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A Kinematic Analysis of Visual and Haptic Contributions to Precision Grasping in a Patient With Visual Form Agnosia and in Normally-Sighted Populations

Robert Whitwell
The University of Western Ontario

Supervisor
Dr. Melvyn Goodale
The University of Western Ontario

Graduate Program in Neuroscience
A thesis submitted in partial fulfillment of the requirements for the degree in Doctor of Philosophy

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KINEMATIC ANALYSIS OF VISUAL AND HAPTIC CONTRIBUTIONS TO PRECISION GRASPING IN A PATIENT WITH VISUAL FORM AGNOSIA AND IN NORMALLY-SIGHTED POPULATIONS

(Thesis format: Integrated-Article)

by

Robert Leslie Whitwell

Graduate Program in Neuroscience

A thesis submitted in partial fulfillment
of the requirements for the degree of
Doctorate in Philosophy

The School of Graduate and Postdoctoral Studies
The University of Western Ontario
London, Ontario, Canada

Abstract

Skilled arm and hand movements designed to obtain and manipulate objects (prehension) is one of the defining features of primates. According to the two visual system hypothesis (TVSH) vision can be parsed into two systems: (1) the ventral ‘stream’ of the occipital and inferotemporal cortex which services visual perception and other cognitive functions and (2) the ‘dorsal stream’ of the occipital and posterior parietal cortex which services skilled, goal-directed actions such as prehension. A cornerstone of the TVSH is the ‘perception-action’ dissociation observed in patient DF who suffers from visual form agnosia following bilateral damage to her ventral stream. DF cannot discriminate amongst objects on the basis of their visual form. Remarkably, however, her hand pre-shapes in-flight to suit the sizes of the goal objects she fails to discriminate amongst when she reaches out to pick them up; That is, unless she is denied the opportunity to touch the object at the end of her reach. This latter finding has led some to question the TVSH, advancing an alternative account that is centered on visuo-haptic calibration. The current work examines this alternative view. First, the validity of the measurements that have underlined this line of investigation is tested, rejecting some measures while affirming others. Next, the visuo-haptic calibration account is tested and ultimately rejected on the basis of four key pieces of evidence: Haptics and vision need not correlate to show DF’s ‘perception-action’ dissociation; Haptic input does not potentiate DF’s deficit in visual form perception; DF’s grasp kinematics are normal as long as she is provided a target proxy; and denying tactile feedback reveals shifts in grasp kinematics away from natural grasps and towards pantomimed (simulated) ones in normally-sighted populations.

Keywords: Two Visual Systems Hypothesis, Vision, Haptics, Tactile Feedback, Visual Form Agnosia, Visuomotor, Sensorimotor, Prehension, Grasping, Dorsal Stream, Ventral Stream

Co-Authorship Statement

Regarding the published work reported in this dissertation, the first author (Robert L. Whitwell) was solely responsible for all phases and aspects of the scientific method except as follows: Chapter 1 was co-authored by Melvyn A. Goodale who revised and edited some sections and provided comments on the remaining sections. Chapter 2 was co-authored by Melvyn A. Goodale who revised and edited all drafts of the manuscript. Chapter 3 was co-authored by A. David Milner, Cristiana Cavina-Pratesi, Caitlin M. Byrne, and Melvyn A. Goodale. A. David Milner provided comments on several drafts of the manuscript. Cristiana Cavina-Pratesi assisted with data collection of patient DF and provided comments on a later draft of the manuscript. Caitlin M. Byrne assisted with data collection of the control participants. Melvyn A. Goodale was involved in the experimental design and revised and edited all drafts of the manuscript. Chapter 4 was co-authored by A. David Milner, Cristiana Cavina-Pratesi, Masihula Barat, and Melvyn A. Goodale. Cristiana Cavina-Pratesi assisted with data collection of patient DF. Masihula Barat assisted with data collection of the neurologically intact control participants. Melvyn A. Goodale was involved in the experimental design and revised and edited all drafts of the manuscript. Chapter 5 was co-authored by Tzvi Ganel, Caitlin, M. Byrne, and Melvyn A. Goodale. Tzvi Ganel was involved in the experimental design and provided comments on a later draft of the manuscript. Catlin M. Byrne assisted with data collection and analysis. Melvyn A. Goodale was involved in the experimental design and revised and edited all drafts of the manuscript. Finally, Chapter 6 was co-authored by Gavin

Buckingham and Melvyn A. Goodale. Gavin Buckingham revised and edited some sections and provided comments on the remaining sections and Melvyn A. Goodale revised and edited a later draft.

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Grasps directed at real targets (viewed through a pane of glass) with veridical haptic feedback ($G_{G\text{-}H}$)

Grasps directed at virtual targets (viewed in the mirror) without haptic feedback ($G_{M\text{-}NH}$)

Grip Aperture (GA)

Final Grip Aperture (FGA)

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Infrared Emitting Diode (IRED)

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Normal Grasping (NG)

Constant Haptic Size (CH)

Haptic Feedback (HV)

Non-Veridical Mirror (NVM)

Visual Feedback (VF)

Veridical Haptic Size (VH)

Veridical Mirror grasping task in which the visual and haptic sizes were matched (VM)

Chapter 1

1 General Introduction

1.1 Patient DF

Just a few days after her 34th birthday in 1988, a young woman was taking a shower in her newly-renovated cottage and was nearly asphyxiated by carbon monoxide from a poorly vented water heater. Although she had passed out from hypoxia, her partner found her before she died and rushed her to hospital. When she emerged from her coma, it was clear that her brain had been badly damaged from lack of oxygen. Her vision was particularly affected. She could no longer recognize common objects by sight or even her husband and friends. In the days and weeks that followed her accident, she showed some improvement, but in the end she was left with a profound visual form agnosia; in other words, she could no longer identify objects on the basis of their shape. Indeed, in later testing, it became apparent that DF (as she is now known in the literature) could not identify even the simplest of geometric figures, although her ability to perceive colour and visual textures remained relatively intact.

DF’s ability to perceive the form of objects is so compromised that she cannot distinguish a rectangular block of wood from a square one with the same surface area (Fig. 1-1A). Such blocks are often referred to as ‘Efron’ blocks, after

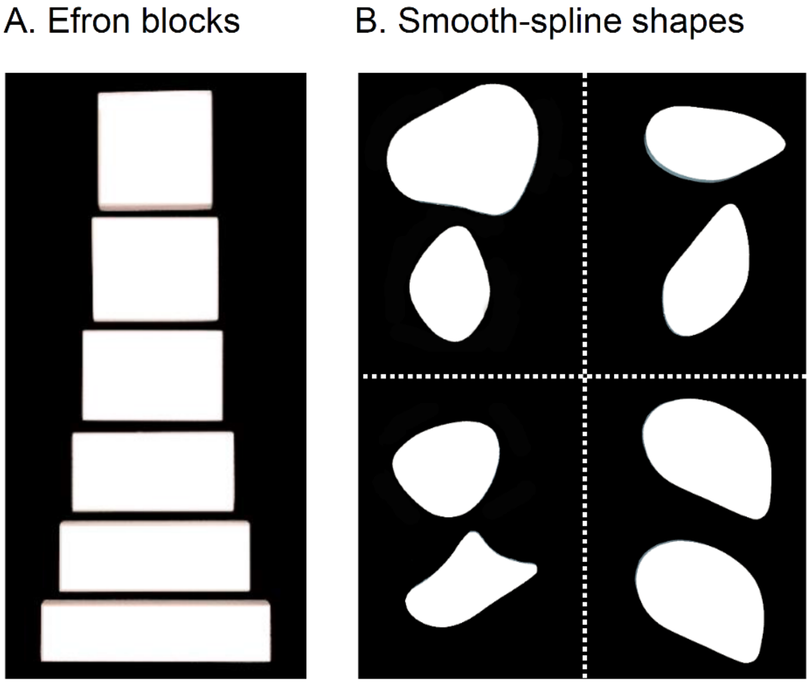


Figure 1-1. Example stimuli that have been used to test object form processing in visual form agnosic patient DF. (A) Examples from a set of Efron blocks that, by definition, are matched for surface area, texture, mass, and color, but vary in width and length (1). In the grasping task, DF reached out to pick the objects up across their width. In a typical perceptual task, she is asked to indicate manually the width of the block by adjusting her thumb and index-finger a matching amount or to provide same/different judgments about pairs of these objects. (B) Examples of the pebble-like shapes used in Goodale et al. 1991. DF was asked to either (i) reach out to pick up the shapes presented at one of two possible positions one at a time or (ii) provide explicit same/different judgments about pairs of shapes when they had different shapes and different orientations (top left), the same shape but different orientations (top right), different shapes but same orientations (bottom left), and same shape and orientation (bottom right).

the psychologist, Robert Efron, who first devised shapes such as these to test for visual form agnosia (Efron, 1969). DF cannot even manually estimate the widths of the blocks by opening her finger and thumb a matching amount (e.g., Goodale, Milner, Jakobson, & Carey, 1991; Goodale, Jakobson, & Keillor, 1994). Nevertheless, one aspect of DF's visually guided behaviour with respect to object form has remained remarkably preserved. When she reaches out to pick up one of the Efron blocks, the aperture between her thumb and finger scales in flight to the object’s width (Goodale et al. 1991; Goodale, Jakobson, & Keillor, 1994; Marotta, Behrmann, & Goodale, 1997; Westwood, Danckert, Servos, & Goodale, 2002; Whitwell, Milner, Cavina-Pratesi, Byrne, & Goodale, 2014; Whitwell, Milner, Cavina-Pratesi, Barat, & Goodale, 2014). Similarly, even though DF cannot distinguish perceptually amongst objects on the basis of their orientation and shape (e.g., Goodale et al. 1991; Milner et al. 1991), she orients her wrist correctly when posting her hand or a wooden card through a slot (Goodale et al. 1991; Hesse & Schenk, 2014; Milner et al. 1991) and places her fingers on stable grasp points when picking up smooth-spline, pebble-like shapes (Fig. 1-1B; see Goodale, Meenan, Bulthoff, Nicolle, Murphy, & Racicot, 1994). In other words, despite a profound deficit in form perception, DF seems able to use information about object form to guide her grasping movements.

