the eye vs. adapting the hand and the role of prediction in motor adaptation

Extensive research of saccadic eye movements has shown that the oculomotor system is capable of robust adaptation. In the typical saccadic adaptation paradigm, a target is presented in the visual periphery, and the participant's task is to look at the target. While the eyes are in flight, the target is imperceptibly perturbed by a small amount, either forward or backwards from its initial location. Initially, saccades miss the perturbed location of the target and a corrective saccade is required. Unlike reaching movements, saccades are too fast to engage in meaningful online correction, though small amounts of online correction have been reported (e.g., Gaveau et al. 2003). However, over the course of repeated exposure to a systematic target perturbation, saccades begin to go directly to the perturbed location of the target. Furthermore, when the exposure phase is over, saccades exhibit aftereffects, such that the eyes continue to overshoot (or undershoot, depending on the direction of the perturbation) the target.

While the mechanisms of saccadic adaptation are not yet fully understood, there is evidence to suggest that visual error is the critical adaptive signal, rather than the motor signal that arises from the corrective saccade (Pelisson et al. 2009). That is, it is the error between intended and actual visual feedback when the eyes fail to reach the target that leads to subsequent modification of the primary saccade, rather than the motor command that is issued to acquire the target following the initial miss. Moreover, there is evidence to suggest that the visual error signal does not rely on direct fovea-to-target error, but actually applies a remapping process by which a visual prediction (based on the eye movement command) is made, and the discrepancy between this prediction and the actual visual feedback provides the error signal (Bays and Husain 2007; Pelisson et al. 2009). Some of the evidence for this process comes from research by Bahcall and Kowler (2000), in which participants were instructed to execute an undershooting (or, rather, 'underlooking') saccade during a saccadic adaptation protocol. Despite this undershoot task, participants still adapted to the target perturbation, suggesting that the system was estimating the visual signal that would arise from the eye movement and comparing this estimate to the actual visual feedback.

It is interesting to consider whether the principles that govern saccadic adaptation are similar to those that govern reach adaptation. Eye and hand movements do differ in several respects that may initially lead one to expect that adaptive processes in the two systems would be very different. For instance, unlike eye movements, hand movements are capable of online corrections. They also involve considerably more degrees of freedom and require more complex sensorimotor transformations. Yet, despite these differences between systems, it seems that in some ways their adaptive processes are very similar. Like saccades, reaching movements adapt to pure target error (Magescas and Prablanc 2006; Cameron et al. 2010). Furthermore, like saccades, the motor command from a secondary corrective movement does not appear to be required for, nor does it appear to enhance, reach adaptation (Magescas and Prablanc 2006; Tseng et al. 2007). It also appears that, as for saccades, adaptation to target error in reaching movements relies on prediction-based error, rather than direct effector-to-target error, as demonstrated by Study 2 of the present document.

Despite these apparent similarities between systems, saccadic adaptation and reach adaptation have been traditionally investigated with very different methods. Saccadic adaptation is typically investigated with a target perturbation protocol, whereas reach adaptation is typically investigated with prism, cursor, or force manipulations of the effector, which introduce, among other things, visual-proprioceptive conflict, a conflict which is not typically present in investigations of saccadic adaptation. It is only relatively recently that target perturbations have been used to investigate reach adaptation (Diedrichsen et al. 2005; Magescas and Prablanc 2006). I suggest that greater use of target perturbation protocols in future investigations of reach adaptation will allow researchers not only to isolate error-based adaptation (avoiding the complicating effects of proprioceptive recalibration), but also allow them to make more meaningful comparisons between eye and hand control systems.

6.2.4 The adaptive effects of terminal versus online error in reaching movements

As already mentioned, one of the differences between reaching movements and saccadic eye movements is the former's ability to be fully corrected online. If a target moves, if the limb is perturbed, or if there is simply too much noise in the motor command, the reach trajectory will be in

error. This initial error in a reach, however, can be overcome through online correction. The processes that govern such corrections are not fully understood, though there is evidence (as presented in Chapter 1) that the fastest, most automatic corrections, may be driven by predictive estimates of the effector's location relative to the target, derived from efference copy that is combined with lagging visual and proprioceptive estimates of effector location (Desmurget and Grafton 2000).

One of the questions that the current project sought to answer was whether the error signals that are used to correct movements online impact the preparation of subsequent movements and lead to aftereffects when the perturbation is removed. Some earlier research that I had carried out (Cameron et al. 2008, Appendix A) suggested that when participants are exposed to repeated saccadically-suppressed online target perturbations, they modify the planning of subsequent reaches (Appendix A). Research by Magescas et al. (2009) suggested, likewise, that participants modified reach planning during exposure to repeated online target perturbations. However, Magescas et al. also showed that, despite these modifications during the exposure phase, there were no aftereffects during the posttest. This contrasted with exposure to terminal error, which led to robust aftereffects (Magescas and Prablanc 2006). Magescas et al. consequently concluded that terminal and online error processing are driven by separate mechanisms.

As outlined in detail in Chapter 4, there were several features of Magescas et al.'s design that may have undermined the development of reach aftereffects that were independent of whether reaches were subject to terminal or online error. The study that I carried out (Chapter 4) attempted to address some of the disparities between online and terminal error conditions that existed in Magescas et al.'s design. The results suggest that, contrary to Magescas et al.'s assertion of distinct mechanisms for terminal and online error processing, both types of error lead to aftereffects. Of course, an outcome that shows similarly-sized aftereffects for terminal and online error processing does not necessarily imply that the same mechanisms underlie their generation. It does, however, suggest that there is an absence of evidence for distinct mechanisms.

Given that much of the present research is based on work by Magescas and Prablanc (2006) and Magescas et al. (2009), and employs very similar protocols to theirs, it is worth considering their suggested mechanisms for reach adaptation and addressing some of the ways in which these mechanisms differ from the ones I am proposing.

Magescas et al. (2009) make the following claims: 1) the critical component of reach adaptation is effector-to-target error, 2) predicted to actual feedback comparisons are not involved in target error adaptation and may not be involved in effector perturbation protocols either, and 3) the effector-to-target error must be present at the end of the movement in order for adaptive processing to occur (i.e., online corrections that eliminate terminal error also eliminate adaptation). Their claims are not without merit, and I will summarize, shortly, the evidence they invoke to support them. However, their claims also rely on some questionable assumptions, some oversight of relevant experimental evidence, and some potential confounds in the design of one of their experiments.

Their first claim, that effector-to-target error is the critical component of reach adaptation, is based on the results of Magescas and Prablanc (2006). In that experiment there was no visual distortion of hand feedback (and, accordingly, no inter-sensory conflict); rather, the location of the target was moved, imperceptibly, between the start and end of the reach. Such a design clearly rules out sensory recalibration as a factor in the adaptation that they observed. However, it does not so clearly rule out predictive processing as a potential contributor to adaptation.

Magescas et al. (2009) suggest that predictive processing is not involved in adaptation to target error by assuming that such processing would only involve comparisons to feedback *during* a movement. In their own words,

[Our results] depart from the generally accepted view that the signal driving adaptation is the mismatch over the course of movement between the expected and actual sensory feedback. (p. 345)....[I]t should be noted that many models...like those proposed for prism adaptation or force fields, use as an error signal the mismatch between the actual visual feedback of the

limb and the forward model's output.... [I]ndeed this error signal is null in the present experiment as there is no such mismatch. (p. 347)

This is a very restrictive view of predictive processing. It restricts prediction of feedback to the flight of a movement, foregoing any predictions about the movement's endpoint relative to its environment. Such a view neglects evidence that predictive processes can be involved in the adaptation of saccadic eye movements, where the only relevant error signal occurs at the end of the movement (Bahcall and Kowler 2000). And, of course, Study 2 of the present document now suggests that such predictive processes *are* involved in reach adaptation to target error, calling into question Magescas et al.'s claims about the absence of such processing in their design.

