Generalisation of adaptation to a visuomotor rotation

from curved to straight line reaching

by

JOE R. L. DUNCAN

A thesis submitted to the Department of Psychology

in conformity with the requirements for

the degree of Master of Science

Queen’s University

Kingston, Ontario, Canada

April, 2009

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Abstract

Numerous studies have investigated motor learning by examining the adaptation of reaching movements to visuomotor perturbations that alter the mapping between actual and visually perceived hand position. The picture of the visuomotor transformation from visual input to motor input that has developed consists of three broad phases: integration of hand and target locations in a common reference frame, calculation of a movement vector between hand and target, and transformation of this movement vector from the common reference frame into motor commands. The process of adapting to a visuomotor rotation is generally viewed as an alteration of the vectorial representation of reach planning. When visual feedback is rotated, the motor and visual directions no longer coincide and the motor command executed is remapped to the subsequent visual direction produced. In the current set of studies, we examined how learning a visuomotor rotation while reaching to a target with a curved hand path generalizes to straight path reaching and novel target directions. We found that there is very little to no generalization of learning between curved reaches and straight reaches when given only endpoint feedback. With continuous visual feedback, we found partial transfer. This suggests that in the absence of visual feedback, the vectorial adaptation hypothesis is insufficient and adaptation to a visuomotor rotation is mediated by the later stages of the visuomotor transformation, when the motor commands specific to the hand path used are being generated.
Acknowledgements

First, I would like to thank my supervisor, Dr. Randy Flanagan, for his guidance, wisdom and sharp insight.

I would like to thank my committee members, Dr. Martin Pare and Dr. Kevin Munhall, for their greatly appreciated feedback and suggestions.

I would also like to thank Dr. Isaac Kurtzer for our many fruitful discussions.

Additionally, a big thank you goes out to my labmates Miles Bowman, Lulu Bursztyn and Christine Tong, as well as my friends and family for supporting me through this process.

Finally, I would like to thank my wife, Sarah Bannoff, for her unwavering support over the years; I would not have been able to do it without her.
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Chapter 1: General Introduction

Research into motor learning has made wide use of visuomotor perturbations to investigate the structure of the learning mechanism itself (Cunningham & Welch, 1994; Krakauer, Pine, Ghilardi & Ghez, 2000; Wigmore, Tong & Flanagan, 2002; Scheidt & Ghez, 2007). A visuomotor perturbation is essentially an alteration of the mapping between motor output and expected visual consequences. Traditionally, they have been implemented using various types of prisms, but many recent studies have used virtual environments. By examining how adaptation to an altered visuomotor mapping generalizes to novel situations, researchers have been able to draw inferences about the computations involved in the adaptation process itself. This line of research dates back as far as Helmholtz (Helmholtz, 1867) who’s pioneering work with reversing prisms demonstrated that participants could adapt to an inversion of visual input. Many different types of visuomotor perturbations are possible. Using prisms, researchers have been able to shift or displace visual feedback as well as invert it in either the horizontal or vertical planes. With virtual displays, researchers have been able to produce any desired arbitrary visuomotor perturbation, with common ones being visuomotor rotations, translations or gains about an arbitrary start location.

The visuomotor perturbation paradigm

Numerous studies have investigated motor learning by examining the adaptation of reaching movements to visuomotor perturbations that alter the mapping between actual
and visually perceived hand position. Early evidence suggested that adaptation to visual displacement from wedge prisms worn over the eyes was due to a combination of “visual shift” and “proprioceptive shift” (Harris, 1963; Craske & Gregg, 1966; Welch, 1974). A proprioceptive shift can be described as a change in the participant's subjective perception of the position of their arm in accordance with the prism; such that they felt that their arm was straight ahead when it appeared straight ahead through the prisms, even though it was in fact pointing off to the side. A change in the felt position of the arm can account for adaptation to a visuomotor perturbation by changing the mapping between visually and proprioceptively perceived arm configurations. Thus, when reaching to a target, the participant need only move their arm to the new proprioceptively perceived position associated with the altered visual perception of the arm at the target. This of course relies on the participant receiving proprioceptive feedback during the movement in order to guide the arm to the correct proprioceptive position. Similarly, a visual shift can be described as a change in the subjective perception of the position of the eyes in the head, such that the participant felt themselves looking straight ahead when in fact they were looking off to the side. Visual shift can account for adaptation to a visuomotor perturbation in a manner similar to proprioceptive shift.

Investigating proprioceptive shift, Baily (Baily, 1972) demonstrated that although participants readily adapt to a visual perturbation using slow, proprioceptively controlled “zeroing-in” movements, this adaptation does not generalize to fast, ballistic movements that are not subject to proprioceptive feedback control (since the movements were finished by the time proprioceptive feedback became available for control). Baily found that participants also readily adapt to the same prism-induced perturbation while making
fast, ballistic movements; adaptation that does generalize to slow proprioceptively controlled reaches. In Baily's task, participants reached in darkness to a visual target. Vision of their hand and arm was obscured during movement and they were only given terminal visual feedback after the motion was complete. For the fast, ballistic movements, participants were instructed to reach directly from the start position to the target, as fast as possible. For the “zeroing-in” task, participants were instructed to extend their arm off to the side (in a different direction each trial) and then oscillate their arm back and forth with diminishing amplitude around the location of the target. By giving participants ample time to make use of proprioceptive feedback in the slow, zeroing-in task but not in the fast ballistic task, Baily was attempting to distinguish between changes in early afferent sensory encoding (proprioceptive shift) and later efferent motor response. The asymmetrical transfer between the fast and slow tasks demonstrates that the adaptation in the fast task cannot be due to proprioceptive shift, and must be mediated by some other mechanism. Baily attributed the adaptation in the fast task to changes in the motor response. A similar mechanism of adaptation was proposed in a review by Welch (Welch, 1974) who investigated the contributions of proprioceptive shift and visual shift (change in subjective felt position of the eyes relative to the head) on adaptation to prism perturbations. Welch found that in order to account for the data from numerous prism studies, particularly for fast ballistic movements with no online feedback (i.e. participants could not see their arm during reach, only after the movement was finished), a third component of adaptation was required. Rather than a change in perception, adaptation to a visuomotor perturbation could also be accounted for by an alteration in motor response. By modifying the motor commands associated with moving
the hand to the target such that the hand attains the target in the altered visual feedback, no change in the proprioceptively perceived hand location or eye orientation is necessary. One advantage of modifying the motor output as opposed to the sensory input is that alterations in motor output do not require feedback during movement in order to attain the goal. This is what Welch called the “assimilated corrective response.”

Positional relationships, such as visually perceived arm position to felt arm position and visually perceived gaze position to felt gaze position, are called kinematic because they deal with static, context free relationships. This is in contrast to dynamic relationships which deal with how the current system state affects the relationship and how the relationship evolves over time. Mapping one position to another is not the only way that kinematic information can be used to provide a mapping between visual input and motor output. Early research focused on kinematic positional mapping (e.g. proprioceptive shift), while later work has focused on mapping of vectors from visual input to motor output. Research by Cunningham (Cunningham, 1989) using visuomotor rotations and computer displays provides strong evidence that adaptation to a visuomotor rotation is equivalent to a remapping of bi-directional movement axes from visual to motor space. Visually obtained spatial directions are mapped to appropriate motor directions. When visual feedback is rotated, the motor and visual directions no longer coincide and the motor command executed is remapped to the subsequent visual direction produced. By examining the pattern of errors exhibited across the workspace during adaptation, Cunningham was able to infer that the representation of directional mapping is ordered by orientation angle. That is, Cunningham suggests that the mappings of bi-directional visual movement axes to their corresponding bi-directional motor movement
axes are stored in a continuous representation ordered by the orientation angle of the visual axes in a similar manner as contour orientation is represented in primate visual cortex (Cunningham, 1989; Hubel & Wiesel, 1974). Thus, re-mapping of a visual axis should affect other visual axes in relation to the rotational distance between them.

Roby-Brami & Burnod (Roby-Brami & Burnod, 1995) used a mouse and computer display to investigate the generalization of adaptation to visuomotor rotation across novel reaching directions. Their results indicated three adaptive responses: online correction during the movement itself (feedback control – see Representation of reach planning below), a change in initial movement direction (a kinematic mapping of vectors from visual to motor space), and a trial-by-trial memorization of motor response (modification of the motor commands themselves, similar to Welch’s assimilated corrective response). Importantly, Roby-Brami & Burnod found that the correction of initial movement direction is represented in relation to the learned reference direction in visual space, similar to the findings of Cunningham (Cunningham, 1989). Thus, after adapting to a visuomotor rotation by reaching to a reference target, the transfer of learning to a target in a new direction depends on the similarity between the novel and reference direction vectors in visual space. This similarity can be approximated as the cosine between the two directions in visual space. This has also been supported by Pine and colleagues (Pine, Krakauer, Gordon & Ghez, 1996) and Krakauer and colleagues (Krakauer et al., 2000) who demonstrated that adaptations to a visuomotor rotation are local to the learned reference direction. In contrast, Krakauer and colleagues (Krakauer et al., 2000) found that adaptation to a visuomotor gain, where the amplitude between hand movement and cursor movement is altered, fully generalizes from a training
direction to novel hand movement directions.

Converging evidence demonstrates that people plan reaching movements in visually-based kinematic coordinates as opposed to intrinsic joint based dynamic coordinates. For instance, if a visuomotor perturbation is introduced gradually to increase the perceived curvature of an otherwise straight hand movement, participants will compensate by curving their actual hand path through space in order to create a visually straight movement (Wolpert, Ghahramani & Jordan, 1995). This suggests that reaches are planned so as to maintain visually straight trajectories regardless of the correspondence between actual hand path and visually perceived hand path. Flanagan and Rao provide a further demonstration in an experiment where participants moved a cursor to a target and the mapping between hand position and cursor position was highly non-linear (Flanagan & Rao, 1995). Reach targets were chosen so that straight trajectories in Cartesian space resulted in curved paths in joint space and vice versa. With practice, participants adjusted their actual hand motion so that the visual feedback produced straight trajectories.

It's important to note that while the visuomotor perturbation paradigm has been used extensively to study motor learning in conjunction with reaching tasks; it is not the only method of studying motor learning in general. Motor learning has also been extensively researched in oculomotor control studies involving saccadic adaptation (Desmurget et al., 1998; Deubel, Wolf & Hauske, 1986; Jurgens, Becker, & Kornhuber, 1981; Quaia, Paré, Wurtz & Optican, 2000), visual pursuit adaptation (Optican, Zee & Chu, 1985) and the vestibulo-ocular reflex (Crawford & Vilis, 1991; Gonshor & Jones, 1976; Miles & Fuller, 1974). As such, any conclusions drawn from motor learning studies
involving reaching under a visuomotor rotation, must necessarily be viewed in the context of reaching itself, and do not necessarily extend to motor learning in general.

*Representation of reach planning*

While research using visuomotor perturbations has shed much light on the nature and structure of the information processes that give rise to motor learning, to get a full understanding of the process it must be situated within the larger context of reach planning itself. What processes are involved in executing a reach in the first place, before any perturbations are applied?

The basic view that reaching consists of two broad phases, a fast velocity initial "launch" phase and a low velocity final "homing" phase has prevailed since it was introduced by Woodworth (Woodworth, 1899). This view is still generally accepted today and has received support from the work of Jeannerod (Jeannerod, 1981, 1984) who demonstrated that reaching to grasp an object consists of two distinct phases, a transport phase where the hand moves rapidly toward the target, and a manipulation phase where the hand slows down on approach to the target and the thumb and forefinger open to the correct width to grasp the object. These two phases of movement broadly correspond to two types of motor control: feedforward and feedback. Feedforward control is the process of creating a movement plan or program and corresponds to Woodworth's launch phase and Jeannerod's transport phase. It is the type of control we are primarily looking at in this series of studies. Feedback control is the process of using sensory input to adjust an ongoing movement to ensure the goal or task is achieved. Woodworth's homing and Jeannerod's manipulation phases are roughly analogous to feedback control. Since
feedback control can alter behaviour during movement (i.e. within a single trial) it can mask or confound the feedforward effects researchers are probing. One common method used to minimize the role of visual and proprioceptive feedback is to use fast, ballistic type movements, so the participant does not have time to process sensory feedback fast enough to affect the movement (as in Baily, 1972). A common method used to prevent the use of visual feedback is to simply remove vision of the hand and/or target during movement (through the use of screens or shutters in prism experiments, or simply removing objects from virtual displays).

Work in the 1990s led to a broad overview of visually guided reach planning (Georgopoulos 1991, Soechting & Flanders 1992), in which the process is viewed in terms of a series of transformations converting sensory information into motor commands. First, the location of the target is transformed from a retinotopic reference frame to a body-centered visual reference frame by taking into account the positions of the eyes and head. At the same time, the location of the hand is calculated in the same reference frame. If the hand is visible, then the same transformations applied to the target are applied to the hand. If the target is not visible, then proprioceptive input about arm configuration (elbow and shoulder angles) is transformed into the common reference frame. Second, the difference vector (direction and distance) between the location of the hand and target in this common reference frame is computed and then transformed into a shoulder-centered reference frame. Lastly the shoulder centered movement vector is transformed into motor commands for the muscles. Researchers used characteristic errors in movement to deduce this series of transformations and to show that it is essentially a modular and sequential process within the central nervous system (Flanders,

More recent work has suggested that the calculation of the movement vector between hand and target is performed in gaze-centered coordinates (Crawford, Medendorp & Marotta, 2004; Blohm & Crawford, 2007). However, the key ingredients are the same. Whether the target and hand locations are transformed into body centered coordinates and then the difference vector is calculated or whether the difference vector is calculated in gaze coordinates and then transformed into body centered coordinates, it is assumed that target and hand locations are transformed into a common reference frame in order to specify the movement as a vector of distance and direction. In either case, the movement vector must still be transformed into shoulder centered coordinates and then into patterns of muscle activation.