1.1.1 Initial Scans of DF’s Brain

As Milner et al. (1991) report in detail, DF underwent several brain scanning session using different imaging techniques within the first 13 months following her accident. Less than two weeks after her accident, computerized topography (CT) revealed small areas of low-densities “at the level of” (p. 406) the internal capsule and the around the body of the left lateral ventricle. A second CT scan conducted approximately seven weeks after the first revealed no abnormality. The first of two single-photon emission computed topography (SPECT) scans was conducted four weeks following her accident and revealed reduced blood-flow across much of the frontal cortex, the left posterior parietal cortex and the occipital-temporal regions. The second of the two SPECT scans 8 months after her accident showed no sign of reduced blood flow in the frontal cortex. At the same time, however, reduced blood flow was observed in the parieto-occipital area. Thus, both the CT and SPECT scans indicate a dynamic post-traumatic environment in which certain regions are more persistently affected than others. Milner et al.'s (1991) report of the magnetic resonance imaging (MRI) scans of DF's brain support this general finding. MRI was conducted between two and three weeks following her accident. The MRI images revealed damage at the level of the lentiform nucleus bilaterally and in the left temporo-occipital cortex. Thirteen months following her accident, however, a second MRI scan revealed signs of bilateral damage to the globus pallidus. The most evident damage was to the occipital cortex bilaterally. According to the report, this damage was largely confined to the inferior and ventrolateral areas and at the polar convexity, extending into the parasagittal occipitoparietal region. Finally, this later scan revealed a widening of the ventricles and sulci.

1.1.2 Visual Form Agnosia, Optic Ataxia, and the Two Visual Systems Hypothesis

Taken together, these early scans revealed persistent damage to the lower lateral occipital regions of DF's brain. Furthermore, these scans revealed little to no evidence of persistent damage to the frontal cortex or the anterior areas of the parietal cortex. Given these findings, it seemed reasonable to assert, as Mon-

Williams, Tresilian, McIntosh, & Milner (2001) did, that DF constitutes a case-study of an “isolated dorsal stream” (p. 135).

At about the same time that DF’s spared visuomotor abilities were being tested, other patients were shown to have severe deficits in skilled visually-guided acts like reaching out to point to or grasp targets. What was remarkable about these patients, however, was their demonstrable lack of any exclusively visual or motor impairments that could explain their reaching and prehensile deficits. For example, these patients could readily perceive the very geometric and spatial features of targets that successful performance on the reaching and grasping or pointing tasks depended on. Critically, these patients showed bilateral lesions to the dorsal stream that left their ventral stream intact (Goodale, Meenan, et al., 1994; Jakobson, Archibald, Carey, & Goodale, 1991; Jeannerod, Decety, & Michel, 1994; Perenin & Vighetto, 1988). This complementary patterns of intact and impaired abilities that can be observed in relatively ‘pure’ cases of visual form agnosia and optic ataxia have long been argued to constitute a double dissociation – one that formed a cornerstone of Goodale and Milner’s (1992) two visual systems hypothesis (TVSH).

1.2 The Two Visual Systems Hypothesis

Shortly after the findings from DF were reported, Goodale and Milner (1992; Milner & Goodale, 1995) published their account of the “division of labour” between dorsal and ventral visual streams in the primate cerebral cortex described a decade before by Ungerleider & Mishkin (1982). The ventral stream involves a series of corticocortical connections between the occipital and inferotemporal cortex and is thought to be hierarchically organized along a posterior-to-anterior axis: from an anatomical standpoint, the more posterior areas in the occipital cortex form the ‘bottom’ of the hierarchy. Cells and structures in the more posterior areas of the ventral stream (e.g. striate, prestriate, and extratriate cortex) have smaller receptive fields, respond more exclusively by visual input (i.e. are more unimodal), and are selective for ‘simpler’ visual stimulus features than those in more anterior areas in the temporal cortex, including the perirhinal cortex, the temporal pole, and other peri-limbic structures (e.g., Kravitz, Vinson, & Baker, 2008; Olson, Plotzker, & Ezzyat, 2007; Tanaka, 1997).

According to the TVSH, the ventral stream mediates our conscious visual perception of the world. In line with this proposal, structures in the occipital and inferotemporal cortex have been implicated in various perceptual and cognitive processes, including long- and short-term memory, reward, value, habit formation and emotion (for review, see Kanwisher & Dilks, 2012; Kravitz, Saleem, Baker, Ungerleider, & Mishkin, 2013). Many (if not all) of these functions involve the identification and elaboration of object features, objects, object ensembles, and scenes along semantic, social, episodic, and emotional dimensions that intersect with attention, thought, reason, and decision making. The ventral stream is thought to service these processes by transforming visual input into scene-based references frames that are largely independent of view-point. This latter feature of ventral representations stands in contrast to the viewer-dependent (effector-based) visuomotor transformations that the dorsal stream. According to the TVSH, an additional point of contrast between the ventral and dorsal streams is in the ‘degree’ or ‘proximity’ of control over goal-directed action. The dorsal stream affects goal-directed action in a direct way, specifying the parameters of the movement. The ventral stream affects goal-directed action in an *indirect* way: rather than specifying the parameters of a target-directed action, the ventral stream identifies and, therefore, helps select an object for the dorsal stream to operate on. It is important to stress here that the TVSH does not require the ventral and dorsal streams to be hermitically sealed off from one another. The ventral stream likely plays a role in retrieving information about ‘hidden’ properties of those objects that are often useful for interacting with it. For example, the weight of the goal object appears to invoke activity in the ventral stream (Gallivan, Cant, Goodale, & Flanagan, 2014). The indirect nature of this influence, however, is evinced by the fact that the Ponzo pictorial size-contrast illusion affects the anticipatory fingertip forces participants apply post-contact but not the anticipatory pre-shaping of the hand during the reach phase of grasping movements (Jackson & Shaw, 2000). Moreover, transcranial magnetic stimulation (TMS) a cortical target in the area of the anterior intraparietal sulcus (aIPS – a dorsal stream structure) disrupts grip aperture and fingertip forces at different time points during the reach phase of grasping movements (Davare et al. 2007).

The dorsal stream involves the dorsomedial occipital and posterior parietal cortex particularly along the intraparietal and superior parietal areas. According to the TVSH, the dorsal stream mediates the visual control of skilled target-directed action. More specifically, the dorsal visual stream can be described as a network of visuomotor nodes that are populated with neurons that code the spatial and geometrical properties of targets in effector-specific reference frames. The cells of these nodes accept as input visual information about the target in one spatial reference frame (e.g., a retinocentric one) along with input about the position of the body or some component of it (e.g., the position of the eye in its orbit), integrates these inputs, and outputs a signal that can be diagnostic of a particular spatial relation between the target and the effector itself. This process is referred to as ‘gain-field modulation’ (e.g., Salinas & Their, 2000). For example, neurons in the posterior parietal cortex code the position of a visual stimulus as a function of the position of the eye in its orbit or as a function of the target with respect to the arm (e.g., Marzocchi, Breveglieri, Galletti, & Fattori, 2008). More generally, spatial reference frame transformations are achieved by cells whose output is modulated by the internal state (e.g., position) of the body (or some part of the body) (e.g., Anderson, Snyder, Bradley, & Xing, 1997; Colby 1998). At the population level, the combined output of these cells serves as input to populations of cells in the motor and premotor areas of the frontal cortex that activate and deactivate muscles and groups of muscles that produce smooth and accurate goal-directed movements of the limb and hand.

The nodes of the dorsal territory of the visuomotor network can also be thought to operate as ‘internal models’ of various aspects of the agent (including the state of his or her body or parts of it) and his/her immediate environment (e.g, Miall & Wolpert, 1996). One class of internal model is the so-called ‘inverse model’ which accepts as input real-time sensory information about the desired state, including the target object, the agent's current state his/her goal (i.e. what is to be done with the goal object) and outputs a program for action (a 'motor program'). According to this conceptual framework, due to noise in signal conduction and propagation within and between the central nervous and musculoskeletal systems, these programs are rarely formulated and executed without some variable degree of error. Thus, these programs are often adjusted and fine-tuned to result in the accurate and smooth goal-directed movements we normally observe.