Their third claim, that online error does not lead to adaptation, is based on their finding of no aftereffects when the target's perturbed location was presented during the movement, rather than at completion. I have addressed in detail (Chapter 4) potential problems with their design that may account for their failure to find aftereffects of the target perturbation. I have not yet addressed, however, their inference that, when online error is introduced, "...as long as the target is perceived as unique and as long as the error is unconsciously corrected online, there is no need to modify the planning of subsequent trials." (Magescas et al. 2009, p. 346). While it is not unreasonable to argue that full correction of an error during a movement might eliminate the need for subsequent change in planning, their statement appears to be refuted by their own data from their exposure phase. Velocity profiles from their study suggest that movements in the exposure phase of the online error condition were being initiated in the direction of the perturbed target location; in fact, this effect appeared to be as substantial as the effect in the terminal error condition.

Unfortunately, the authors do not address the velocity profiles in their discussion. Taken at face value, the profiles would suggest that trial-to-trial movement planning was being influenced by the online error, contrary to their statement that the presence of online correction obviates the need for changes in movement planning. The challenge, then, would be to explain the absence of changed movement planning during the posttest phase. One possibility would be that cognitively-mediated

processes were involved in movement planning during the exposure phase, perhaps as a result of the fairly large target perturbation (7.7 cm), and that the altered planning did not transfer to the posttest.

Alternatively, the changing velocity profiles may not actually reflect changed planning during the exposure phase. The target perturbation in the online condition was tied to the saccade, which typically precedes the onset of the hand movement, and so the perturbed target location may have begun influencing reaches during the hand reaction time period, effectively producing ‘online’ corrections prior to (or very shortly after) reach onset (van Sonderen et al. 1988). However, the authors do not address the possible implications of their exposure phase velocity profiles, nor do they include any data regarding the onset of the eye relative to the hand, so it is unclear how we should interpret such results.

Based on their findings (specifically, the pre- to posttest endpoint effects in the online and terminal error conditions), Magescas et al. (2009) propose a model for reach control and learning in which forward model predictions are involved in online corrections (i.e., control) but not in the modification of subsequent movements (i.e., learning). Their model further suggests that the principal adaptive signal is the comparison between effector *endpoint* and target location. As I have already argued, their claim that forward modeling is not involved in learning is challenged by 1) the tenuous nature of their assumption that target error protocols do not produce conflict between feedback prediction and outcome and 2) Study 2 of the present document, which provides evidence that prediction is involved in target error-based learning. Their assertion that only terminal target-based error contributes to motor learning is challenged by Study 3 of the present document, which showed that online error, too, can lead to reach adaptation. In a later section I will propose a different model, one that retains a role for forward modeling in motor learning and that, furthermore, suggests that forward model-based error signals that possibly occur during online correction might also serve as training signals for future reaches.

6.2.5 The role of a visible target during reach adaptation

None of the studies that I conducted directly compared reach adaptation in the presence of a visual target to reach adaptation in the absence of a visual target. I am somewhat restricted, therefore, in the claims that I can make about the role of the target in reach adaptation. However, some general observations might still be made. First, the fact that adaptation was shown in the first 3 studies, which involved *only* target perturbations (and no perturbation of limb feedback) clearly suggest, along with the initial research by Magescas and Prablanc (2006), that a visual target, all by itself, can drive reach adaptation. This is even the case when there is no visual feedback during the reach and when the reach corrects online to the perturbation, removing all visual hand-to-target error (Study 3). Second, the occurrence of reach adaptation in Study 4, wherein there was no visual target during exposure, suggests, as does much previous work with prism and cursor perturbations (e.g., Held and Hein 1958; Synofzik et al. 2006), that adaptation can proceed in the complete absence of a visual target.

What role might a visual target play during reach adaptation? Does a visual object in the reach environment merely serve as a reference point, adding precision to the visuomotor system's estimate of reach error, or is there something special about an object being the target of a reach? Study 2, in which participants undershot the 'target' yet still exhibited adaptation, does suggest that a visual object can drive adaptation even when it is not the direct target of a reach. However, adaptation in that case did appear to be somewhat less than that which occurred in Study 1, where the perturbed object was the direct target of the reach. This might suggest that, in a target-error protocol, adaptation is enhanced when the perturbed object is the direct target of the reach.

When visual feedback of the limb is perturbed rather than the target of the reach, there is some evidence from prism research that the presence of a visual target enhances reach adaptation (Welch 1986). Presumably, the presence of the target enhances the precision of the error estimate. Again, however, it is not clear whether this effect depends on the target being the goal of the reach or simply being a stable visual element in the environment relative to which error can be assessed. Future studies that directly compare conditions in which the perturbed object is the target of the reach

to conditions in which the perturbed object is simply a neighbouring element in the environment might allow us to answer this question.

6.3 Sensory recalibration versus error-based processing

6.3.1 Multiple causes of reach adaptation

One of the issues raised in Chapter 1 was the difficulty of defining two terms that are at the very center of the present research: motor learning and adaptation. I suggested that adaptation is a specific kind of motor learning, a low-level, implicit process of adjusting internal models (as opposed to forming new ones, which might be conceived as skill acquisition (Shadmehr and Wise 2005)). I also mentioned that one of the common operational definitions of adaptation (and also the one that was applied to the studies in the thesis) is the emergence of aftereffects following exposure to a perturbation of some kind. One of the arguments that I will attempt to make over the course of the remaining discussion is that adaptation, itself, is a multi-component process. I will further suggest that the number and nature of the components in adaptation depends on the nature of the perturbation to which people are exposed, and that only error-based components should properly be termed motor learning. Sensory recalibration, on the other hand, which can also contribute to aftereffects, might be considered a form of perceptual (or sensory) learning, but, I will argue, should be considered an independent process from motor learning.

6.3.2 Revisiting Held's reafference hypothesis

According to Held (1965), motor learning and motor development are driven by the same adaptive process, a process by which the visuomotor system correlates motor commands with sensory feedback. This is not conceived, by Held, as an error correction process, by which the system would learn by overcoming movement error from prior exposure, but rather as a rearrangement of perceptual expectations. For instance, motor command 'x' results in visual feedback 'y', and by learning the systematic relationship between motor commands and visual feedback, we can acquire the ability to operate under novel feedback conditions. For Held it was critical that movement be actively generated; only in this way can motor commands be correlated with sensory feedback. In the absence

of a command, there is nothing to be correlated with the feedback, and no learning can occur. It was also important for Held that adaptation be measured with a protocol that avoided error detection and correction. In Held and his colleagues' experiments, participants were exposed to prismatically-displaced visual feedback of their limb, and they made movements within a featureless, target-less environment.

However, Held's conception of the adaptive process can be re-framed in an error-processing manner, where the error is the mismatch between anticipated feedback and actual feedback. The error, in this case, is not as explicit as the error that arises when a visual target is present and there is a potential visual separation between hand and target. Held's argument can, I would suggest, (apart from mainly being a strong argument for the role of active engagement in motor adaptation) be taken as an argument against the role of *direct* error processing, but not necessarily as an argument against error processing per se.

On the basis of my results and those of others, I will argue that error processing, specifically prediction-based error processing, is an important component of reach adaptation, one that, by definition, relies on active movement control. However, I will also argue that sensory recalibration is a component of reach adaptation, but that its development does not rely on active exposure to a perturbation. Thus, while I will tend to agree with Held in many respects, my perspective is one that breaks adaptation down into two components: an error-based component and a sensory recalibration component. Based on data from the present thesis and from recent studies of sensory recalibration, I will argue that active control is only important for the error-corrective component of adaptation, while the sensory-recalibration component emerges simply from the coincidence of conflicting sensory feedback, whether actively or passively generated.