The basic idea that motion of the hand is controlled visually was first explored by Morasso (Morasso, 1981). By examining the tangential velocity of the hand and the angular velocities and accelerations of the elbow and shoulder joints for a series of different reaches, Morasso found that the main commonality for all reaches was a bell shaped velocity profile of the hand and a roughly straight line hand path, thus suggesting that the nervous system plans the motion of the hand in terms of its trajectory in external visual space.

A more recent approach in motor research has been to examine movement planning in terms of optimal control. On the assumption that the brain plans movements so as to be optimal or near-optimal according to some specified set of criteria (collectively called cost functions), much work has been done to identify what these cost functions are for movement planning. Providing further evidence that reaches are
planned in visual space, Wolpert (Wolpert, 1997) showed that for reach planning the cost function is kinematic. That is, in reaching studies using visuomotor and force field perturbations, participants were shown to adapt their reaches so as to minimize the reaching cost in terms of kinematic variables, such as hand position in visual space, as opposed to dynamic variables such as joint torque change.

Other theories of reach planning also predict straight line hand paths and bell shaped velocity profiles without requiring that the movement actually be planned in visual space. The minimum jerk theory (Flash & Hogan, 1985; Flash 1987) posits that reaches are planned so as to minimize changes in hand acceleration, which results in straight line hand paths and bell shaped velocity profiles in physical space. Uno and colleagues (Uno, Kawato & Suzuki, 1989) have suggested that torque changes are minimized during reach planning, which again results in roughly straight hand paths and bell shaped velocity profiles. However, the visual perturbation experiments of Wolpert and Flanagan & Rao (Wolpert et al., 1995; Flanagan & Rao, 1995) would appear to contradict these ideas.

A number of studies support the idea that reaching movements are planned in terms of a vector consisting of distance and direction. Riehle & Requin found that reach planning results from a process where different movement parameters are calculated and then assembled together to create a motor program (Riehle & Requin, 1989). They found that motion of the hand is coded in terms of both movement direction and distance in visual space, and that direction to the target must be calculated prior to encoding distance. This independence of direction and distance in movement planning was demonstrated by Gordon and colleagues (Gordon, Ghilardi & Ghez, 1993) in a study of the variability of
movement end points. The variability of movement end points in the direction of
movement from hand to target increase with target distance, whereas the variability of
movement end points perpendicular to the direction of movement are constant in angular
terms. This finding also suggests that the movement vector itself is planned from the
hand to the target and not from some other starting point (e.g. shoulder, head, torso etc...).

Working with Rhesus monkeys, Georgopoulos and colleagues (Georgopoulos,
Schwartz & Kettner, 1986) reported that the direction of movement of the hand is
represented by a population code of neurons in motor cortex that are broadly tuned to
motion of the hand in visual space. Each cell responds most strongly to a specific
direction of hand motion in 3D space, and gradually less so as the motion deviates further
from the cell's preferred direction. Motion of the hand is accurately predicted by a vector
sum of the individual cell vectors (preferred direction and cell activation). This research
was extended by Caminiti and colleagues (Caminiti, Johnson, Burnod, Galli & Ferraina,
1990; Caminiti, Johnson & Urbano, 1990) who found that the preferred directions of cells
in motor cortex rotated with the shoulder. That is, the preferred directions exhibited are
relative to a coordinate frame around the shoulder. Despite the fact that cells preferred
direction in extrinsic visual space changes as the shoulder rotates, the population code of
the aggregate cells still accurately predicts hand motion in extrinsic visual space.

Recently, converging evidence from several studies has indicated that the brain
constructs movement commands by combining multiple computational basis functions
with a broad tuning for the desired movement direction of the hand (Thoroughman &
Shadmehr, 2000; Donchin, Francis & Shadmehr, 2003; Wainscot, Donchin & Shadmehr,
2005). This is consistent with the work of Georgopolous and Caminiti and colleagues;
the population codes of preferred directions can easily be construed as the biological correlates of the inferred basis functions for movement direction.

The findings of Georgopoulos and Caminiti remain controversial, however. Other researchers have shown that alternative interpretations can account for the data just as well or better than the interpretation of Georgopoulos and Caminiti (Scott, 2000a, 2000b; Todorov, 2000a, 2000b). In particular, Todorov has developed a model demonstrating that interpreting the activations of cells in motor cortex as directly controlling muscle activation accounts not only for the data in Georgopoulos' and Caminiti's studies, but for a number of other studies as well (Todorov, 2000a). Todorov shows that once arm inertia, joint stiffness and current arm state are factored in, the muscle activations necessary for a given arm movement are highly correlated with the direction of that movement in extrinsic visual space (Todorov, 2000a). In addition, Scott and Kalaska (Scott & Kalaska, 1997) found that when making reaches with similar hand paths but different arm configurations, activity of cells in the motor cortex was more closely correlated with intrinsic joint kinematic variables such as joint torques rather than extrinsic variables such as extent and direction of movement. The main objection to the interpretation of Georgopoulos and Caminiti is that if motor cortex were to code for high level motion planning like direction, then the relatively complex transformation of direction into joint angles and muscle commands would be left for evolutionarily primitive circuits in the spinal cord (Scott, 2000b). This does not rule out the existence of a biological correlate of the basis functions proposed by Thoroughman & Shadmehr, Donchin and colleagues and Wainscot and colleagues, but suggests that if such correlates exist, they are higher up in the cortical hierarchy.
A couple of recent studies have suggested that the brain represents reach plans not only in terms of the visual difference vector between hand and target, but also in terms of the desired final position of the hand (Scheidt & Ghez, 2007; Ghez, Scheidt & Heijink, 2007). This is related to the equilibrium point hypothesis of motor control developed by Feldman and colleagues (Feldman, 1986; Feldman, Adamovich, Ostry & Flanagan, 1990; Flanagan, Ostry & Feldman, 1993) which proposes that the brain specifies an equilibrium position via central motor commands that, in combination with reflex-mediated changes in muscle activity, drive the limb toward the equilibrium position. According to Scheidt & Ghez and Ghez & colleagues, reach planning consists of specifying both the direction and distance from the hand to the target as well as the desired hand end point in terms of the muscle equilibrium necessary to attain it. In this view, reach execution is a two stage process very similar to that proposed by Woodworth (Woodworth, 1899), where the distance and direction to the target serve to initiate the movement to the target, and the desired equilibrium point serves later in the movement to bring the hand to its final position.

*Adaptation of reach planning*

In the picture of visuomotor processing developed so far, there are several possible adaptive mechanisms: visual shift, a change in the felt position of the eye; proprioceptive shift, a change in the felt position of the arm or hand; a re-mapping of motion vectors and an “assimilated corrective response”, a change in the motor commands produced. Additionally, there are several stages of the process; whereby the target and hand locations are transformed into a common frame of reference, the desired
motion of the hand is calculated as a vector in this common frame, and this vector is translated into specific arm motor commands. Adaptation to a visuomotor rotation or shift could therefore occur in one or all of three broad phases of the visuomotor transformation. During early sensory encoding, when relevant sensory input is being received, the integration of that input could be altered. After integration, when movements are being planned in a common reference frame, the direction or angle of the movement vector could be changed. Lastly, the motor output generated to perform the movement could be modified. By integrating what is known about mechanisms responsible for adapting to visuomotor perturbations with what is known about the processes involved in reach planning, we can get a good idea of where in the visuomotor transformation mechanism the adaptive processes play their role. Visual shift and proprioceptive shift must occur in the early stages, when target and hand locations are being transformed. The re-mapping of motion vectors and the assimilated corrective response must occur somewhere in the process of mapping movement vectors to muscle commands.

In terms of visuomotor rotations, it is generally accepted that adaptation to the rotation occurs as a result of a vector re-mapping process (Cunningham, 1989; Roby-Brami & Burnod, 1995; Pine et al., 1996; Krakauer et al., 2000). Executed motor vectors are re-mapped to the consequent visual vectors produced. If either proprioceptive or visual shift played a significant role in adaptation to a visuomotor rotation, then a greater generalisation across the workspace than has been observed would be expected. Similarly, since a number of studies have shown that reach planning takes place in a visual, kinematic space (Wolpert et al., 1995; Flanagan & Rao, 1995; Morasso, 1981),
adaptation of this mechanism would also be expected to take place kinematically as opposed to dynamically (which would be the case for an assimilated corrective response). Thus the prevailing view of adaptation to a visuomotor rotation is that adaptation occurs as an alteration of the direction portion of the vectorial representation of reach planning.

Task and context specific effects in motor learning

A large body of research has shown that learning to reach out to a target while a visuomotor perturbation is applied depends heavily on the context under which the learning occurs. To examine the specificity of motor learning to various contexts and tasks, previous work has tested how adaptation to a visuomotor perturbation transfers or generalizes across changes in arm kinematics and dynamics. These studies have shown partial transfer across changes in movement speed (Kitazawa, Kimura & Uka, 1997), throwing style (Martin, Keating, Goodkin, Bastian & Thach, 1996), arm load (Fernandez-Ruiz et al., 2000), target direction (Krakauer et al., 2000) and initial/ final arm configuration (Baraduc & Wolpert, 2002). In Martin and colleagues (Martin et al., 1996) participants threw clay balls at a target using either an underhand or overhand throwing style while wearing laterally displacing prisms. They found partial generalization of motor learning between overhand and underhand throwing. Martin and colleagues concluded that the mechanism of motor adaptation is a change in the normal relation of the direction gaze with the direction of throw and that the altered relation is privately stored with respect to body part or task. Kitazawa and colleagues (Kitazawa et al., 1997) had participants' reach from a button to a target on a screen in front of them while wearing laterally displacing prisms. In their task, participants reached toward the target
using different velocities (fast or slow). Visual feedback of hand and arm position was provided at the end of the movement but vision of the hand and arm was blocked during movement. After adapting to the prism while reaching with one velocity, participants were tested while reaching with the other velocity. They found partial generalization between fast and slow reaches. They concluded that adaptation occurs in a later stage of the visuomotor transformation where time dependent aspects of movement kinematics are represented (e.g. velocity, acceleration, force...). Baraduc & Wolpert (Baraduc & Wolpert, 2002) had participants perform a reaching task with different initial configurations of the arm while a virtual reality (VR) environment was used to displace the visual feedback in a manner similar to a prism. Participants were given visual feedback throughout the movement. They found graded generalization, where the amount of transfer to novel initial arm configurations scaled with the degree of change in arm configuration, and concluded that the adaptation is not a function of sensory processing (visual or proprioceptive shift) but a change in the transformation of visual input to motor output which is specific to the trajectory of the arm through joint space. Fernandez-Ruiz and colleagues (Fernandez-Ruiz et al, 2000) had participants throw clay balls at a target while wearing laterally displacing prisms. In their study participants threw under varying weight conditions (different masses fixed to the wrist). They found that there was only partial transfer of adaptation between different weight conditions and concluded that the representation of a motor memory is stored under a specific weight condition, and can only be properly retrieved under the same weight conditions.

Further evidence for the specificity of motor learning in general comes from Mah & Mussa-Ivaldi (Mah & Mussa-Ivaldi, 2003). They had participants learn a novel task
with a virtual object (balancing an inverted pendulum in a virtual environment), and demonstrated that the learned responses were specific to both the task and motor commands. The learned skill did not transfer well to the same task using different motor commands, nor did it transfer well to a different task using the same motor commands.

If the specificity of motor learning observed in these studies is due to the motor or task context serving as a cue or index for the learned adaptation, then the partial generalisation observed in those studies must be due to some portion of the learned adaptation being specific and the rest being shared. If the vectorial view of adaptation to a visuomotor rotation is also correct, then the motor or task context of a given reaching movement used when learning the rotation serves in some way to index a portion of the learned vector adaptation. In this case, a predictable, partial generalisation across any given task or motor context should be observed when adapting to a visuomotor rotation.

On the other hand, if the motor or task context does not serve simply as a cue or index for the learned representation, then it must mean that the specific portion of the adaptation occurs via a different adaptive process more closely tied to the motor commands executed, such as the assimilated corrective response proposed by Welch (Welch, 1974) or the equilibrium end point proposed by Ghez and colleagues (Scheidt & Ghez, 2007; Ghez, Scheidt & Heijink, 2007).

Curved vs. straight reaching

Most previous research in the area of motor control for reaching has solely investigated straight line reaching, where participants were either explicitly instructed to reach in a straight line path or naturally chose roughly straight line paths. Such reaching
movements map well to the accepted notion of vector representation of reach plans, where planned movements are specified in terms of the direction and amplitude of the reach. Does the vectorial representation of reach planning hold for hand paths that are not easily mapped on to a single vector? Additionally, previous research has demonstrated that motor learning is specific to motor or task context and only partially generalizes to conditions different from that of training. Is the specificity of motor learning due to simple contextual cueing or indexing effects, or are they the result of additional adaptive processes?

In the current set of studies, we examine how learning of a visuomotor rotation while reaching to a target with a curved hand path generalizes to straight path reaching. We also examine how adaptation of curved reaches made to one target generalizes to novel targets located in different directions from the start position. In both cases, we examine how generalization was affected by the type of sensory feedback provided during adaptation. When examining transfer of learning from curved to straight reaches, we maintained the initial and final hand and arm configurations during the reach. Thus we could examine the effects of the arm trajectory per se, independently of the start and end positions (or the displacement between these positions). By examining how curved reach adaptation generalizes to both novel hand paths and target directions, we can make inferences about how the adaptation is represented. If curved and straight line reach adaptations occur as alterations in the vectorial representation of reach planning, then the pattern of generalization across novel directions should be similar. In addition, good transfer between curved and straight line reaches should be observed. Conversely, if the planning of curved reaches involves processes that are distinct from those engaged when
planning straight reaches, we would not expect good transfer between these different
types of reaches and may also expect a different pattern of generalization across target
directions for curved and straight reaches. By examining the overall pattern of
generalization, we can ask whether hand path during reaching serves simply as a general
context to store or index motor memory or if it can tell us something more about the
process of reach planning and adaptation. If hand path through space acts simply as a
contextual cue for motor learning, then partial generalization of learning would be
expected when switching from curved to straight line reaches.
Chapter 2: General Methods

Participants

Participants in all studies were neurologically intact university students who volunteered to participate after giving informed consent. All participants had normal or corrected to normal vision. The experimental protocol was approved by the Queen’s University Ethics Board.