To begin with, there are two ways in which these updates can be flagged: the first is through direct sensory monitoring of the target variables of the motor program in real-time (i.e. online sensory feedback). In principle, direct monitoring of the ongoing movement appears ideal. However, the time it takes sensory (afferent) signals to be processed and the movements of the muscles to be subsequently updated is thought to be too long: the movement error might change as the movement unfolds and so what was an adequate correction 200ms ago is now inadequate. To make matters worse, noise increases monotonically with the number of synapses that are involved. For these reasons, sensory feedback is considered insufficient for smooth and accurate updating of goal-directed limb movements. Rather than relying exclusively on sensory feedback, adjustments to the motor program are made with the assistance of an additional process that models and predicts the sensory and motor consequences of the motor program or motor outflow. This additional process is referred to as the 'forward model'. The role of the forward model is to hasten the detection of errors in the execution of the motor program and, therefore, hasten corrections to the motor program. The forward model achieves this by accepting as input the motor program output from the inverse model and generating motor and sensory predictions based on the motor program. This way, movement corrections can bypass the sensory apparatus, cutting down on both the noise and time delay that arises out of signal conduction/propagation and processing.

Critical to this internal model-based conceptual framework is the role that learning plays in developing the rules that inverse and forward models apply to constrain the range and scope of their output. Inverse models are believed to be highly contextualized, applying learned contingencies about the kind of actions that are required to utilize particular objects or classes of objects, exploiting various features such as their size, inferred weight, and/or functional use to specify the kind of grasp to direct at a goal object. To pick up a baseball bat, one does not use a precision-pincer grasp (in which only the index-finger and thumb are used). Rather, one uses all of the fingers, including the palm of the hand to achieve a stable grip. In contrast to the inverse model, the forward model learns to predict how the muscles respond or react to descending motor commands. The forward model is also thought to learn the relationships between motor output and sensory re-afference (i.e. the sensory information that arises as a direct consequence of the agent's movement). Storing these classes of relationships (motor to motor and motor to sensory) allow the forward model to output predictions that can be compared with subsequent motor commands and sensory feedback. In the latter case, a comparison of the predicted sensory feedback from the movement itself and the sensory feedback in general is thought to be critical for attributing the source of sensory input as uniquely external.

1.3 Recent MRI Scans of DF's Brain and Updating the TVSH

Of all the brain imaging scans DF underwent, the third of DF's reported MRI scans was by far the most detailed (see James, Culham, Humphrey, Milner, & Goodale, 2003). Taken approximately 15 years following her accident, these scans clearly revealed bilateral damage to DF's lateral occipital cortex (area LOC) which has long been implicated in object recognition (for review, see Grill-Spector, 2003). Also evident in these scans was bilateral damage to the posterior-most extent of the parietal cortex in and around the parieto-occipital sulcus. The damage to this region in the left hemisphere was large enough that the authors identified it as a lesion. The damage to this region in the right hemisphere was far less conclusive and so the authors identified it as atrophy. Thus, by revealing the full extent of DF's dorsal stream lesions, these scans confirmed what some of the earlier scans had only hinted at. Critically, however, James et al. did not restrict their assessment of DF's brain to its structural aspects. These authors also performed functional MRI (FMRI) while DF performed reaching, grasping, and passive viewing tasks. The FMRI results revealed robust activation in the anterior intraparietal sulcus of DF's brain during visually-guided grasping, despite the lesions to the parieto-occipital cortex (POC) and atrophy in the surrounding tissue (see Fig. 1-2). This area in the dorsal stream has long been associated with the planning and execution of prehensile movements in both monkeys (Gallese, Murata, Kaseda, Niki, & Sakata, 1994; Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Nelissen & Vanduffel., 2011; Taira, Mine, Georgopoulos, Murata, & Sakata, 1990) and neurologically-intact humans (James et al. 2003; Begliomini, Caria, Grodd, & Castiello, 2007; Davare, Rothwell, & Lemon, 2010; Frey, Vinton, Norlund, & Grafton, 2005; Króliczak, McAdam, Quinlan, & Culham, 2008; Monaco, Cheng, Medendorp, Crawford, Fiehler, & Henriques, 2013; Rice, Tunik, Cross, & Grafton, 2007; Rice, Tunik, & Grafton, 2006; Tunik, Frey, & Grafton, 2005). Equally as important, these functional scans of DF's brain showed

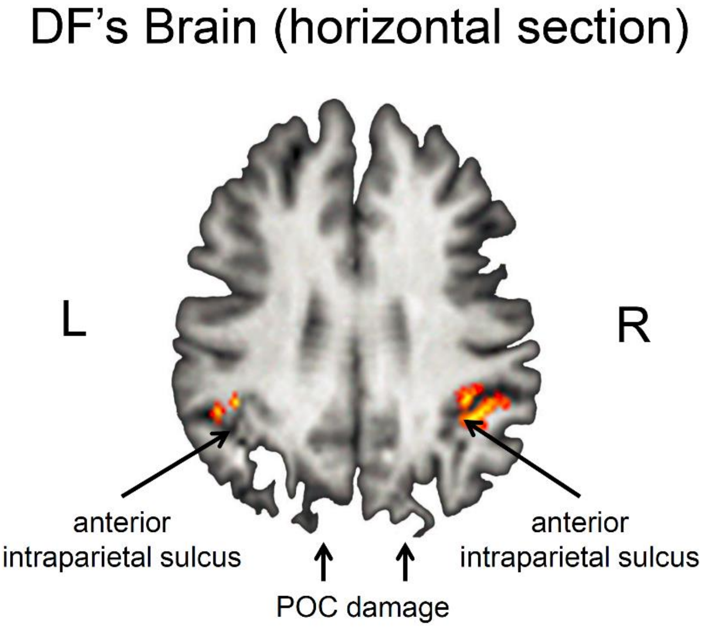


Figure 1-2. Horizontal section through DF's brain illustrating grasp- and reach related activation in the anterior intraparietal sulcus (aIPS). Grasp-specific activation is largely restricted to the right hemisphere. Note that these regions are activated despite the presence of bilateral damage to the parieto-occipital cortex (POC). Unlike healthy controls, there was little or no activation associated with reaching in the POC (James et al. 2003).

no preferential activity whatsoever for intact line drawings of objects when contrasted against scrambled versions of those objects. Thus, the activation in DF’s AIPC occurs despite the fact that she has functionally complete bilateral damage of LOC. This finding suggests that her spared visual control of grasping is mediated by computations in the AIPC that are independent of those in the LOC that are involved in the conscious realization of visual form.

As the earlier scans foreshadowed, DF’s lesions are not restricted to her ventral stream. Her brain shows the typical pattern of diffuse atrophy that is seen in patients who have experienced hypoxia from carbon monoxide poisoning, and the most recent scans indicate that the lesion to POC is now evidently bilateral (Bridge et al. 2013), suggesting that the atrophy has increased in size in these and other areas. In fact, a structural scan performed less than 10 years following the one performed by James is depicted in Figure 1-3 which highlights not only the

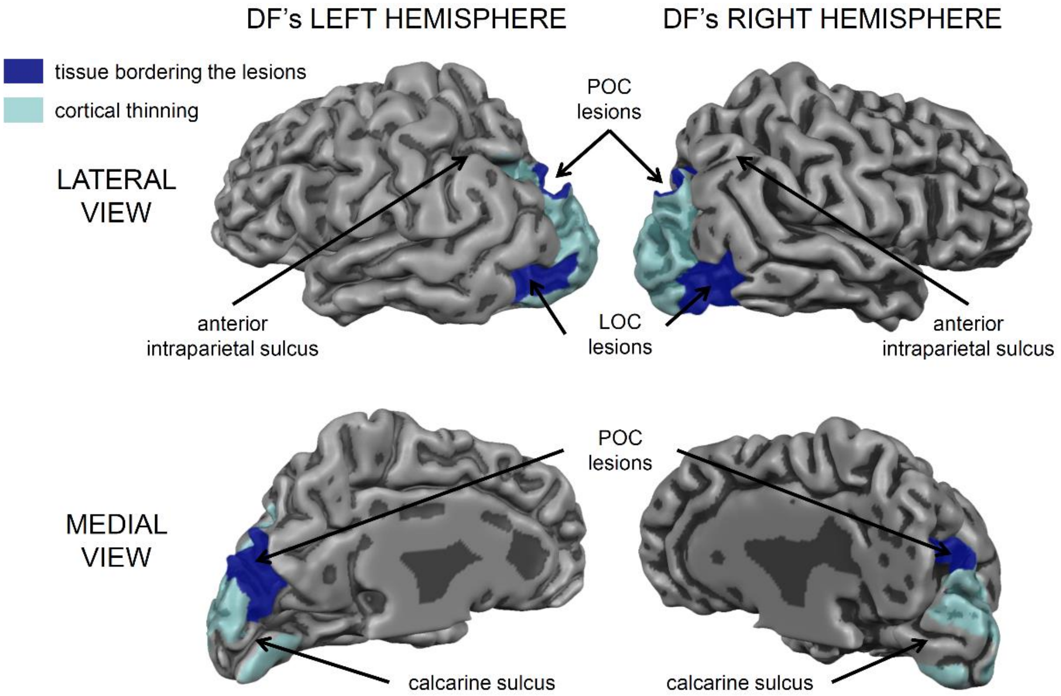


Figure 1-3. A 3D rendering of the cortical grey matter boundary of DF's brain. The peripheral surface of her gyri are depicted as lighter and more reflective, whereas the sulci are depicted a darker grey. The areas of cortical thinning are painted in translucent lighter blue and encompass much of peri- and extrastriate cortex, especially in the left hemisphere (see Bridge et al., 2013 for a detailed analysis). There are also prominent bilateral lesions in the lateral occipital cortex (LOC) and additional lesions in the parieto-occipital cortex (POC) that are highlighted by an opaque darker blue. Importantly, the cortical tissue surrounding most of the calcarine sulcus, corresponding to primary visual cortex (V1) is intact, as are most of the frontal, temporal, and parietal cortices. The small lesion in the anterior part of the upper bank of the calcarine sulcus in her left hemisphere accounts for the partial quadrantanopia in her lower visual field (e.g., Bridge et al., 2013; Hesse, Ball, & Schenk, 2012).

well-known LOC lesions but the POC lesions as well. The POC lesion in the left hemisphere is particularly prominent and extends well into the medial occipital cortex, sparing the tissue around the calcarine sulcus. As Figure 1-3 makes clear, the lesion to the right POC is far more restricted.