6.3.3 Sensory recalibration and error-based adaptation are independent processes

A recent study by Cressman and Henriques (2009) showed that participants recalibrated their proprioceptive sense of static limb position after engaging in a visuomotor adaptation task. The task involved reaching to visual target while visual feedback of the hand was perturbed (either rotated or

translated). Following exposure to the perturbed feedback, participants' reports of limb position were shifted in the direction of the perturbation by about 25% of the visual perturbation magnitude. Their results clearly imply that proprioceptive recalibration occurs during active exposure to a visual perturbation, but it is not clear from their study whether this effect was dependent on participants' active engagement in a target-directed task or whether mere exposure to the perturbed visual feedback (in the absence of a target) would have produced the same effects. Study 4 of the present document contrasts with the Cressman and Henriques study in that, during exposure phases of Study 4, no visual target was present and, therefore, no direct error processing was occurring. When our participants were actively exposed to the perturbed feedback (Active Exposure Session of Study 4), we observed levels of proprioceptive recalibration (22% of the perturbation magnitude) that were very similar to those of Cressman and Henriques (2009). Of course, we applied a different type of perturbation – a cursor gain as opposed to a rotation – so direct comparisons between studies should be made with caution. This cross-study comparison does suggest, however, that direct error processing does not contribute to proprioceptive recalibration during active movement.

The possible independence of proprioceptive recalibration from motor learning is more convincingly demonstrated by the results of the passive exposure session of Study 4. In that condition, not only was there no target, but there was no active control of the movement while the visual perturbation was applied. The resulting shift in participants' perceived position of the unseen limb suggests that proprioceptive recalibration can arise purely from conflicting visual and proprioceptive feedback, independent of whether or not the movement is under the active guidance of the participant.

This conclusion is further supported by recent work by Cressman and Henriques (2010), which shows that passive exposure to rotated visual feedback produces a shift in proprioceptively-sensed limb position. Moreover, their study shows that a similar shift in perceived limb position occurs when participants are actively exposed to visual perturbation but are not exposed to target error. In Cressman and Henriques' (2010) study, participants' active movements were robotically

constrained to a path, such that error between the rotated cursor and the target was locked at zero. They observed small, but equal, shifts in limb position sense and visuomotor adaptation (the latter of which was probed by free reaching to a target) following both active and passive exposure. Specifically, they observed a ~6 degree shift in perceived limb position and a ~6 degree shift in aiming movements following exposure to a 30 degree cursor rotation, regardless of whether participants were actively or passively exposed to the perturbation. These results agree with our finding, in Study 4, that a small amount of visuomotor adaptation can occur as a result of passive exposure. Their results also support the idea that visuomotor aftereffects are a combination of error-based learning effects and sensory recalibration effects.

An interesting question for future research is whether sensory recalibration and error-based learning are both susceptible to credit-assignment considerations. In Study 1, we showed that a visible target perturbation dramatically undermined learning, such that aftereffects of the perturbation were fleeting. I have attributed this effect to the visuomotor system's disregard (from an adaptive perspective) of error that does not derive from internal sources. Such a view is supported by Wei and Kording (2009), who showed that adaptive effects are influenced in a non-linear way by the magnitude of error, such that large errors (which are more likely to have external sources) receive reduced adaptive weighting compared to smaller errors. Thus, for pure error processing, credit-assignment (internal vs. external) seems to be an important consideration for the visuomotor system. However, it is not known whether sensory recalibration processes are governed by the same considerations. In other words, does the amount of trial-to-trial recalibration of sensed limb position depend on the magnitude of the sensory discrepancy, such that larger discrepancies are more weakly weighted?

The foregoing considerations suggest that we may need to re-evaluate previous research that has investigated reach adaptation to perturbed effector feedback. Researchers that approach such adaptation from an error processing perspective potentially neglect the sometimes small, but potentially important, contributions of sensory recalibration. The study by Diedrichsen et al. (2005),

for instance (described in Chapter 2), which examined the behavioural and neural activity associated with movement error induced by a cursor manipulation and compared it to the activity generated by a target perturbation, may have measured neural activity in the cursor group that was driven by enhanced error processing, sensory recalibration, or both. Diedrichsen et al. (2005) attributed the effects to differences in error processing between the target and cursor groups, but there may also be sensory recalibration differences. Future studies may want to control for such possible confounds by also employing pure target error protocols (which eliminate the effects of sensory recalibration) or passive exposure techniques (which preserve sensory recalibration while eliminating all forms of error processing).

6.3.4 Changes in the location map versus changes in the displacement map

In Chapter 1 I discussed Shadmehr and Wise's (2005) model for prism adaptation, which involved modifications in the location map and the displacement map as a result of active exposure to a prism perturbation. Recall that the location map encodes the relationship between joint angles (sensed by proprioception) and the location of the end effector (e.g., the hand). When visual feedback of the hand is perturbed, the location map is realigned to provide an updated proprioceptive estimate of hand location that matches the visual estimate of the hand. The displacement map, on the other hand, encodes the relationship between changes in joint angle and changes in end effector location. Thus, when the hand fails to acquire the target after a reaching movement, the displacement map is realigned such that the computed changes in joint angle eventually produce the desired difference vector.

Notice that in this model, the motor command, which produces changes in joint angle, is directly related to the displacement map only. I propose that the adaptive changes that were observed in target perturbation studies of the present document (Studies 1 through 3) might be conceptualized as changes in the displacement map. That is, when participants in the SacStart group of Study 1, for instance, failed to acquire the imperceptibly displaced target, they updated their internal estimate of the joint angle changes that would be required to transport the hand through the computed difference

vector. Because the target was presumed to be stable in the environment, it was not computation of the difference vector that was presumed to be in error but, rather, the system's displacement map. This might be contrasted with instances where the target perturbation was visible, such as in the ReachEnd group of Study 1, where the system may have recomputed the difference vector during the exposure phase (to carry the hand directly to the perturbed location), rather than produce any lasting change in the displacement map (i.e., the internal model). Finally, because the target perturbation studies did not involve any visual-proprioceptive conflict, I am also suggesting that adaptation to target error does not involve any modification of the location map.

This contrasts with what may be occurring during exposure to a perturbation of the effector. I propose that the adaptive changes that were observed in the passive exposure condition of Study 4 (during which participants had their limb passively moved as a gain-modified cursor was projected from above) reflect modification of the location map. That is, mere exposure to a conflict between vision and proprioception led to an update in the system's estimate of how sensed joint angles relate to the current location of the hand. Because passive exposure did not require the computation of a difference vector, which would only be required for the generation of an active movement, there would have been no involvement (and, accordingly, no modification) of the displacement map. The adaptive changes that were observed in the active exposure condition, on the other hand, probably involved the modification of both the location map and the displacement map, in much the same way that active exposure to prisms would influence both maps.

6.4 A model for error-based motor adaptation

In this section I provide some (very speculative) modifications to the model for motor control and learning that was presented in the introductory chapter (Figure 1.1). Note that this model deals only with adaptive effects that derive from error-based processing; adaptive effects that might arise from sensory recalibration are not treated within this model.

The two modifications that I propose deal with how the inverse model might be influenced by 1) the degree to which movement error is attributed to the actor, and 2) the error signal that might

derive from forward model predictions that occur as the movement unfolds. These modifications to the model are shown in the figure below (Figure 6.1). The new comparator (A) that I have proposed compares the predicted movement outcome with the observed outcome and assesses the degree to which the actor was responsible for the movement error. This error attribution is then used to apply a corresponding weighting to the error signals that train the inverse and forward models. I have added this comparator to the model based on the work of Wei and Kording (2009), Michel et al. (2007), and the results of Study 1 of the present document, which all suggest that learning from reach error is dependent on the degree to which the error is attributable to the self versus the environment.

The new training signal (B) for the inverse model that I have proposed arises from the online error signal. In the current model, that error signal is thought to stem from the error that is generated by a comparison of the predicted sensory feedback and the current location of the reach target. I have added this training signal based on the results of Study 3 of the present document, which suggest that participants adaptively modify subsequent reach planning as a result of exposure to an unperceived online target perturbation. As I have drawn it in Figure 6.1, the prediction-based error signal is responsible for both real-time corrections to an ongoing movement and the subsequent training of the inverse model. Note that for inverse model training I have applied a weighting to this signal that is influenced by the degree to which movement error is attributed to the self versus the environment. For instances where the online target jump is visible (e.g., Diedrichsen et al. 2005) or is large enough to potentially be treated as externally-derived (as may be the case with the 7.7 cm online perturbation applied by Magescas et al. 2009), I am proposing that this training signal is suppressed. However, even though the training signal may be suppressed when the online target perturbation is visible, the real-time online corrections that rely on the same error signal presumably persist (e.g., Pisella et al. 2000; Cressman et al. 2006; Cameron et al. 2007; Komilis et al. 1993). Accordingly, I have not incorporated into the model any weighting of the error signal when it acts as a real-time mediator of the online correction itself.