Apparatus

Participants sat on an adjustable stool at a glass-topped table and held a vertical cylindrical handle with their right hand (see Figure 1). The handle was attached to a lightweight, force-reflecting robotic manipulandum (Phantom Haptic Interface 3.0L, SensAble Technologies – capable of producing up to 10N of force feedback) and mounted on an air sled that enabled the participant to move the handle over the table top with minimal friction. The manipulandum measured the position of the handle with a temporal resolution of 1000 Hz and a spatial resolution of 0.1 mm. An opaque shield prevented participants from seeing their arm at all times. A visual projection system was used to display targets, a start position, and a cursor representing the handle in a horizontal plane aligned with the top of the handle. Specifically, a CRT projector (Electrohome 9500 Ultra) projected the 2D virtual environment onto a projection screen (located above the plane of motion) that participants viewed in a semi-silvered mirror located midway between the screen and the plane of handle motion.
**General Procedure**

At the beginning of each trial, participants were presented with a start position (white circle 2 cm in diameter) and a cursor representing the position of the handle (green circle 2 cm in diameter). Trials were initiated after the participant successfully aligned the handle with the start position. A target (blue circle 2 cm in diameter) was then presented, located 20 cm away from the start position, and the participant was required to reach out to contact the target. In all but one experiment they were asked to make and “out-and-back” reaching movement in which they moved the handle from the start position to the target and back such that they returned to the vicinity of start position within 750 ms of the start of their movement. To provide feedback about movement

![Figure 1. Experimental apparatus. Participants held onto the handle of a force reflecting manipulandum (Phantom Haptic Interface 3.0L), and made reaching movements to visual targets projected on a semi-silvered mirror. Participants were seated such that vision of their arms was blocked. Participants reached with their right hand only (figure shows bimanual reaching).](image-url)
Figure 2. Example of a baseline curved reaching trial, showing the out-and-back progression. A. Spatial plot of reach. B. Plot of X position relative to the start position by time t. C. Plot of Y position relative to the start position by time t.

duration, the start position changed colour to red 750 ms after the onset of movement. In one experiment, they were asked to make an outward movement to the target and stop.

In some experiments the cursor representing the handle position was visible throughout the movement whereas, in others, the cursor was visible only at the start position and target (see below). In addition, in one experiment, force feedback, simulating contact between was handle and target, was provided when the handle contact
the target. An outline of all experiments and the key manipulations involved in each is provided in Table 1.

Participants made two types of reaching movements, either straight movements or curved movements, and were verbally instructed as to which type of movement to make. For straight movements they were simply instructed to reach “as straight as possible” to the target and back. For curved movements, they were instructed to reach “in an arc on the right so as to contact the target on the right hand side”. In order to keep the movements as natural as possible, we did not explicitly control for the degree of hand path curvature beyond these simple verbal instructions. A typical out and back curved reaching movement is shown in Figure 2.

General Data Analysis

The X and Y handle positions in the horizontal plane of movement were recorded at 1000 Hz. Position data were smoothed with a low-pass zero-pass lag Butterworth filter using a 10 Hz cut-off frequency. The smoothed position data were then differentiated to obtain X and Y velocities. For each trial, movement onset and end times were determined by finding the points where the magnitude of the instantaneous tangential handle velocity exceeded and fell below 100 mm/s, respectively. Note that even though participants made out-and-back reaching movements, the tangential velocity of the handle dropped close to zero at the turn around point, which we define as the movement end point.

Mean hand paths were determined by normalizing each trial's duration to 1. We then linearly interpolated the spatial trial data into one hundred slices of the normalized
time and averaged the X and Y positions across all trials.

Based on visual inspection of the data, there did not appear to be any obvious differences in hand path curvature before and after training. Additionally, a preliminary analysis examining curvature in terms of the maximum X extent over the maximum Y extent also indicated that our participants did not significantly change their hand path curvature as a result of training. Based on these observations, we do not pursue a complete quantitative analysis of hand path curvature.

In all statistical analyses, an alpha value of .05 was considered to be statistically significant.

Table 1

*Experimental Outline and Key Manipulations*

<table>
<thead>
<tr>
<th>Study</th>
<th>Hand Path</th>
<th>Testing</th>
<th>Feedback</th>
<th>Notes</th>
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</thead>
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<td></td>
<td></td>
<td>Training</td>
<td>Testing</td>
<td>Targets</td>
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<td></td>
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<td>Straight</td>
<td>20°</td>
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<tr>
<td>Study 2</td>
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<td>0°</td>
<td>Discrete visual</td>
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<tr>
<td>Study 3</td>
<td></td>
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Table 1

*Experimental Outline and Key Manipulations*

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<th>Testing Targets</th>
<th>Feedback</th>
<th>Notes</th>
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<td>Clockwise visuomotor rotation</td>
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<td>Group 3</td>
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<td>Continuous visual</td>
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<td>Study 5</td>
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<td>Discrete visual</td>
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<tr>
<td>Study 6</td>
<td>Curved</td>
<td>Straight 0° visual</td>
<td>Discrete Hand held at target briefly before returning to start</td>
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Chapter 3: Study 1

Introduction

The great majority of studies that have examined how reaching movements are adapted to a visuomotor rotation have focused on straight line reaching movements. One of the key ideas that has stemmed from this work is that reaching movements are planned in terms of the direction and amplitude of the required movement. However, in daily tasks, we often make curved reaching movements. For example, when reaching with the right hand to grasp a bottle from the right side, with the thumb contacting the near side and the other fingers contacting the back, we initially direct the hand to the right of the bottle and then curve the hand in towards the bottle before grasping it. Similarly, if we reach out to touch the right side of a square target object with our fingertip, we will generate a curved hand path (Smeets and Brenner 1999). The aim of this study was to investigate the extent to which curved and straight reaching movements shared common planning processes. On the one hand, it is obvious that curved reaching movements cannot be fully specified in terms of reach direction and amplitude. On the other hand, the planning and generating of straight and curved may share certain processing steps. For example, it may be that both straight line and curved reaching movements involve the initial specification of a movement end point that can be represented in terms of direction and amplitude.

In order to address this issue, we examined how adaptation to a visuomotor rotation while making curved reaching movements generalizes to straight line reaching. During the adaptation phase, participants moved a handle from a start position to a target, located directly in front of them, and back. They were instructed to make a curved hand
path and to contact the right side of the target. They received forces, simulating contact between the handle and the target, when they contacted the target but could not see the handle or the arm. In initial practice trials, the visual and felt locations of the target – which we will refer to as the visual target and the haptic target, respectively – were aligned. However, during the adaptation phase, the position of the haptic target was gradually rotated clockwise around the start position. When the handle contacted the haptic target, participants effectively received visual feedback about the position of the handle because they felt the handle contact the visible target. Thus, by rotating the haptic target, we effectively created a visuomotor rotation in which participants receive distorted visual feedback related to the position of the handle at the end point of the movement. A gradual rotation of the haptic target was used so that participants would not become aware of the perturbation (Klassen, Tong & Flanagan, 2005; Kagerer, Contreras-Vidal & Stelmach, 1997; Ingram et al. 2000; Malfait & Ostry 2004). In the transfer phase following this adaptation phase, we asked participants to make straight line reaching movements to the visible target.

If adaptation of the curved reach involves remapping a vector specifying the direction and amplitude of the movement end point, then we might expect adaptation of curved reaches to generalize fully to straight line reaches. One the other hand, if adaptation involves a re-mapping between the visual target and motor commands specific to the curved hand trajectory, then little or no generalization would be expected.

Krakauer and colleagues (Krakauer et al., 2000) found that adaptation of straight line reaching movements to a visuomotor rotation shows limited generalization to new directions. Specifically, when participants are adapted to a 45° visuomotor rotation when
repeatedly reaching to a target in one direction, partial generalization is seen for targets located 22.5° away from the training target and no generalization is seen for targets located 45° away from the target. In the main experiment described in this study, we adapted participants to a target located directly in front of the participant while they made curved movements and then tested for generalization to straight reaches using the same target. That is, we assumed that any generalization would be strongest for the same visual target. However, it is also possible that generalization is strongest in the initial direction of the curved reaching movement. In straight line reaching, the initial direction of the reaching movement closely coincides with the direction of the target. However, in curved reaching this is not the case. Therefore, we ran an additional control experiment in which generalization was tested for a target located in the direction of the initial part of the curved reaching movement (measured in our main experiment). We also included a control experiment in which generalization was tested in the direction of the rotated haptic target position rather than the visible target.

**Methods**

**Participants**

Sixteen neurologically intact university students volunteered to participate after giving informed consent. Participants were randomly assigned to one of 3 independent experimental groups, with 8 participants in Group 1, and 4 each in Group 2 and Group 3. Groups 2 & 3 served as simple controls for the main experiment (Group 1).

**Procedure**

Participants did not receive any visual feedback of hand position during
movement, but did receive haptic (force reflecting) feedback simulating contact with the target. During the initial practice phase participants made 26 curved reaches to targets located at -20, 0 and 20º, followed by 26 straight reaches to the same targets. Eight reaches were made to each of the offset targets (± 20º) and 10 reaches were made to the target located directly ahead (0º). Practice targets were randomized by trial.

After the practice phase, we instructed participants to make curved reaches to a target located at 0º (the training phase). Over 80 trials, the position of the haptic target was gradually rotated clockwise (0.25º per trial) about the start position, such that, at the end of the first 80 training trials, the haptic target was rotated 20º with respect to the visual target which did not move. Participants made a further 10 curved reaches to the 0 degree target with the rotated haptic target before moving on to the transfer phase.

In the transfer phase we instructed participants to make straight reaches. Participants in Group 1 made 10 reaches to a visual target located at 0º; that is, in the same location as the training target. A haptic target was also provided at 20º where the participant would be expected to reach should the learned rotation transfer completely from curved to straight line reaching. In Group 2, participants made 10 reaches to a visible target located at 56º and a haptic target was also provided at 76º. A target angle of 56º was selected because this corresponded to the average initial direction of the adapted curved movement in Group 1 (see below). In Group 3, participants made 10 transfer reaches to a target located at 20º, with a haptic target also provided at 40º.

Analysis

To characterize reaching performance and adaptation we computed several dependent variables related to reach direction. The initial directional error for the handle
(IDEh) was calculated by taking the angular difference between the vector from the start position to the visual target and the vector from the start position to the handle position 150 ms after movement onset.

We also determined the angular difference between the visual target and the position of handle at the movement end point (ADh). This was calculated as the angular difference between the vector from the start position to the target and the vector from the start position to the position of the handle at the movement end point.

We also expressed the extent of adaptation to the rotation of the haptic target in each trial as a percentage of the target rotation as follows:

\[
\text{PercAdap} = 100 \times \left( \frac{ADh}{HapticAngle} \right)
\]

where PercAdap is the percentage adaptation and HapticAngle is the degree of rotation of the haptic target relative to the visual target.

Generalization of rotational adaptation from curved to straight trajectories was calculated as the ratio of the mean PercAdap observed during the 10 transfer trials to the mean PercAdap observed during the last 10 training trials. This ratio was expressed as a percentage and we will refer to this dependent variable as the percent generalization (PercGen).

Results

Figure 3 shows individual trial and mean hand paths of a representative
Figure 3. Study 1: Individual and mean hand paths for participant P2. Individual trials are shown in black, means are superimposed in blue. A. Curved reaching trials to the training target, located at 0 degrees, during practice. B. Straight reaching trials to the training target during practice. C. Final 10 curved reaches during training. D. Transfer trials, straight reaching.

participant (P2) from Group 1. Figures 3A and B show curved and straight hand paths to the center (0 degree) target during the initial practice phase in which the visual and haptic targets were aligned. Figure 3C shows the final 10 trials in the training phase where the haptic target was fully rotated by 20°. As illustrated in the figure, the participants readily adapted to the rotated haptic target by changing the initial direction of their curved reach
trajectories. Figure 3D shows all 10 trials in the transfer phase where the participant was instructed to make straight line reaches to the (visible) target. As illustrated in the figure, effectively no transfer of adaptation was observed. That is, they reached directly to the visible target rather than the haptic target.

In response to the perturbation during the training phase, participants gradually altered the initial direction error (IDE) of their curved hand trajectories. Figure 4 shows mean IDE values, averaged across the 8 participants in Group 1, as a function of training.
trial. Mean IDE over the training phase changed from an initial value of 56° during the practice phase to approximately 73° at the end of training, which represents a change in IDE due to training of about 15°. None of the participants indicated being aware that the haptic target had rotated.

Figure 5 shows the mean PercGen across participants for each of the three groups. PercGen was calculated for each participant as the ratio of mean PercAdap during testing (while reaching straight) to the mean PercAdap after training (while reaching curved). For group 1 (N=8) a t-test \[t(7) = -2.09, p = .075\] did not reveal a significant difference from zero. We did not conduct t-tests for groups 2 and 3 because of the small Ns (N=4 for both group 2 and 3). However, as can be readily seen from Figure 5, groups 2 and 3 did not exhibit substantial generalisation either. Importantly, in none of the three groups did the adaptation generalize to straight line reaching.

![Figure 5. Study 1: Percent generalization for straight reaches to training target for all groups. Vertical bars show ±1 SEM.](image)
Figure 6 shows mean hand paths before and after training for all three groups.