1.3.1 Implications of the Bilateral Damage to POC in DF's Brain

The bilateral damage to area POC in DF's brain warrants some discussion of the role of this brain area, particularly since it forms part of the dorsal stream. After all, the TVSH would predict that damage to this area would affect visually-guided action. In fact, a mounting body of evidence implicates POC in the control of visually-guided reaching, particularly to targets presented in the periphery (for review see Andersen, Andersen, Hwang, & Hauschild, 2014; Culham & Valyear, 2006; Culham, Cavina-Pratesi, & Singhal, 2006; Filimon, 2010; Karnath & Perenin, 2005). In an important study, Karnath and Perenin (2005) carried out an analysis of lesion sites in 16 optic ataxic patients with unilateral damage to either the left or the right posterior parietal cortex. The authors contrasted these patients with control patients who had sustained damage to their parietal cortex but who did not exhibit optic ataxia. Their analysis showed that the greatest degree of lesion overlap that was unique to the optic ataxic patients occurred in POC and in the precuneus. Critically, all of the patients with optic ataxia showed misreaching errors when reaching out to touch targets presented in the periphery of their contralesional field. Although there is clear evidence that optic ataxia can include visuomotor deficits in central vision (e.g., Buiatti, Skrap, & Shallice, 2013; Ferrari-Toniolo et al. 2014; Jakobson et al. 1991; Perenin & Vighetto, 1988), it is well-known that optic ataxia more frequently manifests itself as misreaching to targets presented in the periphery (Buxbaum & Coslett, 1997; Rossetti, Pisella, & Vighetto, 2003). In fact, peripheral and centrally-guided reaches might well rely on partially-separate networks in the posterior parietal cortex (Clavagnier, Prado, Kennedy, & Perenin, 2007; Prado et al., 2005) Clavagnier et al., for example, have argued that the POC forms part of a fronto-parietal network of areas that is critical for visually-guided reaches to peripherally-presented targets.

Given the damage to DF's POC, it is perhaps not surprising that this region shows unusually little, if any, fMRI activation in this region when she reaches out to touch targets (James et al., 2003) and that she exhibits a gross deficit when reaching out to point to targets in the periphery, but not when pointing to targets presented centrally (Hesse, Ball, & Schenk, 2012; 2014). Thus, DF's deficit in peripheral reaching is likely due to the damage in her POC. There is also some indication that the POC in monkey and in man plays a role in the control of grasps that are directed at peripheral targets (Fattori et al., 2010; Fattori, Breveglieri, Raos, Bosco, & Galletti, 2012; Rossit, McAdam, McLean, Goodale, & Culham, 2013). For example, patient MH, who developed optic ataxia following a unilateral POC lesion, not only shows a deficit in pointing to targets presented in the periphery of his contralesional field, but he also shows a deficit in grip scaling when grasping these same objects. Critically, however, if the objects are closer and he does not have to reach out towards the target before picking it up, MH's grip scaling is normal. This suggests that his grasping deficit is secondary to his deficit in reaching (Cavina-Pratesi, Ietswaart, Humphreys, Lestou, & Milner, 2010). Interestingly, DF also shows a deficit in grip scaling when reaching out to pick up targets located in her peripheral visual field (Hesse, Ball, & Schenk, 2012). But again, this deficit in grasping targets in the periphery might be secondary to her demonstrated deficit in reaching into the periphery, as it is in patient MH.

Nevertheless, DF’s visuomotor performance, even centrally, is not completely normal in all situations. Himmelbach and his colleagues (Himmelbach, Boehme, & Karnath, 2012) revisited DF’s grasping with the aim of testing for a dissociation using the independent sample t-tests recommended by Crawford et al. (Crawford & Garthwaite, 2005). Himmelbach et al. compared her performance (as reported in Goodale et al., 1991; Goodale, Meenan et al., 1994) with that of 20 new age-matched control participants on three different visuomotor tasks: posting a hand-held card through a slot, picking up Efron blocks of varying width, and picking up smooth-spline pebble-like shapes (Goodale et al., 1991; Goodale, Meenan et al., 1994). Although DF’s grip scaling with rectangular objects fell within the range of the new control participants, the grasp points she selected when picking up the pebble-like shapes were not as optimal as those of the new control participants tested by Himmelbach et al. Her performance on the card-posting task was also slightly, but significantly, poorer than that of the controls. Nevertheless, as the authors themselves admit, the tests also revealed that DF’s data set satisfied Crawford, Garthwaite, & Gray’s (2003) criterion for a “strong/differential” dissociation. Unlike the criterion for a “classic” dissociation in which the patient shows a deficit in one task but not the other, the criterion for a “strong/differential” dissociation allows for a deficit in both tasks, but, critically, requires a dramatically greater deficit in one task than in the other. In other words, despite the presence of slight impairments, DF’s performance on the action tasks were consistently better than her performance on the corresponding perceptual tasks – and this difference was much larger for her than it was for the controls.

Although DF's spared visuomotor abilities have been examined in a number of different settings, it is her ability to scale her grip aperture to the relevant dimension of a goal object when picking it up that has been tested most often. No matter how the computations underlying the programming and control of grasping are conceptualized (e.g., Iberall & Arbib, 1990; Iberall, Bingham, & Arbib, 1986; Jeannerod, 1988, 1999; Smeets & Brenner, 1999; Smeets, Brenner, & Biegstraaten, 2002; Smeets, Brenner, & Martin, 2009), there is general agreement that the accurate grasping of a goal object normally requires a visual analysis of the object's shape so that the final positions of the thumb and fingers can be computed correctly with respect to the relevant dimension of the object, such as its width. Any error in this computation could lead to the object being knocked away or fumbled. When assessing DF's grasping ability, investigators have typically relied on the known positive linear relationship between the maximum opening of the hand mid-flight and object's targeted dimension (see Fig. 4). Given the survey of DF's dorsal stream damage discussed above and in light of Himmelbach's findings, we examined DF's grip scaling across a range of studies in which she grasped centrally-located targets (Goodale et al., 1991; Goodale, Jakobson, & Keillor, 1994; Marotta, Behrmann, & Goodale, 1997; Westwood, Danckert, Servos, & Goodale, 2002; Whitwell, Milner, Cavina-