For most of our daily actions, we successfully acquire the target to which we reach, thanks to

online corrections that correct for any error that occurs in the initial trajectory. The proposed model incorporates the idea that the size of this initial error is important for determining how to modify subsequent reaching movements. If the error is quite large, the system may be less inclined to attribute the error to an internal source, and may therefore reduce the weighting of the resulting training signal, similar to what is thought to occur for terminal error (Wei and Kording 2009). However, the extent to which we are willing to attribute the error to ourselves probably also depends on the plausibility of the error arising from an external source. In lab-based settings, where a target and cursor might appear on a screen, for instance, there may be a greater willingness to attribute error to an external manipulation. This contrasts with a scenario in which one reaches for an object in an apparently normal environment, only to find oneself missing the target. In the absence of any knowledge that our limb may have been perturbed, we may be more inclined to weight large errors in the same way as small ones. In other words, top-down factors such as knowledge about possible external sources of error (or the absence thereof) may interact with the error-size effects described by Wei and Kording (2009). Consequently, it may be worth considering the addition of a further component to the model in Figure 6.1, one that makes the forward model-based error attribution partially contingent on one's prior beliefs about the potential for movement error under given conditions.

It may also be worth considering whether agency attribution and training signal generation occur for each individual reaching movement or whether error is accumulated over multiple trials, assessed for systematic bias, and then used for internal model training. That is, the visuomotor system may require multiple samples before determining that an error in programming exists and requires updating. Alternatively, each movement might immediately produce a small change in the internal model, based on the degree of over- vs. under-shooting, and these small changes, averaged over time, would compensate for any systematic error that was initially present.

6.5 Future directions for research

6.5.1 Target versus effector perturbations

One of the arguments that I have made in this document is that a target perturbation protocol can be a useful methodology for investigating error-based processing during motor learning. However, it is also a fairly new protocol, and it is not yet clear to what extent its adaptive effects match those that are produced by effector perturbations. (None of the present studies directly compared the learning effects of target perturbations to those of effector perturbations.) Therefore, it may be helpful for future interpretations of effector and target perturbation effects if, first, experiments are conducted that directly compare the trial-to-trial effects and the aftereffects of these two perturbation types. Although Diedrichsen et al. (2005) have compared cursor, force, and target perturbation effects within a single study, their target perturbation was a visible one, which prevented it from inducing significant adaptation.

I am suggesting, of course, that an effector perturbation should be compared to an *imperceptible* target perturbation (of equivalent size to the cursor displacement used for the effector perturbation), such that reach error can be attributed to the actor in both cases. A useful accompanying protocol for this type of study might be a measurement of the sensory recalibration that is induced by the cursor perturbation, so that, once this is accounted for, the error-based effects of the cursor perturbation can be compared to those induced by the target perturbation.

There are multiple variations that might be considered for these experiments, such as whether the perturbation is presented during the movement (online) or only at the end (terminal), or whether veridical feedback of the effector is present/absent during the movement for the target perturbation conditions. (Recall that, in Magescas and Prablanc (2006) and in the target perturbation studies presented here, visual feedback of the limb was extinguished during its flight.) The variation that I propose as a starting point, however, would simply compare terminal error that is induced by a perturbation of either the cursor or the target. In this design, the cursor and the target would both be visible at the start of the reach, would disappear during the reach, and then would reappear at the end

of the reach (either of which could be displaced by the experimenter, depending on the condition). The participant would know which item represented the hand and which one the target, but they would not consciously know that either one had been perturbed. With this type of design, one could directly compare the adaptive effects produced by the two kinds of perturbation. One could also vary the size of each type of perturbation, as Wei and Kording (2009) did with their effector perturbation, to determine whether error attribution occurs in the same way for each type of perturbation. In other words, is the decrease in error weighting that occurs for a large (e.g., 8 cm) relative to a small (e.g., 2 cm) effector perturbation comparable to that which occurs for equivalent target perturbations?

6.5.2 Neural correlates of adaptation to target error

I speculated in Chapter 2 that adaptation to unperceived target perturbations is mediated by the cerebellum; however, this hypothesis has yet to be tested. Future imaging studies may want to examine this question, for not only will such studies shed light on which regions of the brain are associated with adaptive error processing, but they will also help to determine whether similar cortical areas are responsible for adaptation to effector and target perturbations and, accordingly, whether similar processes might be engaged by each type of perturbation.

Furthermore, in light of the possibility that error-based adaptation and sensory recalibration are independent processes, it may be worth adding neuro-imaging to the behavioural protocols that isolate each type of process. In fact, one may find that those regions of cortical activation that differ between adaptation to target perturbation and adaptation to effector perturbation are the same regions that are responsible for sensory recalibration (which should occur in adaptation to effector perturbations only).

6.5.3 Perceptual sense of agency and its relation to motor adaptation

To date, the impacts of visual and temporal distortions of movement feedback have been investigated separately for motor adaptation and sense of agency. For instance, studies of motor adaptation have shown that aftereffects degrade as the delay between movement completion and feedback presentation is increased during exposure (Held et al. 1966; Kitazawa et al. 1995) and that

sudden, large spatial perturbations induce less robust adaptation than incremental ones (Michel et al. 2007). Research on sense of agency, meanwhile, has shown that participants are more likely to report that a movement is caused by an external source as the spatial deviation of the effector increases, yet the participants never report that temporally-distorted feedback is due to an external source, even though they may recognize that such feedback is biased (Farrer et al., 2008). However, reports of agency and motor adaptation have never been investigated simultaneously, so we don't know how a participant's judgment of agency influences their subsequent learning. Although it seems clear that, at some level, the sensorimotor system must attribute error to itself when it learns, it is not yet known whether this type of attribution directly corresponds to the participant's cognitive assessment of agency.

Future studies may wish to consider how perceptual sense of agency and motor learning are related. For instance, if people are told that recently experienced visual feedback is not their own, does this knowledge influence how they process error from their recently completed movement, or is the sensorimotor system's assessment of error attribution cognitively impenetrable? Alternatively, if participants are simply asked to report, after each movement in an adaptation paradigm, how much of the error in the feedback is a result of their own action, how will this correlate with the amount of motor adjustment that occurs on the subsequent trial?

6.6 Concluding remarks

The research presented in this document was undertaken with the goal of furthering our understanding of motor adaptation. The project was broken into roughly two components, one that dealt with how the motor system learns from movement error with relation to a target, and one that dealt with how motor performance and perception are adaptively influenced by visual perturbation of the effector. Investigations of the first component (target error) examined how awareness of the source of error influences learning, how explicit control and feedback prediction influence learning, and how online corrections to a movement influence learning. Investigation of the second component

(visual perturbation of the effector) examined how processing of visual feedback and its integration with proprioception is influenced by active versus passive movement of the limb.

In brief, I have shown that the motor system is sensitive to the stability of the reach environment: if the target noticeably moves, feedback is processed differently than if the target appears stationary. I also showed that explicit control of a reaching movement does not prevent the motor system from learning implicitly from movement error, and I suggested that this implicit learning relied on predictions about movement outcome, rather than direct processing of hand-to-target error. Furthermore, in Study 3, I showed that learning could occur even when terminal reach error was eliminated by online corrections of the reach. This result permitted the speculation that the forward model-based sensory predictions that are thought to underlie rapid online corrections might simultaneously produce a training signal for the inverse model. Finally, in Study 4, I showed that proprioceptive recalibration could occur in the absence of active movement control.