Figure 6A shows mean curved hand path across all participants in group 1 before training (solid line) and after training (dashed line). Figure 6B shows mean straight hand path across all participants in group 1 before training (solid line) and during transfer (dashed line) Figures 6C and D, and 6E and F show the same for groups 2 and 3. Evaluation of mean hand paths clearly demonstrated that participants did not generalize the rotational adaptation from curved to straight line reaching in any of the three groups.

Since the ADh dependent variable is normalised for target direction, we compared the mean angular differences of the handle (ADh) for straight line reaches before and after training using a single factor repeated measures ANOVA for all participants from all groups. The ANOVA \[ F(1,15) = 2.18, p = .161 \] showed that the mean ADh after training was not significantly different than before training.

**Discussion**

Participants readily adapted to the rotation by altering the initial direction error of the handle (IDEh). On transfer, participants did not exhibit any generalisation of the adaptation to the rotation from curved to straight line reaching. Generalisation for group 1 was not significantly different from zero. Additionally there was no significant difference in the angular difference of handle movement end point between straight line reaches before and after training.
Figure 6. Study 1: Mean trajectories. Panels A, C, and E show, for Group 1, 2 and 3, respectively, mean curved hand paths to the training target before (solid) and at the end of (dashed) training. Blue circles show the visual target (which was aligned with the haptic target before training) and the purple circles show the haptic target at the end of training. Panels B, D, and F show corresponding mean straight hand paths before training (solid) and during transfer (dashed). Blue circles show visual targets and the purple circles show haptic targets when these were different than the visual targets.
One potential confound when examining adaptation based on using the angular difference of movement end points and haptic feedback, is that the force feedback provided automatically results in the end of the movement on contact with the target. Since the target and virtual hand cursor were both 2 cm in diameter, the force feedback provided when the participants contact the target results in a movement end point at least 2cm away from the center of the target. When participants reach in an arc from the right hand side (as they did in this study), it results in an over-estimation of the amount of adaptation (as the participant's movement end point is always rotated further clockwise from the visual target than the angular magnitude of the current visuomotor rotation). An objection could be raised then, that participants are not truly adapted to the rotation, and instead are simply performing the same motion repeatedly, but being stopped earlier in the movement arc by the force feedback mechanism. However, the change in the IDE of the hand as the adaptation progresses demonstrates clearly that participants alter the IDE of the hand path in response to the perturbation (see Figure 5).

The results from the control groups 2 and 3 show that the failure of transfer of a learned adaptation from curved reaching to straight line reaching is not due to the memory being stored relative to an angle other than the one between hand and target. Neither control group shows anymore transfer than group 1.

The fact that participants successfully adapt to the rotation of the haptic feedback while reaching in a curved manner, yet do not show any generalization of this learning to straight line hand paths, suggests that there is no shared representation of learning between different hand paths in the conditions of this study. The absence of any generalization at all is unexpected and surprising, especially so since in previous studies...
of visuomotor transformations with similar conditions, at least partial transfer was been observed. In particular, the task in Kitazawa and colleagues (Kitazawa et al., 1997), involved reaching to a target on a touch screen while wearing displacing prisms. Participants were not given visual feedback during movement and were only shown their error after touching the screen (receiving haptic feedback). In their study, Kitazawa and colleagues found partial generalization of prism adaptation between different movement velocities (but the same hand path). If the trajectory of the hand through space functioned simply as a contextual cue to aid learning in a manner similar to velocity, then partial generalization would be expected. Since there was zero generalization, it indicates that hand path is not merely a contextual cue for learning, but has implications in regard to the actual representation and structure of the learned adaptation itself.

However, it remains possible that the lack of transfer is related to factors other than the hand path itself. It could be that the sensory feedback provided by the haptic modality alone does not allow some components of reach planning to be properly adapted, and those components which can be adapted based solely on haptic information do not share any properties between different hand paths. This issue is examined in study 2. Conversely, it could be the temporal characteristics of the feedback which is responsible for the lack of transfer. Endpoint, terminal feedback alone might be insufficient to allow training of components of adaptation that are shared between different hand paths. This issue is addressed in study 3.
Chapter 4: Study 2

Introduction

In the previous study, we found no transfer between curved and straight line reaching when adapting to a visuomotor rotation, suggesting that there was no shared representation of learning between the two spatial trajectories. Previous studies that have investigated context and task specific effects of learning have found partial transfer of motor learning between various similar contexts (Kitazawa et al., 1997; Martin et al., 1996; Fernandez-Ruiz et al., 2000; Krakauer et al., 2000; Baraduc & Wolpert, 2002). However, in all previous studies on context dependent motor learning, feedback was always given in a visual modality. The aim of this study was to investigate the extent to which sensory modality was a factor in the lack of transfer between curved and straight line reaching in study 1. To this end, we replicated study 1 as closely as possible, using visual (as opposed to haptic) feedback provided discretely at the endpoint of the movement (the target). That is feedback was only provided when the hand cursor intersected with the visual target in order to mimic the haptic forces provided in study 1 when the hand cursor contacted the haptic target.

If the haptic sensory modality is somehow less salient to the adaptation process than the visual modality, then the lack of generalisation observed in study 1 could be explained by the use of haptic feedback to provide endpoint information. In this case we might expect that providing equivalent feedback visually would result in full transfer of learning from curved to straight line reaches. If, on the other hand, the sensory modality of the feedback is functionally irrelevant we might expect little to no transfer from curved to straight line reaching.
Methods

Participants

Eight neurologically intact university students volunteered to participate after giving informed consent.

Procedure

Participants did not receive any visual feedback of hand position during movement, but did receive visual feedback of the hand cursor when it intersected the target. Participants did not receive haptic feedback during this study. During the practice phase participants made 26 curved reaches to targets located at -20, 0 and 20°, followed by 26 straight reaches to the same targets. 8 reaches were made to each of the offset targets and 10 reaches were made to the target located directly ahead (0°). Practice targets were randomized by trial. After the practice phase, we instructed participants to make curved reaches to a target located at 0°. Over 80 trials, the hand cursor visual feedback gradually rotated 20° counter-clockwise (0.25° per trial), such that, at the end of the first 80 training trials, visual feedback of the hand cursor was rotated 20° counter clockwise about the start position. Participants made a further 10 curved reaches to the 0 degree target with rotated hand cursor feedback before moving on to the transfer phase. In the transfer phase participants made 10 straight reaches to a target located at 0°.

Analysis

To characterize reaching performance and adaptation we computed several dependent variables related to reach direction. The initial directional error for the cursor (IDEc) was calculated by taking the angular difference between the vector from the start
position to the visual target and the vector from the start position to the cursor position 150 ms after movement onset.

We also determined the angular difference between the visual target and the position of cursor at the movement end point (ADc). This was calculated as the angular difference between the vector from the start position to the target and the vector from the start position to the position of the cursor at the movement end point.

We also expressed the extent of adaptation to the rotation of the visual cursor in each trial as a percentage of the target rotation as follows:

\[
PercAdap = 100 \times \left(1 - \frac{ADc}{CursorRotation}\right)
\]

where PercAdap is the percentage adaptation and CursorRotation is the degree of rotation of the cursor about the start position.

Generalization of rotational adaptation from curved to straight trajectories was calculated as the ratio of the mean PercAdap observed during the 10 transfer trials to the mean PercAdap observed during the last 10 training trials. This ratio was expressed as a percentage and we will refer to this dependent variable as the percent generalization (PercGen).

**Results**

Figure 7 shows individual trial and mean hand paths of a representative participant (P5). Figures 7A and B show curved and straight hand paths to the center (0º)
Figure 7. Study 2: Individual and mean hand paths for P5. Individual trials are shown in black, means are superimposed in blue. A. Curved reaching trials to the training target during practice. B. Straight reaching trials to the training target during practice. C. Final 10 curved reaches during training. D. Transfer trials, straight reaching.

target during the initial practice phase with no rotation of the visual cursor. Figure 7C shows the final 10 trials in the training phase where the visual cursor was fully rotated by 20° counter clockwise. As illustrated in the figure, the participants readily adapted to the rotated visual feedback by changing the initial direction of their curved reach trajectories. Figure 7D shows all 10 trials in the transfer phase where the participant was instructed to
make straight line reaches to the target. As illustrated in the figure, effectively no transfer of adaptation was observed. That is, they reached directly to the target rather than off to the side (as would be expected if they were to compensate for the visuomotor rotation of the cursor).

The mean adaptation (PercAdap) across participants after the training block was 78%, which is comparable to the level of adaptation (81%) obtained in Krakauer and colleagues (Krakauer et al., 2000) for straight line reaching under a 30 degree rotation.

Generalization (PercGen) from curved to straight line reaching was higher than in study 1 (35.8%), and a single factor repeated measures ANOVA $[F(1,7) = 679.88, p = .000]$ comparing mean angular difference of the cursor (ADc) before and after training for all participants showed a significant effect of curved reach adaptation on straight reaching.

Figure 8 shows mean hand paths before and after training. Figure 8A shows mean

![Figure 8. Study 2: Mean trajectories. A. Mean curved hand paths to the training target for all participants before (solid) and after (dashed) training. B. Mean straight hand paths to the training target for all participants before training (solid) and during transfer.](image-url)
curved hand path across all participants before (solid line) and after (dashed line) training. Figure 8B shows mean hand path across all participants before training (solid line) and during testing (dashed line). Evaluation of mean hand paths demonstrated that participants did not generalize the rotational adaptation from curved to straight line reaching.

Figure 9 shows plots of the first transfer trial for all participants (black lines) and the mean hand path of the first transfer trials for all participants (blue line). The greatest effect of transfer would be expected on the first transfer trial as adaptation could decay over the transfer phase. Thus, an evaluation of the mean first transfer trials indicates that

![Figure 9](image-url)

*Figure 9. Study 2: Trajectories of initial test trials. Black lines show first test trial for each participant. Blue line shows the mean hand path of initial test trials of all participants.*
the lack of transfer observed by examining the mean hand path of all transfer trials for all participants is not an effect of aggregation.

Discussion

Participants readily adapted to the visuomotor rotation by changing the initial direction of the curved reach trajectories. The level of adaptation was comparable to that achieved by Krakauer and colleagues in a similar study (Krakauer et al., 2000). On transfer, participants exhibited a moderate amount of generalization, but did not substantially deviate their hand path from the visual target.

While there is a statistically significant effect of curved reach adaptation on straight line reaching, the plots of the first trial for each participant during the transfer phase clearly indicate that participants are aiming at the visual target (see Figure 8), and not off to the side as would be expected if they were compensating for the cursor rotation. Additionally, plots of the mean straight line trajectories to the training target before and after training reveal that what little effect curved reach adaptation has on straight line reaching is not sufficient to make the participant miss the visual target (see Figure 8). It is clear that the effect is insufficient to cause the participants' hand paths to deviate from the goal. This indicates that there is effectively less transfer than shown by the statistical analysis.

Since this study is identical to study 1 (except for the modality of the feedback given), the marginal generalization observed shows that there is a small effect of modality on generalization from curved to straight reaching, but that effect is not substantial enough to cause a failure in the task. Again, it remains possible that the
general lack of transfer observed in this study could be due to factors other than the change in hand path. Perhaps the lack of transfer is due to the discrete, endpoint nature of the feedback given. Proper adaptation of the representation of learning shared between hand paths may require continuous feedback. This issue is addressed in study 3.
Chapter 5: Study 3

Introduction

In the two studies described in chapters 3 and 4, we observed no generalization of learning when participants adapted curved reaches to a visuomotor rotation and were then tested on straight line reaches. This lack of generalization can be contrasted with the partial or graded generalization observed in previous studies that have examined how adaptation to a visuomotor transformation transfers across changes in arm configuration (Baraduc & Wolpert, 2002), load (Fernandez-Ruiz et al., 2000), movement speed (Kitazawa et al., 1997) and throwing style (Martin et al., 1996). While it is difficult to accurately compare the levels of partial generalizations observed in each of these experiments due to differences in experimental design and data analysis, the amount of generalization observed by Kitazawa and colleagues (Kitazawa et al., 1997) is markedly less than that observed in the other studies mentioned. Importantly, of those studies, only Kitazawa and colleagues used terminal feedback. Participants were only allowed to see their arm after, but not during movement.

In the studies described in chapters 4 and 5, only terminal endpoint feedback was given. That is, participants only received (distorted) visual information related to the position of the cursor at the target. Might a different pattern of generalization be observed if participants were provided with continuous rather than discrete visual feedback related to handle position? The aim of the current study was to investigate what effect continuous visual feedback about the position of the handle has on the generalization of adaptation from curved to straight line reaching. During the training phase, participants in our two main experimental groups made curved reaching
movements to a single target (located directly ahead at 0°) while a visuomotor rotation of either +20° (group 1) or -20° (group 2) was gradually imposed in 0.25° increments over 80. Transfer of adaptation to straight line reaching was then tested for 5 different targets including the training target (0°) and targets located ± 22.5 and ± 45° away from the training target. These additional targets were included to assess how any generalization to straight line reaching depended on target direction. At the same time, we tested for generalization when participant made curved reaches to different target directions.

Krakauer and colleagues (Krakauer et al., 2000) found that adaptation to a visuomotor rotation when making straight line reaches to a single target exhibits limited generalization to targets in different directions. In the study by Krakauer and coworkers, the visuomotor rotation (±30°) was introduced instantaneously (i.e., all at once). It is not known whether similar limited generalization is observed when a rotation is introduced gradually. Previous studies (Kagerer et al., 1997; Ingram et al., 2000) have reported that the gradual introduction of a perturbation both facilitates adaptation and leads to better overall adaptation when compared to instantaneously introduced perturbations – these differences may be due to differences in the way in which adaptation occurs and it is conceivable that directional generalization may be different when adapting gradually versus instantaneously. The test whether this is the case, we included an additional group of participants (group 3) who adapted, during training, to a gradually introduced rotation while making straight reaches to a single target (0°). We then tested for transfer of adaptation when they made straight line reaches to the 0° target and targets located ± 22.5 and ± 45° away from the training target. This group served as a control of our main groups.
Methods

Participants

Twenty-four neurologically intact university students volunteered to participate after giving informed consent. Participants were randomly assigned to one of 3 independent groups, with 8 participants per group.