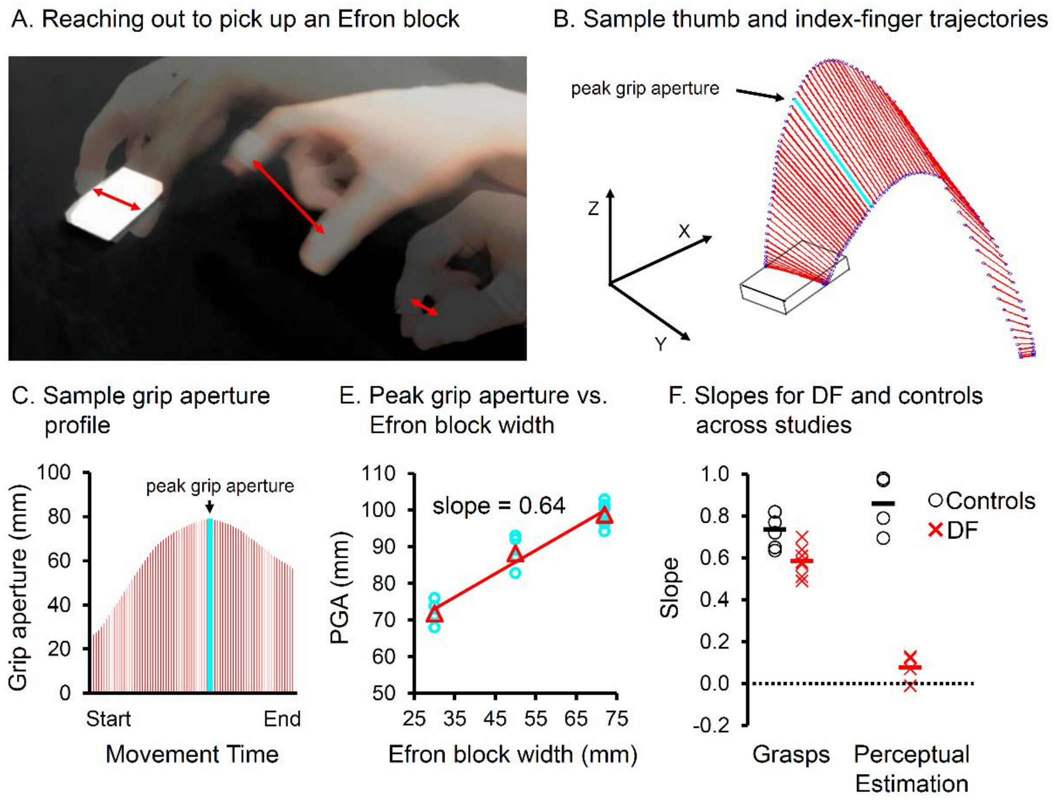


Figure 1-4. The grasping task, measurements of the act, grip aperture, using a slope to summarize the linear relationship between grip aperture and target size and comparing slopes between DF and controls. (A) Superimposed snapshots of a reach-to-grasp action directed at an Efron block. Red double-headed arrows indicate "grip aperture", the Euclidean distance between the tracked markers placed on the tips of the thumb and index-finger (B) sample trajectories of the thumb and index-finger (blue circles) during a precision pincer grasp as the hand reaches out toward the object. The grip aperture is indicated in red. The light blue line reflects the peak grip aperture, which is achieved well-before the fingers contact the object. (C) Grip aperture plotted as a function of time (e.g., percent movement time). The peak grip aperture is again indicated in light blue. (D) Peak grip aperture shows a positive linear relationship to the target size of the object, and so it is thought to reflect the visuomotor system's anticipatory estimate of the target's width. The slopes can be used as indicators of "grip scaling." (E) The slopes for grasping and manual estimation for both the controls (open circles) and DF (X's) across studies in which Efron blocks were used, the visual conditions were "ecological" (i.e., online visual feedback was available), and the controls were gender-matched and age-appropriate for DF. Although DF scales her grasp to the width of the Efron blocks, her slopes are significantly shallower than those of the controls, using either independent or paired-samples variants of the t–test ($p_{\max} < 0.04$). The slopes of DF's manual estimations are essentially zero and clearly different from those of the controls ($p_{\max} < 6\times10^{-3}$). Critically, the difference in slopes between the grasping and manual estimation tasks falls well-outside of the range of the controls ($p_{\max} < 5\times10^{-3}$). In other words, across a number of comparable studies of DF's grasping

and perceptual estimation ability, her performance when grasping Efron blocks is sharply dissociated from her performance when perceptually estimating their width.

Pratesi, Byrne, & Goodale, 2014; Whitwell, Milner, Cavina-Pratesi, Barat, & Goodale, 2014). Critically, the targets in all these studies were drawn from a set of blocks that varied in width and length but were matched for surface area, texture, mass, and colour, so that she could not discriminate one from another in perceptual tests. DF clearly scales her grip aperture to the widths of these targets when reaching out to pick them up (see Fig. 1-4). Nevertheless, she does show a modest, though significant, deficit when compared to the controls. Critically, from study to study, DF's estimations of the widths of these targets remain at chance, whereas, not surprisingly, the estimations made by the controls are essentially perfect. Moreover, a formal test of the difference in performance across the two conditions indicates a significant strong/differential dissociation (Crawford, Garthwaite, & Gray, 2003). In short, over the course of two decades of testing, DF's dissociation between object vision for action and object vision for perception remains as strong as ever.

1.3.2 Limitations to DF's Visuomotor Abilities

As remarkable as DF's visually guided grasping is, however, it is clearly not without limitations. In fact, there are a number of seemingly simple task modifications that have a remarkably detrimental effect on her grip scaling. For example, if a target object is shown to DF and then taken away, she is unable to scale her grasp appropriately when she is asked to show how she would pick it up.

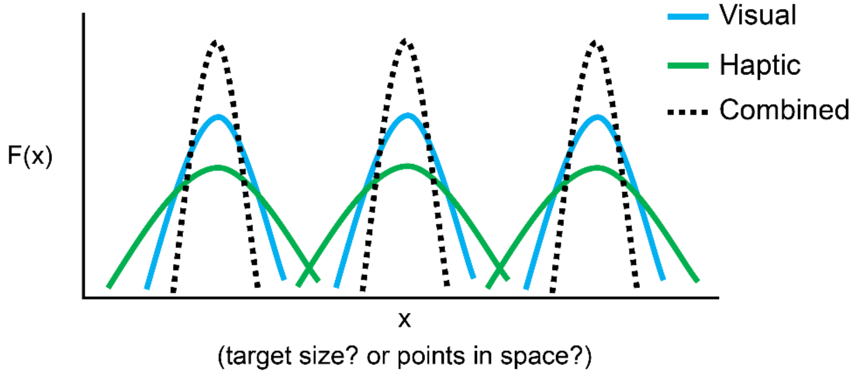
In healthy participants, of course, grip aperture still correlates well with the object's width, even for delays as long as 30 s. In DF, however, all evidence of grip scaling disappears after a delay of only 2 s (Goodale, Jakobson, & Keillor, 1994). DF's poor performance cannot be due to a general impairment in memory: she has no difficulty showing how she would pick up an imaginary orange or a strawberry, objects that she would have encountered before her accident or would have handled in the past. In other words, when she pretends to pick up an imaginary orange, her hand opens wider than it does for an imaginary strawberry (Goodale et al. 1994). Moreover, she is as accurate as normally-sighted controls when asked to open her finger and thumb a particular amount (e.g., "show me how wide 5 cm is") with her eyes closed. Indeed, her manual estimations in this task are much better than they are when she is asked to indicate the width of an Efron block placed directly in front of her. It is important to note that even though the grasping movements made by normal participants in the delay condition are scaled to the width of the remembered objects, they look very different from those directed at objects that are physically present. This is because the participants are 'pantomiming' their grasps in the delay conditions, and are thus relying on a stored perceptual representation of the object they have just seen. Presumably, DF's failure to scale her grasp after a delay arises from the fact that she cannot use a stored percept of the object to drive a pantomimed grasping movement because she never 'perceived' the target object in the first place.

Delayed pantomimed grasps are not the only grasping task that DF has problems performing. DF's grip scaling is also particularly poor when she must reach out to pick up a disk by inserting her thumb and pointer-finger into two, let alone three, circular holes cut into the disks. Interestingly, when the holes were coloured differently in a follow-up version of the task, there was some evidence that her grip scaling improved in both the two-hole and three-hole variants. In fact, unlike the version of the task in which the holes were the same colour, DF remarked that she could see the holes as distinct objects when they were coloured differently. This finding suggests that her performance on this task might have benefitted from some ventral stream involvement. Importantly, however, even when the holes were different colours, her grip scaling was still well below the levels of grip scaling observed in the controls (Dijkerman et al. 1998). Although there is some evidence indicating a role for the ventral stream in processing the distance between the three holes for the purposes of grip scaling, in-line with the TVSH the ventral stream's principal role in this task appears to be target selection. Accordingly, DF's problem scaling her grip aperture to the distance between the two, or even three holes, stems from her inability to determine in the simplest two-hole case which of the holes to send the pointer-finger (or thumb) towards. This failure in target selection also explains why, even in the two-hole variant, DF inserted her pointer-finger through the wrong (bottom) hole on approximately 40% of the trials. Given the fact that DF's grip scaling when reaching out to pick up visible targets is well-above chance and only modestly affected, it seems prudent to conclude that the task of inserting her fingers into holes cut into disks relies more on ventral stream processing than does more natural grasping tasks.

Support for the interpretation that inserting the fingers and thumb into holes imposes demands that the dorsal stream is not capable of meeting also comes from a follow-up investigation in which DF was asked to insert her pointer-finger and thumb through two square (rather than circular) holes cut into a clear plastic sheet (McIntosh et al. 2004). Unlike the Dijkerman et al. (1998) study, the space between the two square holes was filled-in with a black rectangular strip to simulate the appearance of a rectangular object in an effort to make the conditions of the task resemble those under which natural grasps are performed. To the authors own surprise, this manipulation did not ameliorate her poor grip scaling (McIntosh et al. 2004). Again, a failure in target selection can account for DF's problems in this task. Thus, when the task deviates from its most-familiar and ecologically valid version, DF's performance suffers quite noticeably.

Finally, DF's grip scaling ability was recently shown to be particularly poor when haptic feedback was consistently denied. Using an ingenious mirror apparatus, Schenk (2012a) demonstrated that DF's grip scaling is completely abolished in a task in which the target remains visible (as a virtual image in the mirror) yet is physically absent (behind the mirror) so that when her hand closes down on the apparent edges of the virtual target, it closes down on 'thin air'. Schenk argued that DF's failure to show grip scaling in this situation is due to the absence of haptic feedback which she would normally use to compensate for her poor visual abilities. According to Schenk (2012a,b), DF's grip scaling relies on the integration of visual and haptic feedback about location of the finger and thumb endpoints. Presumably, this bimodal integration is applied in a predictive manner on subsequent trials. Nevertheless, when such haptic feedback is absent, Schenk argues, DF's ability to grasp objects falls apart because her degraded form vision cannot, by itself, support visually guided grasping. A schematic illustration of the principles Schenk alludes to but neglects to flesh out in any detail can be found in Figure 1-5. There are two critical assumptions he is tacitly relying on.