Overall, the results support models of motor learning that implicate predictive processes. They also suggest that how we learn from movement error is influenced by the extent to which we attribute the error to ourselves. Furthermore, the results suggest that sensory recalibration and error-based learning operate independently. These discoveries contribute to our understanding of how the sensorimotor system flexibly responds to the small (and sometimes large) errors that we encounter during daily action and how it integrates visual and proprioceptive information about the locations of its various parts. Whether these contributions will ultimately have practical implications, such as for the development of therapies for sensorimotor impairments, is difficult to predict. Therapeutic successes with displacing prisms for spatial neglect (Pisella et al. 2006) and mirror boxes for phantom limb pain (Ramachandran and Rogers-Ramachandran 1996) do, however, offer hope that adaptation methodologies will not only broaden our understanding of perceptual and motor disorders, but potentially provide some relief to those who are afflicted with them.

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Appendix A: Preliminary study of visuomotor adaptation to online error induced by a target jump¹⁷

A.1 Introduction

Online control allows the motor system to overcome error in a movement's initial trajectory. Under normal circumstances, this error probably arises from a combination of noise in the motor system and an impoverished estimate of a target's location (i.e. from peripheral vision, prior to an orienting saccade) (Desmurget and Grafton 2000). Once the effect of noise is recognized and/or a saccade is executed, a corrective motor command can be issued to reduce the error. Examination of reaches to double-step targets suggests that this corrective command can manifest very quickly (within 150ms after a target perturbation (Prablanc and Martin 1992)) and may be driven by forward modeling of the effector based on the outgoing motor command (Desmurget and Grafton, 2000; 2003; Bard et al. 1999). This forward modeling, in conjunction with available sensory information, permits a projection of the effector's endpoint, which can be compared to the target position; any error between the projection and the target can be used for a corrective command, well ahead of any delayed sensory feedback from the moving limb. The present study investigates the motor learning that might arise from an online error signal caused by an unperceived target jump. If the error is systematic, might the visuomotor system adjust its planning, such that the initial error of subsequent movements is reduced?

Diedrichsen, Hashambhoy, Rane, and Shadmehr (2005) have compared the learning that results from reaching errors due to prismatic shift, force field perturbation, and target jump. They found that the prismatic shift and the force perturbation led to an adjustment in the internal model¹⁸, whereas the target jump produced little or no learning. Diedrichsen et al. (2005) attribute this to the

¹⁷ The data herein have been previously presented at the annual meeting of the Canadian Society for Psychomotor Learning and Sports Psychology (SCAPPS) in 2008 as "Online correction to an unperceived target jump modifies subsequent motor planning" by Cameron, Franks, and Chua.

¹⁸ Internal models store the relationship between motor commands and movement outcomes. An inverse model converts the desired movement into motor commands, while a forward model predicts movement outcomes from motor commands.

nature of the error in each condition. Prismatic and force perturbations produce execution errors (i.e. errors in the motor command), while visible target jumps produce a change in the movement goal. We predict that if the target jump was undetectable (such as during a saccade), the motor system might interpret the error as an error of execution, leading to adaptation.

The present study directly tests whether motor learning occurs when a participant responds to an unperceived target jump. Participants aimed to a target that was consistently jumped in the same direction during the orienting saccade. The pairing of the jump and the saccade prevented any detection of the jump (Bridgeman et al. 1975). This was done not only to encourage the motor system to treat the error as an execution error but also to ensure that any adjustment in motor planning by the participants was not the result of a conscious strategy.

A.2 Methods

A.2.1 Participants

Ten participants (ages 20-29; 7 male, 3 female) from the student population of the University of British Columbia took part in the experiment. One of the participants was the first author. All participants were right-handed and had normal or corrected-to-normal vision. Participants provided written informed consent and received \$10 for participation. The study was conducted according to the ethical guidelines set by the University of British Columbia and the Declaration of Helsinki.

A.2.2 Apparatus

Participants were seated at an inclined Plexiglas surface in a darkened room. The low light degraded vision of the hand but did not eliminate it. Stimuli were projected onto the surface from below by red light emitting diodes (LEDs). Four LEDs were used for the experiment: an eye-fixation LED to the left of the participant's midline and 3 target LEDs (hereafter referred to as targets 1, 2, and 3) to the right of the participant's midline (Figure A.1). A chin rest, located mid-way between the eye-fixation LED and target 2, maintained eye position at approximately 60cm from the Plexiglas surface. LED onset and offset were controlled by an intel celeron PC running DOS.

Electrooculography (EOG) was used to monitor saccadic eye movements. Disposable Ag-AgCl electrodes were placed at the outer canthi of the eyes, and a reference electrode was placed on the participant's forehead. The EOG signal was pre-amplified (by a factor of 10000) and band-pass filtered (.3 – 30Hz) by an AC pre-amplifier (Grass Telefactor P55). Online monitoring of the EOG signal allowed the experimenter to set a voltage threshold corresponding to the midpoint of the saccade. This threshold was then used to trigger target jumps during trials.

Movements to the targets were executed with a stylus. An infrared emitting diode was fixed to the front of the stylus, near the tip. An Optotrak 3020 system (Northern Digital), sampling at 500Hz, recorded the 3-dimensional position of the diode during each trial. The stylus's microswitch tip recorded movement lift-off and touchdown.

A.2.3 Procedure

Participants began each trial with their eyes at fixation and the stylus at the home position. The trial began when the EOG signal was steady at baseline. Following a random foreperiod, a target would appear at position 1, 2, or 3 and the fixation would simultaneously disappear. Participants were instructed to look and point to the target when it appeared. They were also instructed to make their movements as quickly and accurately as possible. (If movement times exceeded 500ms or were less than 200ms, participants were instructed to speed up or slow down their movement accordingly.) The experiment consisted of 3 parts, though participants were never made aware of this division. The first part (PRETEST) consisted of 45 trials and involved manually aiming to a stationary target at one of three locations (1, 2, or 3). The second part (ACQUISITION) consisted of 120 trials and involved manually aiming to a target randomly located at position 1 or 2 that would always jump one position to the right at the midpoint of the orienting saccade (i.e., 1 to 2 or 2 to 3). The third part (POSTTEST) consisted of 30 trials and involved manually aiming to a stationary target at position 2. In all parts of the experiment the target disappeared 200ms after the midpoint of the saccade.