Procedure

Participants received visual feedback of hand position (the hand cursor) continuously throughout movement. Participants did not receive haptic feedback during this study. During the initial practice phase for groups 1 and 2, participants made 50 curved reaches to targets located at -45 °, -22.5 °, 0 °, 22.5 ° and 45°, followed by 50 straight reaches to the same targets. Ten curved reaches and 10 straight reaches were made to each of the targets. Practice targets were randomized by trial. Participants in group 3 only made 50 straight reaches (to the same targets as above) during practice.

After the practice phase, we instructed participants in groups 1 and 2 to make curved reaches to a target located at 0° (the training phase). Participants in group 3 were told to make straight reaches to the same target. For groups 1 and 3, hand cursor visual feedback was gradually rotated counter-clockwise (0.25° per trial) about the start position, such that, at the end of the first 80 trials, the hand cursor was rotated 20° counter-clockwise with respect to the handle position. For group 2, hand cursor feedback was rotated clockwise in the same manner. Participants made a further 10 training reaches to the 0° target with rotated cursor feedback before moving on to the transfer phase.
In the transfer phase, participants in groups 1 and 2 made a series of “maintenance” trials, interspersed in a 3:1 ratio with “probe” trials. For maintenance trials, participants reached to the training target at 0º and were given continuous visual feedback of the rotated cursor throughout movement. For straight reach probe trials, participants reached without visual feedback to one of the five practice targets. For curved reach probe trials participants reached to one of the -45º, -22.5º, 22.5º and 45º degree targets. A total of 3 probe reaches of each trajectory type were made to each target, for a total of 27 probe reaches and 81 maintenance reaches. The transfer phase for group 3 also consisted of maintenance and probe reaches in a 3:1 ratio, but all reaches were straight. Participants in group 3 made a total of 25 probe reaches (5 probes to each of the five practice targets) and 75 maintenance reaches.

**Analysis**

To characterize reaching performance and adaptation we computed several dependent variables related to reach direction. The initial directional error for the cursor (IDEc) was calculated by taking the angular difference between the vector from the start position to the visual target and the vector from the start position to the cursor position 150 ms after movement onset.

We also determined the angular difference between the visual target and the position of cursor at the movement end point (ADc). This was calculated as the angular difference between the vector from the start position to the target and the vector from the start position to the position of the cursor at the movement end point.

We also expressed the extent of adaptation to the rotation of the visual cursor in each trial as a percentage of the target rotation as follows:
\[ PercAdap = 100 \times \left(1 - \frac{ADc}{Cursor \text{Rotation}}\right) \] Eq. 2

where PercAdap is the percentage adaptation and CursorRotation is the degree of rotation of the cursor about the start position.

Generalization of rotational adaptation from curved to straight trajectories was calculated for each probe direction as the ratio of the mean PercAdap observed during the probe trials to the mean PercAdap observed during the last 10 training trials. This ratio was expressed as a percentage and we will refer to this dependent variable as the percent generalization (PercGen).

Results

Figure 10 shows individual trial and mean hand paths for a representative participant (P7) in group 1. Figures 10A and B show curved and straight hand paths to all targets during the initial practice phase in which there was no visuomotor rotation. Figure 10C shows the final 10 trials in the training phase where the cursor was fully rotated counter clockwise by 20°. As illustrated in the figure, the participants readily adapted to the rotated feedback by changing the initial direction of their curved reach trajectories. Figures 10D and E show all curved and straight probe trials (respectively) to all probed targets during the transfer phase. As illustrated in the figure, partial transfer of adaptation to the training target was observed. All three groups showed a high degree of mean adaptation over the last 10 training trials with a fixed rotation (see Figure 11).
Figure 10. Study 3: Individual and mean hand paths for P7 in group 1. Individual trials are shown in black, means are superimposed in colour by target (-45º cyan, -22.5º red, 0º blue, 22.5º green, 45º purple). A. Curved reaching trials to all targets during practice. B. Straight reaching trials to all targets during practice. C. Final 10 curved reaches during training. D. Transfer trials, curved reaching. E. Transfer trials, straight reaching.
Groups 1 and 3 both had mean percentage adaptations of approximately 84%, which again corresponds well with the percentage adaptation result achieved by Krakauer and colleagues (81%) for straight line reaching (Krakauer et al., 2000). Group 2 had a mean percentage adaptation of 103%. A single factor ANOVA \( F(2,21) = 4.09, p = .032 \) between all three groups comparing percentage adaptation for the last 10 trials of the training phase showed a significant difference. However, subsequent ANOVAs only showed a significant difference between groups 2 and 3 \( F(1,14) = 10.06, p = .007 \) but no significant differences between groups 1 and 3 \( F(1,14) = 3.62, p = .078 \), or between groups 1 and 2 \( F(1,14) = .13, p = .720 \).

Figure 12 shows the mean PercGen across participants for each of the three groups and all 5 targets when probing transfer using straight reaches. PercGen was calculated for each participant and target as the ratio of mean PercAdap during testing.
(while reaching straight) to the mean PercAdap after training (while reaching curved).

Both groups 1 and group 2 exhibited partial generalization of adaptation from curved line reaching to straight line reaching for the training target. With respect to directions other than the trained direction, groups 1 and 2 showed peaked generalization functions when transferring to straight line reaching, with generalization falling off on either side of the peak. Unexpectedly, the peak generalization of adaptation from curved to straight line reaching for both groups 1 and 2 was not at the trained target, but the target nearest in
direction to the direction of the induced visuomotor rotation itself. Group 2 showed a lower degree of generalization overall than did group 1. As expected, neither group 1 nor group 2 generalized as well as group 3 to straight line reaching. Group 3 (which served as a control group for straight line to straight line transfer) showed a generalization function very similar to that observed in Krakauer and colleagues (Krakauer et al., 2000) except broader and flatter across novel directions. A two factor, 3x5 ANOVA comparing the percent adaptation of hand cursor AD for straight reaches during transfer (across all three groups and all five directions), showed significant main effects for both group $[F(2,105) = 14.75, p = .000]$ and direction $[F(4,105) = 2.78, p = .030]$ as well as a significant interaction $[F(8,105) = 3.49, p = .001]$ between group and direction.

Figure 13 shows the mean PercGen across participants for each of the three groups and all 5 targets when probing transfer using the same reach trajectory as training (i.e. for groups 1 and 2 training was done with curved reaches and graph shows mean PercGen using curved reaches, for group 3 training was done with straight reaches and graph shows mean PercGen using straight reaches). PercGen was calculated for each participant and target as the ratio of mean PercAdap during testing to the mean PercAdap after training. For groups 1 and 2, generalization from curved reaching to curved reaching across directions was much higher globally than for curved to straight, and exhibited a generalization function very similar to the straight line to straight line generalization function of group 3. A two factor, 2x5 ANOVA comparing the percent adaptation of hand cursor AD for curved reaches during transfer (across groups 1 and 2 and all five directions), showed no significant main effects for direction $[F(4,70) = 1.41, p = .239]$ or group$[F(1,70) = 2.46, p = .121]$, as well as no significant interaction $[F(4,70) = 0.35, p = \ldots]$
Figure 13. Study 3: Percent generalization for curved reaching across all directions (groups 1 and 2). Percent generalization for straight reaching across all directions in group 3 is plotted for comparison. Vertical bars show ±1 SEM.

A 3x5 ANOVA comparing the results from curved to curved generalization in groups 1 and 2 against the straight to straight generalization in group 3 showed significant main effects for both group [$F_{(2,105)} = 4.25, p = .017$] and direction [$F_{(4,105)} = 2.64, p = .038$], but no significant interaction effect [$F_{(8,105)} = .27, p = .976$].
Figure 15 shows mean hand paths before and after training and during testing for all three groups to all targets. Figure 15A shows mean curved hand paths across all participants in group 1 before training (solid lines), after training (dotted line) and during testing (dashed lines). Figure 15B shows mean straight hand paths across all participants in group 1 before training (solid lines) and during testing (dashed lines). Figures 15C and D show the same for group 2. Figure 15E shows mean straight hand paths across all participants in group 3 before training (solid lines), after training (dotted line) and during testing (dashed lines). Qualitative evaluation of the mean hand paths before training, after training and during transfer showed clear evidence of partial generalization from curved reaching to straight reaching for the training target.

Figure 14. Study 3: Trajectories of initial test trials. Black lines show first test trial for each participant. Blue lines show the mean hand paths of initial test trials of all participants. A. Group 1 B. Group 2
Figures 14A and B show plots of the first straight reach transfer trials to the training target for all participants in groups 1 and 2 (respectively). Unlike Study 2 plots of the first trial for each participant during the transfer phase clearly indicated that participants were not aiming at the visual target, but partially in the direction of the learned rotation.

Discussion

Participants readily adapted to the rotation by altering the initial direction of reach. On transfer, participants exhibited partial generalisation of the adaptation to the rotation from curved to straight line reaching. The generalisation function across directions when changing from a curved reach trajectory to a straight reach trajectory was markedly different than when training and transfer were both conducted using straight reaches. In contrast the generalisation function across directions when training and transfer were both conducted using curved reaches was almost identical to that when training and transfer were conducted using straight reaches. On transfer, participants’ hand movements in groups 1 and 2 were clearly not aimed at the visual target.

The significantly higher level of adaptation achieved in group 2 compared to the other groups stands out as anomalous, with no obvious explanation. The higher level of adaptation is potentially an illusion, due to the fact that the direction of motion near the end of the movement is congruent with the rotational displacement of the hand cursor. This may be causing a slight overestimation of the counter-clockwise rotation of the movement end point in group 2 (and conversely, in group 1 when the direction of motion
Figure 15. Study 3: Mean trajectories. Panels A and C show, for group 1 and 2, respectively, mean curved hand paths before (solid) and after (dotted) training and during transfer (dashed). Panels B and D show, for group 1 and 2, respectively, mean straight hand paths before training (solid) and during transfer (dashed). Panel E shows, for group 3, mean straight hand paths before (solid) and after (dotted) training and during transfer (dashed). Blue circles show the visual targets.
at the end of movement and the cursor rotation are incongruent, a slight underestimation of the clockwise rotation of the movement end point). Regardless of the cause of the higher level of adaptation in group 2, that higher level of adaptation is the cause for the apparent lower level of generalization observed globally for group 2 when compared to group 1 (see Figure 12); since generalization as we have defined it is calculated (see Eq. 3) relative to the level of adaptation (PercAdap) obtained after training. It is clear, however, that the absolute level of movement end point deviation during transfer is similar between groups 1 and 2 (see Figure 15).

In both groups 1 and 2, there is only partial transfer of the learned rotation from curved reaching to straight reaching, especially when looking at generalization to the training target. Unlike study 2, it is clear from these results that the amount of transfer is sufficient to cause participants' hand paths to deviate from the visual target. This indicates that there is a shared component of visuomotor adaptation for different hand paths, but that this component is dependent upon continuous sensory feedback in order to properly adapt.

The significant difference in hand cursor AD across directions when transferring to straight line reaching was expected based on the findings of Krakauer and colleagues (Krakauer et al., 2000). However, the shape of the generalization function observed when transferring from straight line reaching to straight line reaching was somewhat broader and flatter than that found by Krakauer and colleagues. This may be due to slight differences in the experimental paradigm or apparatus and serves to highlight the importance of the straight to straight control condition (group 3).

The significant differences in hand cursor AD between groups and the interaction
between group and direction, when transferring to straight line reaching, suggests that there is also an aspect of learning which is encoded differently depending on the hand path. The interaction is due to the shape of the curved-to-straight generalization curves of groups 1 and 2. In both groups, the peak of the curve appears to be in the direction of the rotation itself (i.e. in group 1 participants adapt to a 20 degree cursor rotation and the most transfer is observed for the target at 22.5°, while in group 2 participants adapt to a -20 degree rotation and the most transfer is observed for the target at -22.5°). The idea that the direction of the visuomotor rotation may affect how an adaptation learned while reaching in an arc transfers to a straight line reach is suggestive of a difference in encoding, but further research along these lines is required.

The lack of interaction between group and direction when comparing hand cursor angular differences (ADc) for curved reaching to curved reaching transfer in groups 1 and 2 against straight to straight transfer in group 3 indicates that adaptation to a visuomotor rotation in a curved reaching task generalizes across directions in a similar manner to straight reaching. A plot of the generalizations functions from curved to curved in groups 1 and 2 and the straight to straight generalization function from group 3 shows that they are indeed very similar (see generalization graph in Figure 13).

While the generalization pattern across directions for curved reaching is similar to that of straight reaching, the generalization pattern across directions when switching from curved to straight hand paths is strikingly different. The similar generalization functions for curved to curved transfer vs. straight to straight transfer would suggest some commonality of the representation of adaptation between different hand paths, however the partial transfer observed for the training target and the different generalization
function when transferring from curved to straight reaches would also suggest that there's an essential component of the representation which is not shared between hand paths. As mentioned earlier however, the differences between this study and studies 1 and 2 suggest that whatever portion of the representation of learning is shared between hand paths is dependent on receiving continuous feedback throughout the movement.