A. Schematic outline of the bimodal estimates for healthy individuals



B. Schematic outline of the bimodal estimates for DF

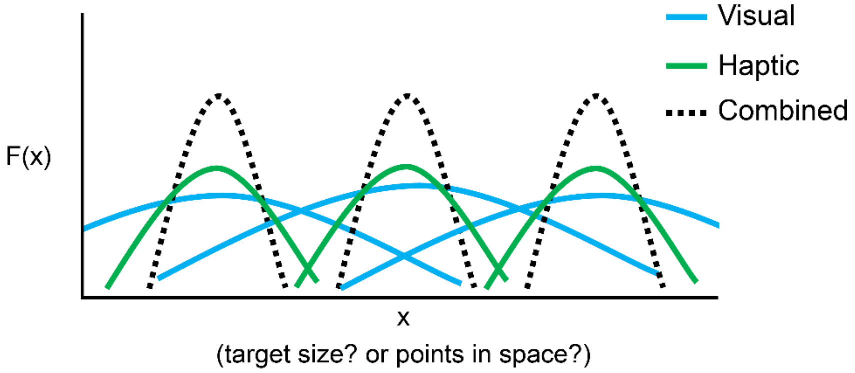


Figure 1-5. A schematic depiction of the process of bimodal integration of unimodal (visual and haptic) estimates of target size or points in space. Normally, visual estimates of target size (or a point in space) are more precise (less variable) than those derived from haptics (see e.g. Ernst & Banks, 2002). When these estimates are combined optimally, the resultant integrated estimates are more precise than either of the two unimodal estimates alone. According to Schenk's (2012a,b) compensation hypothesis, DF reflects a special case in which her visual estimates are severely compromised. Critical to Schenk's argument, DF still possesses some degraded capacity to provide visual estimates of target size (or points in space as Schenk argues), albeit they are very noisy and fairly unreliable on their own. Her

> normal haptic perception, however, is then combined with the degraded visual estimates to yield more precise bimodal estimates of target size which, presumably, are applied in a predictive manner.

First, Schenk assumes that DF's spared grip scaling depends on a visual analysis of the points in space that correspond to the edges of the target, but there is no aspect of Schenk's (2012a) experimental design that can support this notion. Second, by invoking a compensation-based account of DF's grasps, Schenk invokes a monolithic view of visual processing. In other words, Schenk assumes that the human visual system comprises a shared pool of visual information from which all manner of response modes draw from. Under this assumption, it would have been equally as valid to provide haptic feedback after DF provides each of her estimates of target size as this would then provide her the same sources of information that Schenk (2012a,b) alleges she uses when DF reaches out to pick up visible targets, but he did not perform this complimentary experiment.

Milner, Ganel, and Goodale (2012) have offered an alternative, more straightforward explanation: According to their account, grasping tasks in which the target is visible but not available to touch are actually pantomime tasks in which the participant has to pretend to contact the object. For the visuomotor systems in the dorsal-stream to remain engaged, they argue, there must be some sort of tactile confirmation that the visible target has been contacted at the end of the movement. In the absence of such feedback, participants revert to pantomiming (simulating) their grasping movements, introducing a necessary ventral stream contribution to the task. This conclusion is supported by the fact that the slopes of the function relating grip aperture to object width in the normal participants in the absent-object task are much steeper than those typically observed in normal grasping in which the target object is physically present (see Chapter 5). In fact, the slopes resemble those seen in manual estimations of object width, suggesting that participants are indeed resorting to pantomiming a grasping movement when the target object is absent. In other words, they are relying on a perceptual representation of the target to drive their behaviour rather than engaging more ‘encapsulated’ visuomotor networks in the dorsal stream that normally mediate visually guided grasping. DF, of course, is at an enormous disadvantage in this situation because she does not perceive the form of the virtual image in the mirror and thus cannot generate a pantomimed response. As a consequence, her grip aperture bears no relationship to the width of the target in this situation.

To test this idea I recently examined DF’s grasps using the same mirror set-up used by Schenk (2012a). In my experiments (see Chapters 3 and 4), however, there was always an object behind the mirror for her to grasp. Importantly, the width of that object never changed, even though the width of the object viewed in the mirror varied from trial to trial (Whitwell et al., 2014a, 2014 *in press*; see Chapters 3 and 4 respectively). With this arrangement, DF always experienced tactile feedback at the end of the movement, but the feedback was completely uninformative about whether or not her grasp was properly tuned to the width of the object in the mirror. Contrary to what Schenk would have predicted, I found that DF continued to show excellent grip scaling in this task. In other words, DF was able to use visual information in a feedforward manner to scale her grasp in the complete absence of reliable haptic feedback. Tactile contact by itself was evidently enough to keep the visuomotor systems in her dorsal stream engaged.

As I discussed above, under a monolithic version of the visuohaptic integration account, the reason DF is unable to manually estimate the width of an object is that, unlike in the grasping task, she experiences no haptic feedback about the object's width after she makes each estimate. I tested this prediction directly by allowing DF to pick up the object immediately after she had made her estimate (Whitwell et al., 2014a, 2014 *in press*; see Chapters 3 and 4 respectively). Again, contrary to what Schenk would have predicted, we found that DF continued to be unable to indicate the width of the object despite having accurate haptic information about the width of the target after every estimate. Thus, an explicit estimate of size, reflecting what she perceived (or perhaps more correctly, did not perceive) of the object's width, could not take advantage of the haptic feedback.

Before delving into experiments concerning the role that haptic feedback plays in mediating DF's and healthy participants' grasping abilities, I turn first to a methodological examination of peak grip aperture – a gold standard, principal measure of the visuomotor system's estimate of target size. I show how a common analysis of grip aperture in and of itself can lead to remarkably erroneous inferences about the visuomotor system's processing of target size but that the peak grip aperture remains robust to these problems. The results of these experiments bolster support for the continued use of the peak grip aperture of reach-to-grasp movements as a critical and valid indicator of anticipatory visuomotor estimation of target size.

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Chapter 2

2 Grasping without vision: Time normalizing grip aperture profiles yields spurious grip scaling to object size

Why do investigators of grasp kinematics rely on the *peak* grip aperture of reach-to-grasp (prehensile) movements to test for effects of interest? Measurements of the coordinated prehensile movements of the fingers, hand, and limb constitute a rich time-series data set – grip aperture can be computed along all of these time points. So, why not compute grip aperture at time points before or after the peak amplitude of this measurement is achieved? In fact, some investigators have done exactly this, driven by an initial hypothesis that predicts a time-dependent effect. However, as things turn out there are at least two related reasons why testing grip aperture pre- and post-peak time points can introduce serious problems.

The first reason stems from the mechanics of grasping movements: following the peak grip aperture, as the thumb and fingers approach one another to collide with opposing edges of the target, the distance between the thumb and fingers will ultimately reflect the distance between those edges. This is best illustrated by imagining yourself pinching a simple wooden block. If the block is small, then the distance between the tips of the thumb and index-finger is also small. If the block is large, the distance between the tips of your thumb and pointer-finger is large. Imagine now that we recorded your hand and limb as you reached out to pick up each of these two blocks one after the other. If we ran the film backwards starting from the point at which your hand made firm contact with the object, you would first watch the subtle adjustments of your fingers along the surface of the opposing edges of the target. Soon enough, the film of your fingers and hand would appear as if you were releasing the object. You would watch as your hand and fingers retreated back to their starting position. Importantly, it would become immediately apparent to you that your grip aperture reflected the true size of the target well after the 'release' of the object occurred. In other words, points in time beyond peak grip aperture run the risk of being determined not by any anticipatory planning on the part of visuomotor processes but by the physical constraints of the object itself.

The second reason arises from the problem of sample stability and the curve registration process that attempts to solve it. The variability in the estimate of the sample distribution decreases with more observations. In other words, an investigator places more confidence in the sample point estimate with a larger sample size. When dealing with time series data sets that vary in temporal and spatial dimensions, one option is to perform curve registration procedures to standardize or normalize the data set to a fixed number of data points. This has the great advantage of ensuring that the sample stability of each point estimate across all time points (for example) is not biased by differences in sample size. This procedure is inevitably carried out by standardizing the raw data to another variable (e.g., the number of data points in the time-series curve, time, or distance). Typically, the 'standardizing variable' is acquired from the data itself although this is not always the case. Nevertheless, once the curves for each trial are registered, grouped according to one condition or another, and finally aggregated, tests for some effect of interest then proceed through each time point (or some subset thereof) along the averaged standardized curves. Unfortunately, when the effect of interest affects the variable used to standardize the dependent measure, one cannot safely disentangle (1) a direct effect of interest on the dependent measure from (2) an indirect or spurious effect that is mediated via the standardizing variable. This chapter reveals that the relationship between the effect of interest and the variable used to standardize the measure of interest can wreak havoc on the aforementioned inferences all along the trajectory.