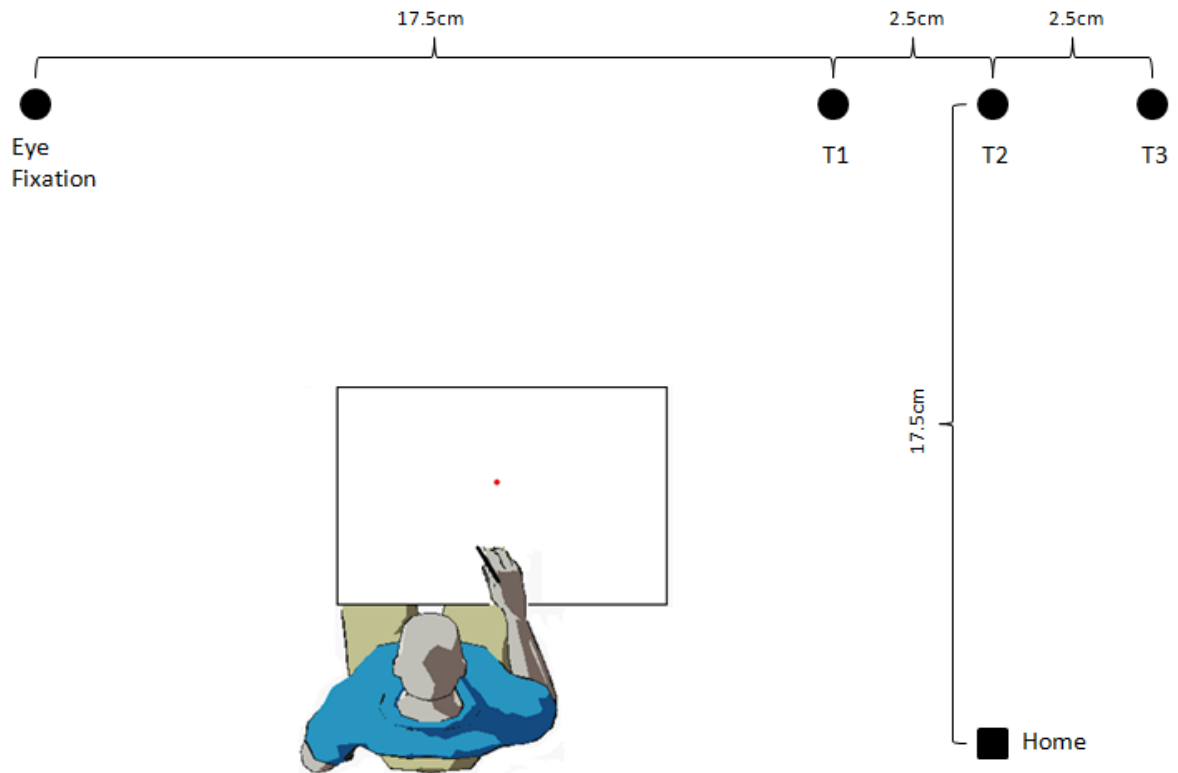


Figure A.1 The stimulus array. Eye fixation, T1, T2, and T3 were red light emitting diodes, only one of which was visible at any given moment. Inset: a bird's eye view of the participant seated at the display surface.

A.2.4 Data reduction

EOG data were low-pass filtered at 30Hz with a dual-pass second-order Butterworth filter. Saccade onset was defined as the voltage minimum prior to a large positive deflection in the signal. Saccade termination was defined as the peak of this positive deflection. Hand displacement data were low-pass filtered at 10Hz with a dual-pass second-order Butterworth filter. Instantaneous velocity was determined by differentiating displacement using a two-point central finite difference algorithm. Acceleration was derived by differentiating velocity using the same algorithm. Movement start and end were defined by the release and contact of the stylus's microswitch.

A.3 Results

A.3.1 Movement planning adapts to the target jump

The trajectories depicted in Figure A.2A suggest the following behavior. In early acquisition, the movement initiates toward target 2 then deviates online to target 3. In late acquisition, the movement initiates toward target 3 and terminates at target 3. In early posttest, the movement initiates toward target 3 then deviates online toward target 2. Finally, in late posttest, the movement initiates toward target 2 and terminates at target 2. These results are consistent with the hypothesis that a saccadically-triggered target jump produces adaptation: motor commands have been altered so as to compensate for the error introduced by the jump.

To quantify this effect, we examined the lateral position of the hand at peak velocity (Figure A.2B). Peak velocity is a kinematic marker that typically falls within the preplanned portion of the movement (Heath et al. 1998). In the present study, peak velocity occurred, on average, 86ms after movement onset (Table 1), so feedback is unlikely to have influenced the movement at this stage. We applied a statistical analysis similar to that of Bernier et al. (2005). We compared the lateral spatial position of the hand at peak velocity across 4 phases of the experiment: the last trial of the pretest, the last trial of acquisition, the first trial of the posttest, and the last trial of the posttest. A one-way repeated measures ANOVA revealed a significant effect of phase, $F(3, 27) = 10.44$, $p = .001$. Post-hoc analysis (Tukey's HSD at $p < .05$) revealed significantly more rightward deviation at peak velocity in late acquisition and in early posttest than in the pretest and in late posttest. Late acquisition did not differ significantly from early posttest, and pretest did not differ significantly from late posttest (Figure A.2B). These analyses confirm that the target jump produced a change in movement planning that subsequently decayed when the target-jump trials ceased.

Table A.1 Mean eye and hand movement measures. Standard deviations are presented in brackets. ‘Eye:Jump’ refers to the lag between the eye movement start and the target jump (negative value indicates the eye preceded the jump). ‘Jump:Hand’ refers to the lag between the target jump and hand movement start (negative value indicates that the jump preceded the hand). For the acquisition phase, endpoint error is with respect to the target’s final (jumped) position. PV = peak velocity, MT = movement time, RT = reaction time.

Phase	Target	Eye RT (ms)	Hand RT (ms)	Time to PV (ms)	PV (mm/s)	Eye:Jump (ms)	Jump:Hand (ms)	Hand MT (ms)	Endpoint direction error (mm)	Endpoint extent error (mm)
Pretest	t2	183.29 (38.11)	270.95 (39.35)	81.25 (45.96)	1110.48 (192.90)	-31.08 (4.27)	-56.58 (26.73)	288.86 (64.87)	1.45 (8.76)	-3.36 (7.79)
	t3	189.61 (53.68)	274.15 (48.82)	80.61 (56.83)	1145.09 (198.96)	-31.30 (4.64)	-53.24 (30.03)	285.83 (58.79)	0.97 (8.03)	-2.03 (8.20)
Acquisition	t2-t3	181.74 (41.27)	260.57 (41.47)	86.39 (53.87)	1108.28 (206.70)	-32.42 (5.54)	-46.41 (31.70)	288.91 (66.42)	-1.18 (7.71)	-1.52 (8.11)
Posttest	t2	185.30 (45.59)	263.75 (41.00)	89.58 (51.29)	1086.67 (171.08)	-35.53 (8.20)	-42.91 (32.10)	292.63 (56.96)	4.70 (8.76)	-2.00 (7.98)