This study only examined transfer of learning from curved to straight hand paths. It could be that the lack of generalization seen is due to something inherent in a curved movement in particular (as opposed to any arbitrary hand path) that makes learning of a visuomotor rotation either more difficult or more specific. This issue is addressed in study 4 by examining the generalization of learning from a straight hand path to a curved hand path.
Chapter 6: Study 4

Introduction

We could not investigate the transfer of learning from straight line reaching to curved reaching using discrete haptic feedback because it was earlier found that participants could not adapt to a visuomotor rotation using straight line reaching when only given discrete haptic end point feedback (Marr, Duncan, Fernandez-Ruiz & Flanagan, 2007). However, participants could adapt to a visuomotor rotation using straight line reaching when given continuous online visual feedback. To determine whether the lack of transfer observed in our previous studies was a result of the particular hand path chosen for training (for the most part curved in preceding studies) in this study we investigated how adaptation to a visuomotor rotation transfers from straight line reaching to curved reaching. A substantial increase in the level of generalization when switching from straight to curved hand paths when compared to switching from curved to straight hand paths could indicate that curved reaches specifically contributed to the lack of transfer previously seen. Additionally we investigated how adaptation to straight line reaches generalizes across both direction and trajectory. Based on the work of Krakauer and colleagues (Krakauer, 2000), there should be full generalization from straight line reaching to straight line reaching with a peaked generalization function centered on the training target.

Methods

Participants

Eight neurologically intact university students volunteered to participate after
giving informed consent.

Procedure

Participants received visual feedback of hand position (the hand cursor) continuously throughout movement. Participants did not receive haptic feedback during this study. During the practice phase participants made 50 straight reaches to five targets located at -45, -22.5, 0, 22.5 and 45°, followed by 50 curved reaches to the same targets. 10 straight reaches and 10 curved reaches were made to each target. Practice targets were randomized by trial. After the practice phase, participants were instructed to make straight reaches to a target located at 0°. Visual feedback of the hand cursor was gradually rotated 20° counter-clockwise about the start position over 80 trials (0.25° per trial). Participants made a further 10 training reaches to the 0 degree target with rotated hand cursor feedback before moving on to the transfer phase. During the transfer phase, participants made a series of “maintenance” reaches, interspersed in a 3:1 ratio with “probe” reaches. For “maintenance” reaches, participants made straight reaches to the training target at 0° and were given continuous visual feedback of the rotated hand cursor throughout movement. “Probe” reaches were made without any visual feedback. Curved probe reaches were made to the five practice targets at -45, -22.5, 0, 22.5 and 45°. Straight probe reaches were made to the targets located at -45, -22.5, 22.5 and 45°. A total of 3 probe reaches of each trajectory type were made to each target, for a total of 27 probe reaches and 81 maintenance reaches.

Analysis

To characterize reaching performance and adaptation we computed several dependent variables related to reach direction. The initial directional error for the cursor
was calculated by taking the angular difference between the vector from the start position to the visual target and the vector from the start position to the cursor position 150 ms after movement onset.

We also determined the angular difference between the visual target and the position of cursor at the movement end point (ADc). This was calculated as the angular difference between the vector from the start position to the target and the vector from the start position to the position of the cursor at the movement end point.

We also expressed the extent of adaptation to the rotation of the visual cursor in each trial as a percentage of the target rotation as follows:

\[
PercAdap = 100 \times \left(1 - \frac{ADc}{CursorRotation}\right)
\]

where PercAdap is the percentage adaptation and CursorRotation is the degree of rotation of the cursor about the start position.

Generalization of rotational adaptation from curved to straight trajectories was calculated as the ratio of the mean PercAdap observed during the 10 transfer trials to the mean PercAdap observed during the last 10 training trials. This ratio was expressed as a percentage and we will refer to this dependent variable as the percent generalization (PercGen).

Results

Figure 16 shows individual trial and mean hand paths of a representative participant (P4). Figures 16A and B show curved and straight hand paths (respectively)
Figure 16. Study 4: Individual and mean hand paths for P4. Individual trials are shown in black, means are superimposed in colour by target (-45 cyan, -22.5 red, 0 blue, 22.5 green, 45 purple). A. Curved reaching trials to all targets during practice. B. Straight reaching trials to all targets during practice. C. Final 10 straight reaches during training. D. Transfer trials, curved reaching. E. Transfer trials, straight reaching.
to the training targets during the initial practice phase with no rotation of the visual
cursor. Figure 16C shows the final 10 trials in the training phase where the visual cursor
was fully rotated by 20° counter clockwise. As illustrated in the figure, the participants
readily adapted to the rotated feedback by changing the initial direction of their reach
trajectories. Figures 16D and E show all trials in the transfer phase for curved and
straight reaches (respectively). As illustrated in the figure, partial transfer of adaptation
was observed from straight line reaching to curved reaching.

The mean adaptation (PercAdap) across participants after the training block was
94.4%.

Figure 17 shows the mean PercGen across participants for this study as well as for
study 3 group 1. PercGen was calculated for each participant and target as the ratio of
mean PercAdap during testing to the mean PercAdap after training. Generalization
shown for this study is from straight reaching to curved reaching and for study 3 group 1
is from curved reaching to straight reaching. Generalization from straight line reaching to
curved reaching for the most important target (the training target) was comparable to the
percent generalization achieved for the same target in study 3 group 1 when transferring
from curved reaching to straight reaching under similar conditions (38.9% vs. 45.3%, see
Figure 17). We compared cursor adaptation across directions between transfer from
straight to curved in the current study and transfer from curved to straight in study 3
group 1 using a two factor ANOVA. It showed a significant main effect for group \( [F_{(1,60)}
= 4.92, p = .030] \) but none for direction \( [F_{(4,60)} = 2.29, p = .070] \) and no significant
interaction \( [F_{(4,60)} = 1.22, p = .313] \).
Figure 17. Study 4: Percent generalization for curved reaching across all directions in study 4 and for straight reaching across all directions in study 3 group 1. Vertical bars show ±1 SEM.

Figure 18 shows generalization (PercGen) from straight line to straight line reaching for both this study and study 3 group 3. Since we trained subjects on the center target, it was not probed during the transfer phase. The PercGen value plotted in the graph for the central target in this study is based on a single catch trial (a trial equivalent to a probe trial with no visual feedback given) at the end of training and is plotted for clarity and completeness. As expected, participants showed a high degree of generalization, with a peaked generalization function centered on the training direction. The observed pattern of generalization from straight line to straight line reaching was
again very similar to that observed by Krakauer and colleagues (Krakauer et al., 2000). A two factor ANOVA showed significant main effects for group \([F_{(1,60)} = 7.21, p = .009]\) and direction \([F_{(4,60)} = 5.56, p = .000]\), but no significant interaction \([F_{(4,60)} = 1.61, p = .182]\), when comparing straight line to straight line generalization across directions between this study and study 3 group 3. However, since the straight line generalization to the training target for the current study was based on a single catch trial at maximum adaptation for each participant, it may not be very reliable. An identical ANOVA omitting the training target showed no significant main effect of group \([F_{(1,48)} = 3.48, p = .068]\), a significant main effect of direction \([F_{(3,48)} = 3.60, p = .020]\) and no significant

Figure 19 shows mean hand paths before and after training and during testing for all participants and all targets. Figure 19A shows mean hand paths for straight line reaching before (solid) and after (dotted) training and during transfer (dashed). Figure 19B shows mean hand paths for curved reaching before training (solid) and during transfer (dashed). Qualitative evaluation of the mean hand paths before and after training showed the expected pattern for straight line to straight line reaching. For straight line to curved reaching, the transfer trials showed a marked change in the shape of the trajectories themselves, but a contrarily small change in the movement end point.

**Discussion**

Participants readily adapted to the rotation by altering the initial direction of reach. On transfer, participants exhibited partial generalization of the adaptation to the
rotation from straight to curved reaching. The generalization function across directions when switching from a straight hand path to a curved hand path was very similar to the generalization function observed when switching from a curved hand path to a straight one.

In regards to the general question of whether learned visuomotor rotations are differentially adapted depending on the hand path, a further clue that they are is the shape of the curved hand paths during transfer in this study. A comparison of the change in curved hand paths from practice to transfer between the current study (see Figure 19) and study 3 group 1 (see Figure 15A), shows that the change in curved hand paths after training is qualitatively different. In study 3 group 1, the hand paths appear to essentially rotate with the perturbation; however, in the current study the curved hand paths after training appear to “bow out” more, while the movement end points change very little. Since the only difference between the two studies was the hand path used for training, these differences must be attributed to some difference related to the hand path in the learned adaptation.

The main question of this study is addressed by comparing its results to those in study 3 group 1. As in study 3 group 1, only partial transfer to the most important target (the training target) is observed when switching to a hand path different from that used during training. Since the level of generalization to the training target observed in this study is very comparable to that observed in study 3 group 1 (curved to straight transfer), it indicates that the lack of transfer between curved and straight reaching is not due to some factor specifically inherent to a curved trajectory, but related more generally to the differences between curved and straight hand paths (and likely the more general case of
differences between any two arbitrary hand paths). Additionally, the overall level of
generalization is higher for curved-to-straight than for straight-to-curved, indicating that
the lack of transfer observed from curved reaching to straight reaching cannot be due to
using curved reaches in during adaptation. There may still be some learning effects that
are idiosyncratic to specific hand paths used (which could account in some part for the
different generalization functions across directions observed for straight to curved and
curved to straight transfer) but the general effect of an overall reduction in generalization
across the board appears to be due to a change in hand paths, and not the specific hand
paths themselves.
Chapter 7: Study 5

Introduction

In the two studies described in chapters 3 and 4, we found that adaptation to a visuomotor rotation using curved reaching and discrete feedback did not generalize to straight line reaching, suggesting that motor learning for curved reaches is represented in a different manner than for straight line reaching. As many previous studies have shown, insight into the representation of learning can be gained by investigating how an adaptation to a visuomotor rotation generalizes across different directions. In this study we replicated the learning conditions of studies 1 and 2 (adapting curved reaches in a single direction with only discrete end point feedback) and examined the transfer of learning to different directions, while maintaining the same curved hand path. By examining the generalization of adaptation to a visuomotor rotation using curved reaching with discrete end point feedback across different directions, we can assess the effect of the continuity of feedback on generalization. If discrete feedback alone was enough to cause partial or no transfer, then we should see less transfer (or a different pattern of generalization across directions) in this study than in study 3 group 1 when testing transfer from curved reaching to curved reaching with continuous visual feedback. On the other hand, if discrete feedback does not impair adaptation, then we should see the same level and pattern of generalization as in study 3 group 1.

Methods

Participants

Eight neurologically intact university students volunteered to participate after
giving informed consent. All participants had normal or corrected to normal vision.

Procedure

Participants did not receive any visual feedback of hand position during movement, but did receive visual feedback of the hand cursor when it intersected the target. Participants did not receive haptic feedback during this study. During the practice phase participants made 50 curved reaches to five targets located at -45°, -22.5°, 0°, 22.5° and 45°. Ten curved reaches were made to each target. Practice targets were randomized by trial. After the practice phase, participants were instructed to make curved reaches to a target located at 0°. Visual feedback of the hand cursor was gradually rotated 20° counter-clockwise about the start position over 80 trials (0.25° per trial). Participants made a further 10 training reaches to the 0 degree target with rotated hand cursor feedback before moving on to the transfer phase. During the transfer phase, participants made a series of “maintenance” reaches, interspersed in a 3:1 ratio with “probe” reaches. For “maintenance” reaches, participants made curved reaches to the training target at 0° and were given visual feedback of the rotated hand cursor when it intersected the target. “Probe” reaches were made without any visual feedback and were made to the five practice targets at -45, -22.5, 0, 22.5 and 45°. A total of 5 probe reaches were made to each target, for a total of 25 probe reaches and 75 maintenance reaches.

Analysis

To characterize reaching performance and adaptation we computed several dependent variables related to reach direction. The initial directional error for the cursor (IDEc) was calculated by taking the angular difference between the vector from the start position to the visual target and the vector from the start position to the cursor position
150 ms after movement onset.

We also determined the angular difference between the visual target and the position of cursor at the movement end point (ADc). This was calculated as the angular difference between the vector from the start position to the target and the vector from the start position to the position of the cursor at the movement end point.

We also expressed the extent of adaptation to the rotation of the visual cursor in each trial as a percentage of the target rotation as follows:

\[
PercAdap = 100 \times \left( 1 - \frac{ADc}{CursorRotation} \right)\]

Eq. 2

where PercAdap is the percentage adaptation and CursorRotation is the degree of rotation of the cursor about the start position.

Generalization of rotational adaptation from curved to straight trajectories was calculated for each probe direction as the ratio of the mean PercAdap observed during the probe trials to the mean PercAdap observed during the last 10 training trials. This ratio was expressed as a percentage and we will refer to this dependent variable as the percent generalization (PercGen).

Results

Figure 20 shows individual trial and mean hand paths for a representative participant (P5). Figure 20A shows curved hand paths to all targets during the initial practice phase in which there was no visuomotor rotation. Figure 20B shows the final 10
Figure 20. Study 5: Individual and mean hand paths for P5. Individual trials are shown in black, means are superimposed in colour by target (−45° cyan, −22.5° red, 0° blue, 22.5° green, 45° purple). A. Curved reaching trials to all targets during practice. B. Final 10 curved reaches during training. C. Transfer trials, curved reaching.

As illustrated in the figure, the participants readily adapted to the rotated feedback by changing the initial direction of their curved reach trajectories. Figure 20C shows all probe trials to all targets during the transfer phase. Participants showed a high degree of mean cursor adaptation over the last 10 training trials (92.9%).

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Figure 21 shows the mean PercGen across participants for all 5 testing targets during the transfer phase. The observed generalization function across directions was very similar to that observed for the generalization of curved to curved reaching in study 3 group 1. A two factor ANOVA showed no significant main effects for group \( F(1,65) = 0.11, p = .740 \) or direction \( F(4,65) = 1.65, p = .172 \), as well as no interaction \( F(4,65) = .35, p = .840 \) when comparing the generalization from curved reaching to curved reaching across all directions between this study and study 3 group 1.