This chapter explores how this problem manifests following a very common method of curve registration that involves using time to standardize grip aperture. This chapter reveals that peak grip aperture remains robust to problems associated with curve registration. In the first of two experiments, participants were asked to reach out to grasp different-sized cylinders in the absence of any informative visual information about the cylinder presented on each trial. The movement-time standardized grip aperture profiles yielded spurious effects of cylinder size beyond the point at which peak grip aperture was achieved. Peak grip aperture itself yielded no such effect. The spurious effects were driven by the effect of cylinder size on the movement time. In the second experiment, participants are asked to plan their grasps on the basis of a memory of previewed targets. Critically, the previewed target could be swapped out for any one of two different sized ones during the delay before participants initiate their movement.

Again, the standardized grip aperture profiles yield spurious effects of the final (unseen) target size beyond the point at which peak grip aperture was achieved, independent of the size of the previewed target. Furthermore, peak grip aperture remained robust to these spurious influences. Similar to the first experiment, the size of the unseen substitute target affected the time taken to complete the reach-to-grasp movements, introducing a size-dependent effect on the movement-time standardized grip aperture profiles.

2.1 Introduction

An informative and prolific line of research in visuomotor control involves the study of goal-directed limb movements, such as reaching and grasping (see Culham and Valyear, 2006; Grafton, 2010; Jeannerod, 1999; Smeets and Brenner, 1999). Kinematic studies of these skilled movements typically involve large time-series data sets derived from repeated measurements of sensors attached to the hand and limb. In many cases the data are time-normalized to standardize the number of data points for each trial. Investigators do this to compare the normalized profiles of kinematic measures between or among conditions across the standardized ‘bins’ of, typically, time (e.g., Danckert et al., 2002; Dixon & Glover, 2009; Glover & Dixon, 2001a; Glover & Dixon, 2001b; Glover & Dixon, 2002a; Glover & Dixon, 2002b; Heath, Mulla, Holmes, & Smusowitz, 2011; Heath and Rival, 2005; Himmelbach et al., 2006; Paulignan et al., 1991a; Paulignan et al., 1991b; Rand, Squire, & Stelmach, 2006; Whitwell, Lambert, & Goodale, 2008; Whitwell & Goodale, 2009). Problems can arise, however, when measurements that are extracted from these normalized profiles are correlated with the variable used to standardize them in the first place. If grip aperture (which is typically scaled in flight for the size of the goal object) is measured at the same time bin in the normalized profiles for a series of grasps directed at goal objects of different sizes, a correlation between grip aperture and target size may simply reflect the fact that the duration of the movement is itself correlated with target size.

To illustrate this point, consider a typical grasping experiment in which participants are instructed to reach out and pick up goal objects of different sizes. We know that participants use vision to scale their grip aperture in flight to the size of the target presented on a particular trial (Jakobson & Goodale, 1991; Paulignan et al., 1991a; Whitwell & Goodale, 2009), and that participants can even do this in visual open-loop where they see the target at the outset but not during the execution of the movement (Jakobson and Goodale 1991; Rand et al. 2007; Whitwell et al., 2008; Whitwell and Goodale, 2009). Now imagine a situation in which blindfolded participants reach out and grasp targets of different size. Common sense tells us that they would not show any grip scaling at all. Under these conditions, the participants would undoubtedly reach out tentatively, with a wide grip aperture to avoid fumbling as they grasped the smallest sized targets, and then close their hand down on the target. This would inevitably mean that their hand would take longer to make contact with the edges of a small target than it would for a larger one. In other words, the smaller the target, the longer the duration of the movement. If one were then to time-normalize the movements, a spurious relationship between grip aperture and target size would emerge in these profiles. Most of each of these two grasping movements would look similar, even the time-normalized ones, but as the hand closed down on the target, the time-normalized grasp for a small target would show a smaller grip aperture than the time-normalized grasp for a large target. In fact, the further along the time-normalized profiles, the more discrepant the difference in real time between these tentative blind grasps for small and large objects (see Fig. 2-1).

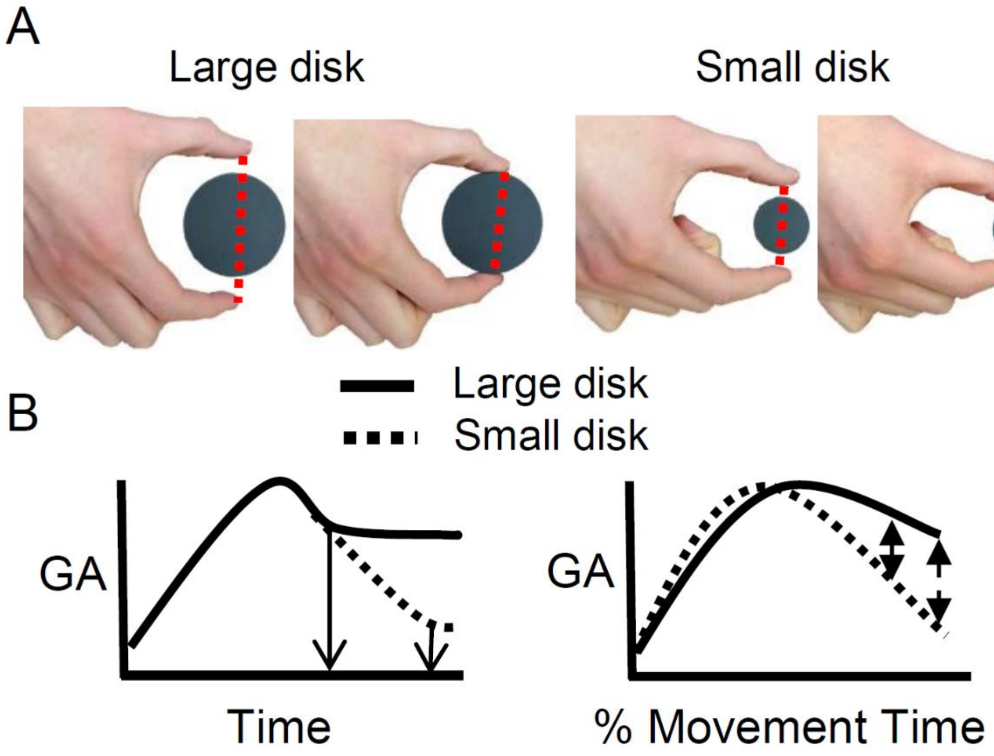

Figure 2-1. Schematic illustration of the relationship between grip aperture, target size, and movement time and the effect of time normalizing grip aperture.
Panel A: The thumb and index-finger just prior to and at the moment of target contact. Despite the fact that the fingers have not made contact with the target, it is clear that the distance between them, grip aperture, will reflect the target's size. Panel B: Grip aperture profiles to large and small disks in raw time (left) and in normalized time (right). The downward-facing arrows in the raw time profiles (left graph) mark the time of contact with the target and the end of the movement. The raw grip aperture traces are identical apart from the fact that the trace for the smaller disk lasts longer and achieves a smaller values. This occurs, of course, because the smaller disk leaves more room (and time) for the fingers to close

down on and so the fingers take longer to make contact with it. Normalizing these data points to overall movement time introduces spurious grip scaling – differences (indicated by the double-headed arrows) in the opening of the hand that were never programmed.

To put it concretely, imagine that the movement time for a blind grasp towards a small object takes 500 ms while the same grasp directed towards a large object takes only 400 ms. At the beginning of the movement (e.g., 10% of the way), the linear difference in real time would be only 10ms. But by 90% of the way through, this difference in real time would have ballooned to a difference of 90 ms – creating a spurious difference in grip aperture for the two different targets. These and other systematic errors associated with normalized data of this kind can lead to erroneous conclusions about the operation of the underlying visuomotor networks.

In the present set of experiments, we looked at the effects of normalizing grasping data from blindfolded participants using a variant of a task that has already been used to study on-line adjustments in grip scaling in a patient (IG) who suffers from optic ataxia following bilateral lesions of the posterior parietal cortex (Himmelbach et al., 2006). In their experiment, the size of the target changed unexpectedly during the execution of a grasping movement. The authors reasoned that measures of grip aperture taken towards the end of a movement would more accurately reflect the contributions of a residual visuomotor ability to adjust the grasp than would measurements taken at the beginning of the movement (see also Glover, 2003, for a similar assumption regarding the relative contribution of movement planning and online motor control). Unfortunately, the authors based their assessment of IG's grip scaling on time-normalized measurements of grip aperture even though movement time was affected by target size. As a result, the apparent correlations they observed between grip aperture and target size at the end of the movements in IG, like those of the thought experiment described above, may simply have been a consequence of a comparison of grip aperture at two different points in time – points which would necessarily correlate with target size – rather than any residual ability to adjust the grasp to changes in target size. To test this possibility, we examined the effects of normalization on 'blind' grasping in two experiments. In the first experiment, we asked blindfolded subjects to reach out and grasp targets of different sizes that they never saw. In the second experiment, we gave the subjects a preview of the target and then asked them to grasp it or a substitute target while blindfolded. On some trials of the second experiment, the previewed object was swapped out for an object of a different size during the delay period (see the "delayed real-grasping" task in Milner et al., 2001 for a similar protocol). Thus, although the target did not change during the movement, the movement itself was planned based on visual input about the previewed target and so the question was whether evidence for an adjustment to the different size of the unseen new target would emerge in the normalized grip aperture as the response unfolded. We predicted that by normalizing the grip trajectories we would find 'evidence' for grip scaling and online adjustments in blindfolded participants, which of course should not be possible.