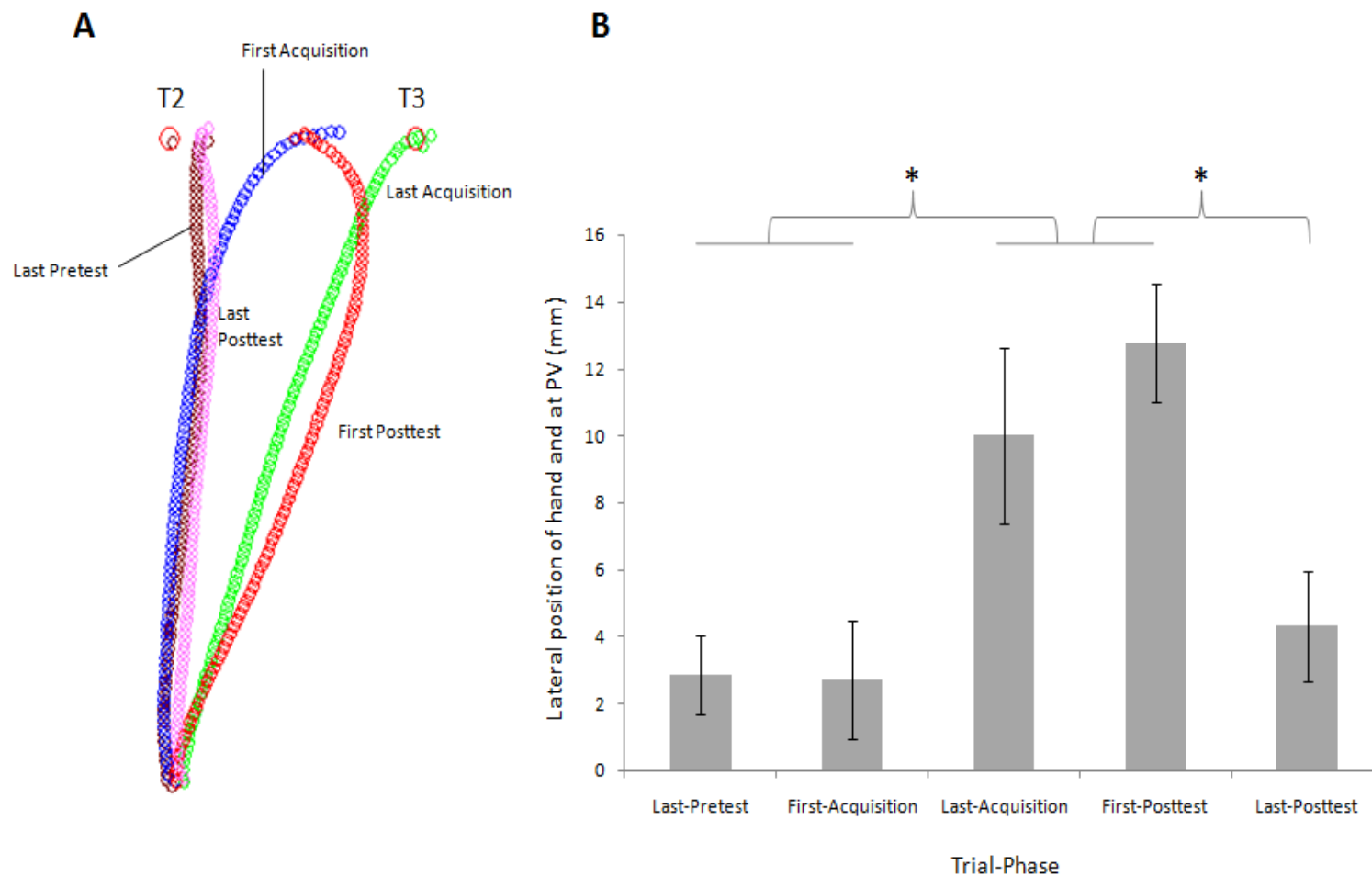


Figure A.2 A) Mean trajectories of aiming movements to T2 for key trials. Each trajectory reflects the mean of all 10 participants. The means have been normalized across displacement: each trajectory was sampled at 100 equally-spaced points along the curve and then the mean position at each sample was plotted. B) Mean lateral displacement of the hand at peak velocity for key trials of the study. All data is for trials in which the target initially appeared at T2. Error bars represent \pm one standard error of the mean.

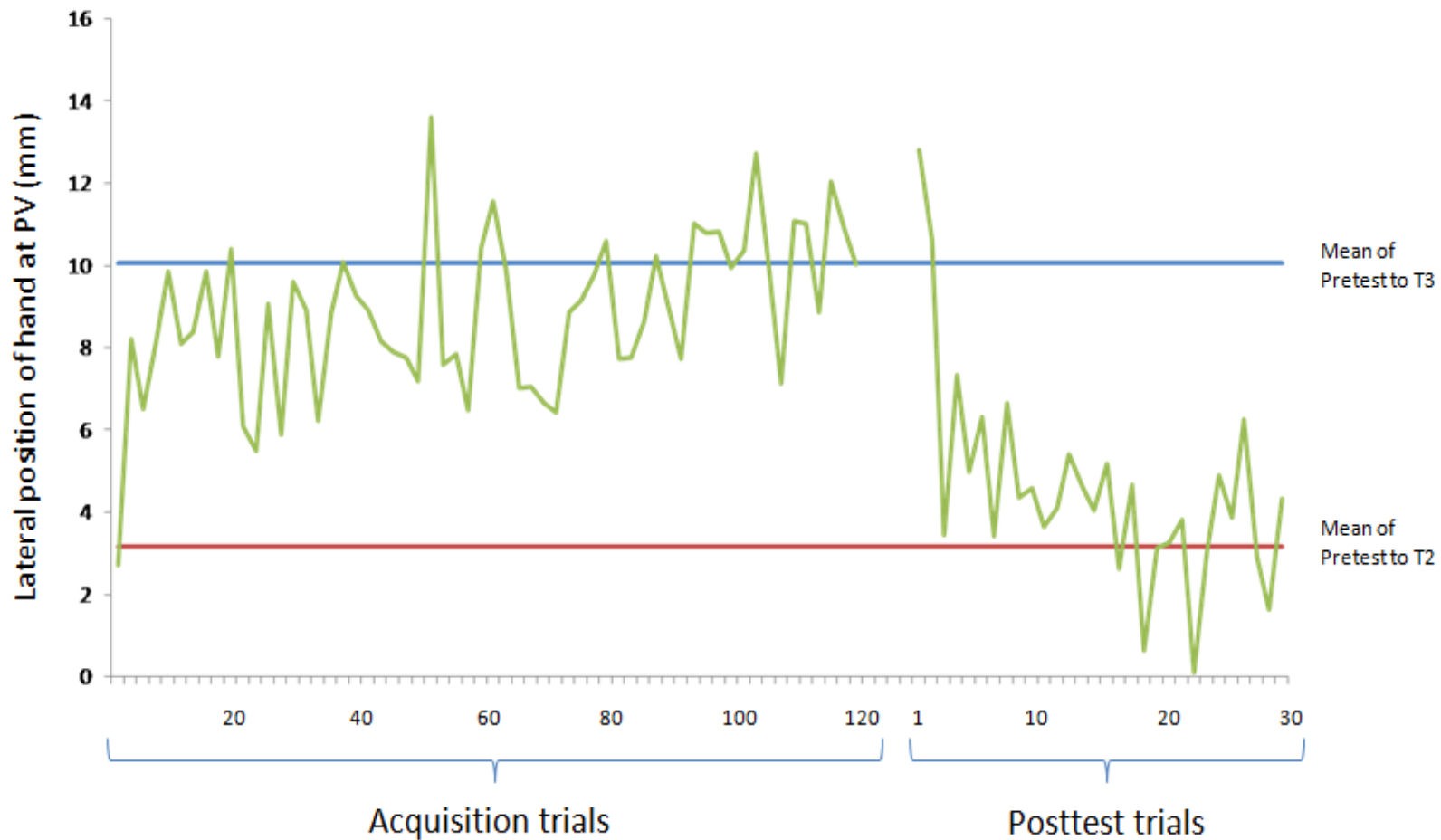


Figure A.3 Mean lateral position of the hand at peak velocity (PV) across trials. Each data point reflects the mean of all 10 participants. Note that data are presented only for trials in which the target first appeared at T2 (the target first appeared at T1 for half of the 120 acquisition trials, but these trials are not presented here).

The progression of learning is illustrated in Figure A.3. Participants appear to have adjusted their trajectory planning quite early in acquisition. Likewise, participants appear to have re-adjusted their movement trajectories quite early in the posttest. Possible reasons for these effects are addressed in the discussion.

A.3.2 Perceptual report of the target jump

People do not detect small target displacements during a saccade, particularly if the jump is less than 20% of the saccade distance (Bridgeman et al. 1975). Even when there is an accompanying arm movement that is corrected online, people remain unaware of the jump (Goodale et al. 1986). Indeed, people appear to have conscious access to neither the target jump nor the corresponding limb correction (Chua and Enns 2005).

To ensure that our manipulation successfully prevented awareness of the jump, we asked participants at the end of the experiment whether they noticed anything happen to the target during the trials. No one reported noticing the target jump. We then specifically asked whether they noticed the target jump during any trials. Again, no one reported noticing the jump. These results imply that the adaptation to the target jump was not the result of a cognitive strategy.

A.4 Discussion

A.4.1 Online error can drive motor learning

When a target jumps during an orienting saccade, the accompanying limb movement is smoothly corrected online to achieve the new target position (Goodale et al. 1986; Prablanc and Martin 1992; Desmurget et al. 1999). However, even when the jump is not paired with a saccade and is, therefore, consciously accessible, the same fast online correction occurs (Komilis et al. 1993; Pisella et al. 2000; Cressman et al. 2006). While the online response itself does not differ between these two cases, the motor learning that arises from the jump-induced error appears to differ considerably. Diedrichsen et al. (2005) showed that an online response to a *visible* target jump does not change future motor commands. We have shown here that the response to an *invisible* target jump

does affect future motor planning. After exposure to a systematic rightward target jump, participants initiated their movements in the direction of the target's final location rather than its initial location.