Figure 22 shows mean hand paths before (solid) and after (dotted) training and during transfer (dashed) for all participants and all targets. Qualitative evaluation of the mean hand paths before and after training showed a generalization pattern for curved to curved reaching very similar to the pattern obtained for study 3 group 1 (see Figure 15A).
Figure 22. Study 5: Mean trajectories. Mean hand paths for curved reaching before training (solid) after training (dotted) and during transfer (dashed).

Discussion

The lack of difference between the results of this study and the results of study 3 group 1 when testing transfer from curved reaching to curved reaching suggests that the absence of continuous online visual feedback has no significant effect on the ability to learn a visuomotor rotation or the generalization of that adaptation to novel directions. Despite only receiving end point feedback in this study, there is no discernible difference between participants’ behaviours in this study and study 3 group 1. This implies that the lack of transfer in studies 1 and 2 is not due simply to the paucity of feedback, but to an interaction of feedback and hand path used during training. Moreover it implies that there are multiple, redundant methods of adapting to a visuomotor rotation and that
continuous visual feedback is necessary for generalization across hand paths, but not for generalization across direction.
Chapter 8: Study 6

Introduction

Two recent studies (Scheidt & Ghez, 2007; Ghez, Scheidt & Heijink, 2007) have suggested that the brain plans reaching movements in terms of both the spatial trajectory of the hand and the final position of the hand. The idea that the brain may specify the final position of the hand (or arm as a whole) can be related to the equilibrium point hypothesis of motor control developed by Feldman and colleagues (Feldman 1986; Feldman et al. 1990; Flanagan et al., 1993). According to this hypothesis, the brain specifies an equilibrium position via central motor commands that, in combination with reflex-mediated changes in muscle activity, drive the limb toward the equilibrium position. The studies by Ghez and colleagues found minimal transfer of adaptation to a visuomotor rotation between an out-and-back reaching task (referred to as “slicing”) and a reach and hold task, where the participant reached to a target and held their hand in a constant position for a brief period at the target (referred to as simply “reaching”). Online visual feedback was given during the slicing task, but not during the reaching task. For the reaching task, visual feedback was only given once the movement was complete. Importantly, both tasks involved straight line reaching.

Ghez and colleagues (Scheidt & Ghez, 2007; Ghez, Scheidt & Heijink, 2007) suggested that learning the spatial trajectory component of adaptation requires online visual feedback during movement, whereas learning the end point position component requires static positioning of the hand at the location to be learned. These authors suggested that the lack of interference between their slicing and reaching tasks is due to the fact that these tasks selectively involve adaptation of the spatial trajectory and end
point positioning components, respectively.

In studies 1 and 2 of this thesis, in which we found effectively no transfer between curved and straight line reaches, visual feedback was not provided during movement and there was no period of static positioning at the target. That is, participants made out-and-back movements to the target and received visual feedback related to hand position only in the vicinity of the target. Thus, from the viewpoint espoused by Scheidt and Ghez, it is not clear how participants in studies 1 and 2 adapted to the rotated visual feedback.

The aim of the current study was to investigate whether static positioning of the hand at the target would lead to transfer between curved and straight line reaches. If, as proposed by Scheidt and Ghez, static positioning at the target lead to adaptation of the final position of the hand, then the trajectory of the hand should not matter and full transfer should be observed between curved and straight line reaches. To test this prediction, in the current study we repeated study 2 with a reach-and-hold task in which we instructed participants to hold their hand at the end point for a brief period after the initial movement. Visual feedback about the position of the hand was only provided at the end point. This should allow for training of the positional component of adaptation proposed by Scheidt & Ghez and Ghez and colleagues (Scheidt & Ghez, 2007; Ghez, Scheidt & Heijink, 2007).

Methods

Participants

Eight neurologically intact university students volunteered to participate after giving informed consent. All participants had normal or corrected to normal vision. The
Experimental protocol was approved by the Queen’s University Ethics Board.

Procedure

Participants did not receive any visual feedback of hand position during movement, but did receive visual feedback of the hand cursor when it intersected the target. Participants did not receive haptic feedback during this study. For all reaches, participants were required to reach out to the target and hold the hand cursor at the target for 2 seconds before returning to the start position. During the practice phase participants made 26 curved reaches to targets located at -20, 0 and 20º, followed by 26 straight reaches to the same targets. 8 reaches were made to each of the offset targets and 10 reaches were made to the target located directly ahead (0º). Practice targets were randomized by trial. After the practice phase, participants were instructed to make curved reaches to a target located at 0º. Over 80 trials, the hand cursor visual feedback was rotated 20º counter-clockwise (0.25º per trial), such that, at the end of the first 80 training trials, visual feedback of the hand cursor was rotated 20º counter clockwise (about the start position) from the actual position of the hand. Participants made a further 10 curved reaches to the 0 degree target with rotated hand cursor feedback before moving on to the transfer phase. In the transfer phase participants made 10 straight reaches to a target located at 0º. No feedback of any kind was given during transfer reaches.

Analysis

To characterize reaching performance and adaptation we computed several dependent variables related to reach direction. The initial directional error for the cursor (IDEc) was calculated by taking the angular difference between the vector from the start position to the visual target and the vector from the start position to the cursor position.
150 ms after movement onset.

We also determined the angular difference between the visual target and the position of cursor at the movement end point (ADc). This was calculated as the angular difference between the vector from the start position to the target and the vector from the start position to the position of the cursor at the movement end point.

We also expressed the extent of adaptation to the rotation of the visual cursor in each trial as a percentage of the target rotation as follows:

\[
PercAdap = 100 \times \left( 1 - \frac{ADc}{CursorRotation} \right)\]

Eq. 2

where PercAdap is the percentage adaptation and CursorRotation is the degree of rotation of the cursor about the start position.

Generalization of rotational adaptation from curved to straight trajectories was calculated for each probe direction as the ratio of the mean PercAdap observed during the probe trials to the mean PercAdap observed during the last 10 training trials. This ratio was expressed as a percentage and we will refer to this dependent variable as the percent generalization (PercGen).

Results

Figure 23 shows individual trial and mean hand paths for a representative participant (P3). Figures 23A and B show curved and straight hand paths (respectively) during the initial practice phase in which there was no visuomotor rotation. Figure 23C
Figure 23. Study 6: Individual and mean hand paths for P3. Individual trials are shown in black, means are superimposed in blue. A. Curved reaching trials during practice. B. Straight reaching trials during practice. C. Final 10 curved reaches during training. D. Transfer trials.

shows the final 10 trials in the training phase where the cursor was fully rotated counterclockwise by 20°. Figure 23D shows all trials from the transfer phase. Participants showed a high degree of mean cursor adaptation (PercAdap) over the last 10 training trials (93.4%), but minimal generalization (PercGen) from curved reaching to straight reaching (19.2%). A single factor repeated measures ANOVA \[ F_{(1,7)} = 0.18, \ p = .6867 \] comparing mean angular difference of the cursor (ADc) before and after training for all
Figure 24. Study 6: Trajectories of initial test trials. Black lines show first test trial for each participant. Blue line shows the mean hand path of initial test trials of all participants.

participants showed no significant effect of curved reach adaptation on straight reaching. As with study 2, plots of participants’ first transfer trials demonstrated that they were still primarily reaching towards the visual target during transfer (see Figure 24). Additionally a qualitative evaluation of mean hand paths shows that participants only slightly altered their straight line hand paths in response to the perturbation such that their aim did not deviate much from the visual target when transferring to straight line reaching (see Figure 25). A single factor ANOVA $[F_{(1,14)} = .87, p = .368]$ comparing the mean angular
differences of the hand (ADh) during transfer between this study and study 2 showed no significant differences between the two studies.

Discussion

While this study shows less generalization than study 2 (19.2% vs. 27.4%), it also shows much higher adaptation, which could account for a large portion of the difference in generalization between the two studies. Despite the addition of a brief “hold” period to the basic task, the results for this experiment are largely identical to those for study 2. This is supported by the fact that there are no statistically significant differences between the hand ADs during transfer between this study and study 2.

According to the ideas put forth in Scheidt and Ghez and their colleagues (Scheidt & Ghez, 2007; Ghez, Scheidt & Heijink, 2007), adapting to a visuomotor rotation depends on two adaptive mechanisms, a trajectory component (viewed as the traditional vectorial representation of reaching: distance and direction) and an end-point position component. In our previous studies, the task always involved “out and back” reaching movements, and in several studies (1, 2, & 5) did not involve continuous online feedback during movement. In the view put forth by Scheidt & Ghez and Ghez and colleagues (Scheidt & Ghez, 2007; Ghez, Scheidt & Heijink, 2007), the trajectory component requires continuous online visual feedback and the end point position component requires static positional feedback at the movement end point. Neither requirement was met in studies 1, 2 & 5, in which case the hypothesis proposed by Scheidt and Ghez and colleagues (Scheidt & Ghez, 2007; Ghez, Scheidt & Heijink, 2007) predicts minimal to no transfer. This is precisely what is observed in both studies 1 and 2 (but not in study 5
Figure 25. Study 6: Mean trajectories. A. Mean hand paths for curved reaching before training (solid) and after training (dashed). B. Mean hand paths for straight reaching before training (solid) and during transfer (dashed).

However). This hypothesis also predicts that using continuous online visual feedback would lead to at least partial transfer through adaptation of the trajectory component, which is what is observed in studies 3 and 4.

If the lack of transfer observed in studies 1 and 2 was due to the lack of end point positional training, and not to differential representations of adaptation based on hand path, then the addition of end point positional training in this study should increase generalization. However, this is not what is observed. Including static end point positional feedback in the reach and hold task does not result in greater generalization. The results of the current study are essentially indistinguishable from those of study 2, indicating that the lack of transfer observed in studies 1 and 2 is not due to a failure to provide static end point positional feedback.
Chapter 9: General Discussion

The broad aim of our research was to elucidate the representations and computational processes involved in planning reaching movements of the arm. The current body of knowledge suggests that reach planning is broadly represented in terms of the direction and distance from the hand to the target. In terms of the process of reach planning, the predominant view is that the positions of the target and hand are transformed into a common visual reference frame in order to calculate this desired movement vector. The movement vector is then transformed into the appropriate muscular control signals to cause the hand to move to the target.

The basic approach we took in our research was to use the visuomotor perturbation paradigm to investigate how adaptation to a perturbation while using one type of reach trajectory generalises to different reach trajectories. Specifically we focused on how adaptation to a visuomotor rotation while reaching with a curved trajectory generalises to a straight trajectory. We had participants adapt to a visuomotor rotation while reaching in a curved path, after they successfully adapted to the rotation we tested whether this adaptation transferred to straight line reaching and novel directions. By examining the patterns of generalisation of learning from curved reaching to straight reaching under various conditions we were able to make some inferences about the nature of the underlying representation and processing of reach planning.

Previous work on adaptation and transfer using the visuomotor perturbation paradigm has investigated how adaptation transfers across speed (Kitazawa, Kimura & Uka, 1997), throwing style (Martin et al., 1996), arm load (Fernandez-Ruiz et al., 2000), target direction (Krakauer et al., 2000) and initial/ final arm configuration (Baraduc &
However these studies invariably used straight movements, and as such did not and could not provide a challenge of vectorial view of reach planning. A recent alternative to the purely vectorial representation of reach planning comes from Scheidt and Ghez (Scheidt & Ghez, 2007; Ghez, Scheidt & Heijink, 2007) who propose that reaching planning involves two processes, similar to Woodworth’s ideas of a launch and homing phases of reaching (Woodworth, 1899), one corresponding to the typical vectorial view and a second, overlapping process that specifies the movement end point in terms of intrinsic joint positions and muscle equilibriums. The studies by Scheidt and Ghez, while challenging the notion that reach planning is represented solely in terms of the difference vector between hand and target, nevertheless again used only straight movements and thus did not provide a challenge to the adequacy of a vectorial representation for planning of arbitrary reach paths.

Since previous studies on adaptation and transfer of reaching all relied on straight line reaches, we chose to use curved reaches in order to examine the adequacy of the vectorial view for reach plan representation when the reach path was not trivially consistent with the difference vector from hand to target. If curved and straight reach planning were represented in the same way (i.e. vectorially), then adaptation to a visuomotor rotation would transfer at least partially under all conditions from one hand path to the other. Additionally, the pattern of generalisation across novel directions when switching between different hand paths would be similar in shape. We did not find either.

The first steps we took (study 1) suggest that learning a visuomotor rotation is dependent on the path of the hand through space during training. In study 1, participants reached to a visual target, but did not receive visual feedback of handle position during
movement; they received haptic feedback forces when the handle contacted the (rotated) haptic target (the visual target never changed). The dependency of learning on hand path is shown by the fact that although participants successfully adapt to a visuomotor rotation of haptic end point feedback while reaching in a curved path, this adaptation does not generalise at all to straight line reaching. Study 1 also demonstrates that this is not due to the learned representation being stored relative to directions other than the vector from hand to target (such as the initial direction of the curved movement, or the direction of the rotation). This is evidenced by the fact that learning does not transfer to straight reaches for either of the control directions tested.

Study 2 was essentially the same as study 1 (minus the control conditions) except that participants were given visual instead of haptic feedback at the target (but again, no visual feedback during movement). Study 2 shows that there is some small effect of modality (i.e. there is slightly more transfer when using visual as opposed to haptic feedback of the hand position), but that the general lack of transfer from curved to straight hand paths observed is due to the change in hand path itself. This is supported by the fact that although there is slight transfer of learning from curved reaching to straight reaching, the transfer is insufficient to cause their hand cursor to miss the visual target when reaching straight.

In study 3, participants received online visual feedback of hand cursor position during movement, but did not receive any haptic feedback. Participants adapted to a visuomotor rotation while making either curved (groups 1 and 2) or straight (group 3) reaches. After adaptation participants were tested using both curved and straight reaches to targets spaced around the training direction. Study 3 shows that the generalization
function across directions from curved reaching to straight reaching is fundamentally different than that of curved to curved or straight to straight reaching transfer. When transferring from curved reaching to straight line reaching, the greatest amount of transfer is seen for the target direction that is opposite to the direction of rotation itself. That is, for a counter clockwise rotation, the peak of the generalisation function is at the first clockwise target, and vice versa for a clockwise rotation. When the hand paths for training and testing are congruent, the peak of the generalisation function is at the training target (as expected). Additionally, study 3 demonstrates that some portion of the representation of visuomotor learning is shared between curved and straight hand paths, but is dependent on continuous visual feedback. This is shown by the fact that there is substantial partial transfer from curved reaching to straight reaching. As this was not seen in study 2 (discrete visual feedback) the difference in the amount of transfer seen in study 3 is due to the addition of online feedback, which means that a substantial amount of shared representation between curved an straight reaches is only present when participants are given online visual feedback.

Participants in study 4 performed the same task as in study 3, but used straight reaches during the training phase and curved reaches during the transfer phase. Thus study 4 reverses the direction of transfer and examines the transfer from straight reaching to curved reaching with continuous visual feedback. Study 4 provides evidence that the observed lack of transfer is not specific to a curved hand path itself, but is a more general effect of switching from one arbitrary hand path to another. This is supported by the fact that participants show partial transfer from straight line reaching to curved reaching, and the observed pattern of generalisation across directions is similar to that observed when
transferring from curved to straight reaching, and unlike that which is observed when training and testing reaches are congruent. Thus the lack of transfer observed when transferring from curved reaching to straight reaching cannot be due to any factors specific to a curved hand path itself, as the same effect is seen when transferring from straight line reaching to curved reaching. The effect is therefore more likely to be due to a change in hand path rather than the specific hand paths chosen for training or testing.

In study 5 participants performed curved reaches for both training and testing phases, with visual feedback of cursor position only provided at the target. We tested the participants on targets located in directions spaced around the training direction. The level of adaptation achieved and the pattern of generalisation across directions are the same as those for the curved to curved transfer observed in study 3 group 1, which used an identical task but provided continuous visual feedback of cursor position. Study 5 demonstrates that the failure of transfer from curved to straight reaching with discrete feedback is not due to a poverty of adaptation caused by the limited feedback given. Thus the lack of transfer observed when only discrete feedback is given cannot be due to the discrete nature of the feedback, or we would see less overall generalisation or a different pattern of generalisation in study 5 when compared to the curved to curved transfer in study 3 group 1.

Lastly, study 6 shows that lack of transfer observed from curved to straight hand paths when given only discrete endpoint feedback, is not due to a failure to provide static feedback at the movement end point. Study 6 is identical to study 2, except that participants were required to hold their hand at the target for a brief period before returning to the start position. Visual feedback of the cursor was only given when the
rotated cursor was at the target. Participants trained by reaching in a curve to the target, holding the cursor at the target briefly and then returning to the start position. In the testing phase, they reached out to the visual target (with no visual feedback of cursor position) using a straight reaching motion and held their hand still briefly before returning to the start position. If the lack of transfer observed so far was due to the failure to train the second, equilibrium point reach planning process (by not providing static endpoint feedback) proposed by Ghez and colleagues (Scheidt & Ghez, 2007; Ghez, Scheidt & Heijink, 2007) then we should have observed greater transfer in this study. We did not. The results of study 6 are largely similar to study 2, with little to no transfer occurring between curved and straight reaching movements.

The overall picture that emerges from these studies is that a large portion of the representation of a visuomotor perturbation appears to be specific to the hand path used during training, while an additional shared component is independent of the hand path used but dependent on continuous visual feedback. The accepted, vectorial representation of movement plans for reaching, (where reaches are viewed as being represented by a direction and distance from hand to target), does not appear sufficient to adequately explain the results observed with curved reaches. The potential alternative view of reach planning offered by Ghez and colleagues (Scheidt & Ghez, 2007; Ghez, Scheidt & Heijink, 2007) is promising in that it acknowledges the need for an additional component of reach planning and the insufficiency of the vectorial view. However, as the results of study 6 indicate, it remains inadequate to explain our results. While the additional component of their model specifying the final hand position in terms of muscle equilibrium would indeed not require continuous visual feedback, the final hand positions
of two different hand paths to the same target would share the same final hand position. Thus, according to their view, we should not see the hand path dissociation that is observed.

While many other studies assume the vectorial representation of reach planning, they have not been able to address the adequacy of such a representation for various reasons. In the study by Martin and colleagues (Martin et al., 1996) participants learned to throw using different styles (underarm or overarm) while wearing prisms that effectively rotated their visual feedback. On a superficial level, the trajectories produced by the thrown object can be viewed as a vector in a visual space, however when speaking of movement planning the true vectors concerned are the movement vectors of the hand. Since the underarm and overarm movements themselves are quite different, it is clear that the spatial displacement of the hand is different in both cases. Additionally, since the initial and final arm configurations are different the motor vectors themselves are also different. While it may superficially seem that the results of Martin and colleagues can be explained using the vectorial representation of movement planning, their study cannot be taken as an endorsement of it. Baraduc and Wolpert (Baraduc & Wolpert, 2002) get a little bit closer, in that they maintain the initial and final positions of the hand, thus the difference vector in visual space remains the same between conditions. However, they varied the initial configuration of the arm itself, thus changing the difference vector in motor coordinates between conditions. The vectorial view accounts for learning of a visuomotor rotation as an alteration in the mapping between visual and motor vectors, however this re-mapping cannot be accurately probed if one or the other of the vectors is different during testing. In the study by Krakauer and colleagues (Krakauer et al., 2000),
both the visual and motor difference vectors were maintained across conditions, however, they only tested straight line reaches, which can be trivially equated to alterations in visual/motor vector mappings. This equivalence is not readily obvious for curved reaches.

In our studies, we varied only the trajectory of the hand through space, but kept the initial and final configurations of the hand and arm the same. Thus both the visual difference vector between hand and target and the motor difference vector between arm positions and configurations were kept relatively constant. Additionally, we examined curved reaches, where the movement to be executed in visual space does not map directly onto the visual difference vector between the hand and target. This allowed us to assess the adequacy of the vectorial representation of reach planning to account for arbitrary reach trajectories.

Of course a number of previous studies have shown that adaptation seems to be quite specific to the motor commands involved, which suggests that movement planning and adaptation are represented in terms of motor commands. Studies examining adaptation to visuomotor perturbations where movement speed (Kitazawa, Kimura & Uka, 1997) or load (Fernandez-Ruiz et al., 2000) were varied suggest that some component of learning the visuomotor perturbation is specific to the motor commands and muscle activations involved. Similarly, the more general motor adaptation study by Mah and Mussa-Ivaldi (Mah & Mussa-Ivaldi, 2003) demonstrates that motor learning appears to be specific to the joint torques involved rather than end effector forces produced. If motor adaptation were a matter of re-mapping movement vectors in different coordinate frames (according to the vectorial representation view) then it should be more
highly correlated with end effector forces than joint torques. If the adaptation to a visuomotor rotation was accounted for simply by an alteration of vector mappings, then there should also be partial transfer from curved to straight reaching under all conditions. This is not observed. However, there does appear to be some shared representation of learning between different hand paths, but that shared representation depends upon continuous online feedback during movement. This raises several questions. What parts or components of the sensorimotor transformation are being differentially adapted based on hand path? What parts are shared and how or why do they depend on continuous feedback?

The broad process of sensorimotor transformation involved in reach planning described in the introduction consists of three main phases. First, hand and target positions are both transformed into a common reference frame. Second, the difference vector between hand and target in the common reference frame is calculated to guide reaching. Lastly, this vector is transformed into motor commands to execute the movement. If we assume that this process of sensorimotor transformation is essentially correct, we can examine what components of that framework are responsible for producing the differential adaptation we observe. The shared representation portion of visuomotor learning is dependent on continuous visual feedback, so should fit into the framework where vision is required or predominant. The most likely candidates are the early stages of the transformation, when target and hand location are transformed into a common reference frame and when visual motion vectors are transformed to shoulder centered coordinates. Adaptation could be occurring in the mapping of retinotopic to visual coordinates, essentially what has been described as “visual shift”, however
previous work has found that the contribution of visual shift to learning a visuomotor transformation is quite small (Welch, 1974). It is unlikely to account for the generalization we see. Adaptation could also be occurring in the mapping of proprioceptive hand coordinates to visual coordinates, essentially what has been called “proprioceptive shift”, however, previous research has demonstrated that proprioceptive shift only accounts for learning in slow movements that can be controlled proprioceptively, and not for fast movements of the type used in our studies (Baily, 1972; Welch, 1974). It is therefore also unlikely that proprioceptive shift is the seat of the shared representation we observe. Of the components with visual inputs, this leaves the transformation of vectors from the common reference frame to shoulder centered coordinates. This is very closely related to the re-mapping of bi-directional movement axes between visual and motor space proposed by Cunningham (Cunningham, 1989); the vectors in shoulder centered space can be easily interpreted as the motor axes proposed by Cunningham. A good candidate for the shared representation of learning between two different hand paths then, is the mapping between visual motion vectors and shoulder centered motion vectors. Given continuous visual feedback, it should be possible to alter the direction of the planned movement vectors themselves so as to compensate for the visuomotor rotation.

For the representation of learning that is specific to hand path, and does not rely on continuous visual feedback, good candidates can be found in the later stages of visuomotor transformation. Both the transformation of vectors centered on the shoulder to joint coordinates and the transformation of joint coordinates to muscle commands are good candidates here. Any change in the mappings at either stage would be necessarily
specific to the hand path used, as different hand paths will have, by definition, different sequences of joint angles and muscle activations. This is essentially what Welch (Welch 1974) would call an “assimilated corrective response”. In this view the hand path specific adaptation corresponds to the adaptation or modulation of joint angle trajectories associated with motion vectors centered on the shoulder or muscle commands associated with those joint angle trajectories.

The identification of these components of the visuomotor transformation process as being responsible for the observed differences in representation can explain much of the experimental data. In studies 1 and 2, adaptation of joint or muscle coordinates necessary to produce the desired movement could allow for learning of the rotation, but this learning would be specific to the hand path used for training. When only discrete feedback at the movement endpoint is provided, visual feedback of the actual movement vector produced is absent, thus it seems unlikely that re-alignment of vectors between the common reference frame used for planning and the shoulder centered insertion point of the arm could occur. Transfer between two different hand paths would only be expected to the extent that they shared sequences of joint angles and/or muscle activations. Since a straight reach and a curved reach have very little in common with respect to joint and muscle spaces, very little to no generalization of learning would be expected. In studies 3 and 4, the presence of online visual feedback would allow for the alteration of vector direction during movement planning and generalization would be expected to the extent that different hand paths share similar visual motion vectors, since we know from Krakauer and colleagues (Krakauer et al. 2000) that learning to adapt a motion vector in visual space generalizes to other nearby directions. Consequently, more generalization
would be expected with online visual feedback since the basic vectorial movement plan should be the same regardless of hand path. The different generalization functions across directions observed when switching between hand paths could be due to the portion of learning still accounted for by the late stage, hand path specific adaptations.

Limitations

It is important to note that, while we have found some significant differences in learning and adaptation for different hand paths, we examined arm reaching movements under specific constrained conditions. As such our findings may only be applicable to other similar contexts and may not apply to motor learning as a general phenomenon. For instance it is difficult to see how our findings could be applied to other popular motor learning tasks such as saccade and visual pursuit adaptation. For experimental simplicity, movements in our task were constrained to simplified reaching movements in a horizontal plane where initial and final arm positions were maintained. This experimentally expedient restriction however, may limit the applicability of our findings to more natural, unrestricted movements where the entire workspace can be explored.

Additionally, we did not explicitly control for hand path curvature, nor did we perform a quantitative analysis of hand path curvature on the experimental data. Without deliberately controlling or analysing hand path curvature over the experimental course, our results can say nothing about the effect of the degree of curvature on learning and adaptation.

Future Directions

While this series of studies has clearly demonstrated some compelling differences in how learned visuomotor perturbations are represented for different hand paths, they
have raised many more questions. The results obtained suggest how the representations may differ, but do not provide enough evidence for firm conclusions about the exact mechanisms at work. Much further research is necessary to confirm or deny the speculative hypotheses generated here to explain the observed differences.

Several possible avenues of future research present themselves. Much benefit could be gained from building a formal computational model of the associative processes discussed in the context of visuomotor processing and adaptation. Building a model would allow predictions and consequences of the ideas presented to be generated and explored. Additional empirical research with a finer focus could answer more specific questions about the representation of motor learning. For instance, if learning visuomotor rotations with only discrete feedback relies on later stages of the visuomotor transformation as it gets closer to motor output, then such learning should be more specific to kinematic parameters such as elbow and shoulder orientation. This could be explored by studying how learning a visuomotor perturbation with discrete feedback generalizes to other parts of the work space (e.g. different start positions, different arm orientations, etc...). Also, such specificity at the later stages of transformation should allow for at least some learning of opposite rotations simultaneously. Another avenue of exploration is in the mechanism of generalization at such late stage learning, which should not be as dependent on visual vectors as it is when continuous visual feedback is given, but should be much more dependent on similarities in intrinsic spaces such as joint or muscle spaces. This could be explored by testing generalization between hand paths that have controlled differences between trajectories in such intrinsic coordinates. Lastly a fruitful avenue of research would be to control and examine the effects of degree of
hand path curvature on learning and adaptation.

This series of studies has identified some important distinctions in motor learning and has laid the ground work for future research to identify and explore the mechanisms and causes of these differences. Much research into the implications of these studies remains to be conducted.
References


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