Magescas and Prablanc (2006) recently showed that visuomotor adaptation can result solely from terminal error, in the absence of any visual/proprioceptive conflict. They introduced error by shifting the position of the target, in small steps, after the completion of a manual aiming movement. The target was blanked at the onset of an orienting saccade, the reach was executed, and then the target was re-illuminated at a shifted location after movement completion. In this way, they prevented any feedback control of the movement and demonstrated robust adaptation based purely on endpoint error. Our experiment, on the other hand, focused on the adaptive influence of online error. Whereas Magescas and Prablanc (2006) induced the error at the end of the movement, we induced error during the manual response and minimized terminal feedback by blanking the target prior to movement touchdown. Thus, it appears that terminal error and online error can independently drive motor learning.

A prism study by Jakobson and Goodale (1989) is consistent with the idea that online error can drive learning. When participants in their study were exposed to a 5deg prismatic shift, movements were corrected online to counteract the error induced by the prisms, such that there was no terminal error even for the earliest movements. Furthermore, they showed rapid adjustment of motor planning: compensation for the prisms was achieved within the first few trials. This is similar to our finding that participants adapted their initial trajectories very early in acquisition (Figure A.3).

However, one major difference between our findings and those of prism studies is the duration of the aftereffects. We showed very rapid decay of the adapted response (Figure A.3). Even though our perturbation escaped participants' awareness (a feature which, in prism studies, enhances the duration of the aftereffects (Michel et al. 2007)), participants de-adapted within only a few trials. On the one hand, this rapid decay makes sense, in that we would expect the same processes that produced the adapted motor commands in the first place (which occurred within only a few trials) to produce de-adaptation. On the other hand, the rapid decay suggests that our manipulation engaged

only a subset of the processes involved in prism adaptation. It may be, for instance, that, in the absence of a visual/proprioceptive conflict (and the subsequent realignment), readjustment of motor commands can occur quite rapidly. Another factor probably contributing to the rapid decay of the aftereffect is the presence of error in the posttest. Most prism studies (as well as the no-prism Magescas and Prablanc (2006) study discussed earlier) do not provide any error feedback during the posttest. Our posttest, however, naturally involved online error, as the target no longer jumped to the location to which the initial portion of the movement trajectory was directed. Error would, therefore, be registered by the visuomotor system from the very first trial of the posttest. The persistence of adaptation may have also been negatively influenced by the participants' active return to the home position prior to each trial. Our apparatus did not permit us to passively return the participant's limb to the home position. As the home position was stationary (and did not, consequently, induce any error during the return reach), the adaptive effect of the jump trials may have been weakened.

A.4.2 Saccadic adaptation

It is likely that our systematic target jump produced saccadic adaptation, in which the gain of the saccade command is gradually increased (or decreased, depending on the direction of the jump) to compensate for the error induced by the target jump (e.g. Wallman and Fuchs 1998). Some studies have suggested that saccadic adaptation can transfer to the limb, such that aiming movements become biased in the direction of the saccadic adaptation (e.g. Bekkering et al. 1995). Is it possible, therefore, that our results reflect transfer of saccadic adaptation rather than a modification of the internal model for the limb?

Two lines of evidence strongly suggest that most, if not all, of the adaptation we observed in the limb motor commands is independent of saccadic adaptation. First, transfer of adaptation is weaker for saccadic lengthening (the type of adaptation that would occur in our study) than for saccadic shortening (Kroller et al. 1999). In fact, Kroller et al. (1999) showed almost no transfer of saccadic adaptation to the hand for saccade lengthening. Even when the eye and hand were coupled in pre- and posttest (the condition most directly comparable to our design), Kroller et al. (1999) showed

only a 6% transfer of adaptation, which amounted to a hand shift of only 4% of the target jump distance.

The second line of evidence relates to the nature of the orienting saccade. Cotti et al. (2007) have recently shown that volitional saccades and reflexive saccades produce very different levels of transfer of adaptation to the hand. They found that adapted volitional saccades transfer to the hand, while adapted reflexive saccades do not. The saccades in our experiment fall clearly into the reflexive category, as outlined by Cotti et al. (2007), whose reflexive saccades had a mean latency of 236ms (± 35) and were made to a suddenly appearing target. (Their volitional saccades were made between two continuously visible targets and had latencies greater than 500ms.) Like Cotti et al.'s (2007) reflexive saccades, our saccades were executed to a suddenly appearing target and had a mean latency of 184ms (± 43).

A.4.3 What error signal drives the learning?

Many previous studies of visuomotor learning have perturbed sensory feedback rather than the veridical location of the target. Prism goggles, for instance, have been used to laterally shift the visual field, which produces movement error during early practice. The initial error is caused by the misperception of the target location, resulting in incorrect movement planning. Error is eliminated with practice, and people adapt to the shift, such that when the goggles are removed, movement error is in the direction opposite the prismatic shift. The prismatic shift produces at least 3 types of discrepancy: a discrepancy between the perceived and actual location of the target, a discrepancy between the received and expected visual feedback of the effector, and a discrepancy between visual and proprioceptive feedback. During adaptation, the latter two discrepancies are eliminated, such that expected visual feedback is congruent with actual visual feedback and proprioceptive feedback has been realigned so as to coincide with visual feedback. Although the realignment of proprioceptive feedback may affect the duration of prismatic aftereffects (Bernier et al. 2005), it is the adjustment of internal models caused by the prismatic shift (Baraduc and Wolpert 2002) that is of particular interest here. Adaptation apparently relies on a comparison of predicted and actual sensory outcome (Tseng

et al. 2007): The forward model is altered until its predictions coincide with sensory feedback, and this leads to adjustment of the inverse model (Wolpert et al. 2001). It is the adjusted inverse model that is thought to produce error when an adapted participant reaches after removing the goggles.

Our hypothesis that movements would adapt to the target jump stemmed from the idea that forward modeling plays a role in both the online control of rapid aiming movements (Desmurget and Grafton 2000; 2003) and motor learning (Wolpert et al. 2001). If the error driving online control is based on a comparison between the forward model projection and the visual target, a learning signal might be generated that has a similar effect to the learning signal driving prism adaptation, in which the forward model's prediction is compared to actual sensory feedback (Tseng et al. 2007).

Although our results are consistent with this premise, the experiment only tested whether learning occurred. It did not directly test the nature of the online error signal. A true test would require eliminating visual and proprioceptive feedback of the limb, such that online error could only arise through forward modeling.

A.5 Conclusion

Our results show that aiming movements adapt to a systematic online target jump. Participants were unaware of the jump, suggesting that adaptation was independent of any cognitive strategy. We propose that the adaptation is driven by the error between the displaced target and the forward model prediction of effector endpoint.

Appendix B: Ethics certificate of approval



The University of British Columbia
Office of Research Services
Behavioural Research Ethics Board
Suite 102, 6190 Agronomy Road, Vancouver, B.C. V6T 1Z3

CERTIFICATE OF APPROVAL- MINIMAL RISK RENEWAL

PRINCIPAL INVESTIGATOR: Romeo Chua	DEPARTMENT: UBC/Education/Human Kinetics	UBC BREB NUMBER: H03-80057
INSTITUTION(S) WHERE RESEARCH WILL BE CARRIED OUT:		
Institution UBC Other locations where the research will be conducted: N/A		Site Vancouver (excludes UBC Hospital)
CO-INVESTIGATOR(S): Melanie L Lam Brendan Cameron Ian M. Franks James T. Enns Jarrod P.G. Blinch		
SPONSORING AGENCIES: Natural Sciences and Engineering Research Council of Canada (NSERC) - "Sensory and perceptual contributions to the preparation and execution of goal-directed action"		
PROJECT TITLE: Sensory and Perceptual Contributions to the Preparation and Execution of Goal-Directed Action		
EXPIRY DATE OF THIS APPROVAL: February 18, 2011		
APPROVAL DATE: February 18, 2010		
The Annual Renewal for Study have been reviewed and the procedures were found to be acceptable on ethical grounds for research involving human subjects.		
<p style="text-align: center;">Approval is issued on behalf of the Behavioural Research Ethics Board</p> <hr/> <p style="text-align: center;">Dr. M. Judith Lynam, Chair Dr. Ken Craig, Chair Dr. Jim Rupert, Associate Chair Dr. Laurie Ford, Associate Chair Dr. Anita Ho, Associate Chair</p>		