2.2 Experiment 1

2.2.3 Methods

2.2.3.1 Participants

Ten self-reported right-handed individuals (M = 31.4 years, SD = ±8.8 years) provided their informed consent and were compensated $10 for their time.

2.2.3.2 Apparatus, Procedure, and Design

Participants were seated in front of a table with the tips of the thumb and index-finger of their right hand pinched together resting on the start position (a small Felt disk). One infrared emitting diode (IRED) was attached to the distal interphalangeal joint of the thumb and a second IRED was attached to the interphalangeal joint of the index-finger. The positions of the IREDs were tracked for 2 s from the start of the trial using the CERTUS optoelectronic recording system (Northern Digital Inc., Waterloo, ON, Canada) at 400 Hz. For the practice and experimental trials, the participants wore PLATO goggles (Translucent Technologies, Toronto, ON, Canada) that were controlled by the experimenter and were used to occlude the participants' view of the workspace during the experimental trials. The lenses of these goggles default to a translucent state that blocks the wearer's view.

On a given trial, an auditory tone cued the participants to reach out to pick up any one of four possible target disks using a precision pincer grasp with the thumb and index-finger. The target disks were located 16 cm from the hand's starting position (see Fig. 2-2A). To ensure that the position of the disks did not vary from trial to trial, each disk was positioned over a short peg that was fixed to the test table. Once the participant lifted the disk, he or she placed it back down on the table before returning to the starting position and resuming the starting hand posture. All four disks were 1.5 cm tall and varied only in terms of their diameter in increments of 8 mm. The smallest disk was 2.8 cm in diameter while the largest disk was 5.2 cm in diameter.

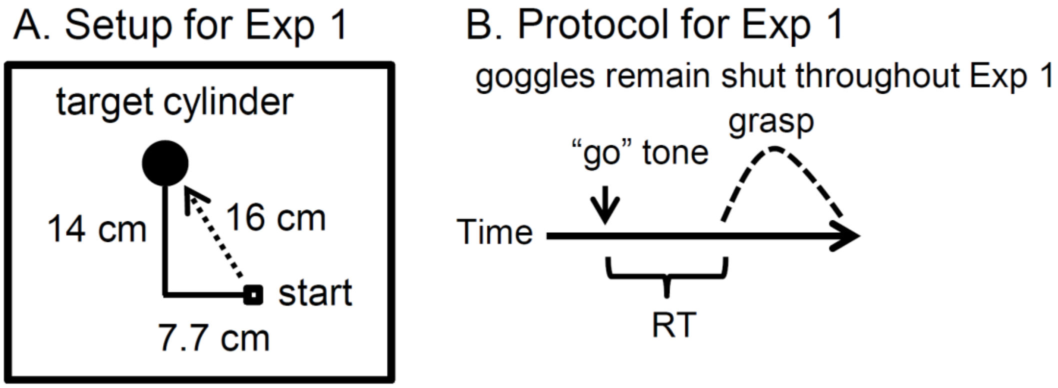

Figure 2-2. Setup and protocol for Experiment 1. Panel A: Setup for Experiment 1. The dashed arrow indicates the direction in which the participant reached out to pick up the target. Panel B: Trial protocol for Experiment 1. The goggles remained shut for the duration of this experiment. An auditory "go" tone cued the participant to reach out blindly to grasp the target disk.

Critically, the lenses of the goggles remained in their default (i.e. view obstructing) state for both the practice and experimental trials (see Fig. 2-2B). Thus, during the practice and experimental trials, the participants could not see the disks or the workspace and, therefore, had to rely on whatever memory of the disk's position that they had accrued. To minimize any tendency for participants' to probe for the target's position on each trial, the participants were instructed to contact the opposing sides of the disk with the thumb and index-finger at the same time and to avoid leading their reaches with their index-finger to find the target.

The participants were also instructed to return to the start position and resume the starting hand posture once they were finished lifting the target disk and placing it back down.

Before the practice and experimental trials were administered, a series of calibration trials were administered to compute the centre of the disks in 3 dimensional Cartesian coordinates and measure each disk's diameter. For these trials, the participants had a full view of the workspace and the target. The participants were asked to place the tips of their thumb and index-finger on opposing sides of a given disk such that the centre of the pads of their finger tips lay at the ends of a visible line on the top of the disk that bisected the top of the disk into two equal halves. They did not lift the disk during these trials and were asked to keep their grip as stable as possible for a 2-s period of data collection. This procedure was repeated several times for each of the four disks.

Next, the goggles were closed and remained so until the end of the experimental test session. Participants were given as many practice trials as it took for them to perform the task comfortably and proficiently as judged by the experimenter and the participant. This was achieved within 10 trials for all participants. These practice trials were not recorded. Note that for these practice trials and the subsequent experimental trials, participants never saw the disks again.

Following the practice trials, 241 experimental trials were administered. The trial order was pseudo-randomized such that a given target disk was equally as likely to be immediately preceded by itself or any of the other disks. This precaution was taken to guard against the possibility that participants might purposefully or inadvertently use haptic feedback from a given trial to scale their grip aperture for the subsequent trial. Specifically, this trial order prevented haptic feedback from the current trial from systematically biasing measures for one target size or any subset of targets. Of course, since the first trial does not have an immediate trial history, an extra trial was added to the total to satisfy the criterion outlined above, which meant that one disk was presented 61 times. All other target disks were presented 60 times. During the experiment, trials in which the experimenter noticed that the participant missed or fumbled the object were repeated at the end of the experiment.

2.2.3.3 Data and Statistical Analysis

The raw positional data for each IRED was processed and analyzed offline using custom in-house software. The raw data was low-pass filtered at 20 Hz. This filtered data set was then used to compute the 3-dimensional velocity and acceleration for each IRED, and the Euclidean distance between the IREDs on the thumb and index-finger (grip aperture, GA).

The onset of the movement (reaction time, RT) was defined as the time at which the thumb IRED exceeded a threshold velocity of 50mm/s for 200ms. The peak grip aperture (PGA) was defined as the maximum grip aperture achieved within a search window from the onset of the movement (i.e. RT) to the end of the movement. The time at which PGA was achieved (tPGA) was the time from movement onset to the PGA. The end of the movement was determined as the frame before the velocity of the thumb IRED first fell below 50mm/s. A velocity-based movement time (MT_V) was defined as the time from the onset of the movement to the velocity-defined end of the reach. An additional temporal window over which to normalize grip aperture was determined based on Himmelbach et al.'s (2006) definitions. This distance-based window (MT_D) began when the thumb IRED reached a frontoplanar boundary 7 cm from the target and towards the participant along the participant's sagittal plane (the time from movement onset to this distance-based boundary, t_D) and ended when either the thumb or index-finger IRED crossed a boundary 10 mm from measured edge of a given disk. There was nothing particularly interesting about the t_D in the current experiment, other than the fact that it corresponded to the point at which the target would change in size in some of the conditions of Himmelbach et al.'s investigation. However, the additional criterion used to define the end of the movement was initially designed to minimize the possibility that finger contact with the object would affect the analyzed measurements of grip aperture (see Himmelbach et al.; see also Franz et al., 2005). Notably, Himmelbach et al., did not elaborate on how the target boundaries in their study were determined, but they did report that the "end of the movement was reached when either the thumb or the index-finger were getting closer than 5 mm to the target disk." (p. 2751). We used a similar distance-based envelope around the disk to define the end of the movement. This distance-based end of movement definition was based on participant-specific measurements of disk centre, diameter, and height that were determined from calibration trials run before the experiment. Both the centre of the disks and the distance between the thumb and IRED fingers while participants touched the contact edges of the disk with these fingers were determined from these calibration trials.

In order to minimize the number of data points in which the participants touched the target disks, a boundary that extended from the centre of the disks out beyond the side and top of the disk was computed to reject sample points, on each trial, in which either the thumb or index-finger IRED crossed the boundary. This boundary was computed by adding 10 mm to half the measured diameter (the radius) for each object during the calibration trials and adding 17.5 mm (7.5 mm – half the height of the disk – plus 10 mm) to the measured height of the center of the disk. Since participants were directed to centre the distal pads of their thumb and index-finger on the sides of the objects, the definition for the height boundary seemed reasonable. Note further that we added 5 mm more to the object boundary than Himmelbach et al. (2006). This meant that the movements were terminated further away from the edge of the disk (and therefore relatively earlier in the reach) than they were in Himmelbach et al's analysis. The radius of the thumb and index-finger IRED to the centre of the disks was calculated for each sample frame on each trial. Thus, according to the additional distance-based definition designed to exclude the influence of finger-object contact, the movement was terminated when either the IRED on the thumb or the IRED on the index-finger fell below both the radius and height thresholds. For each trial, grip aperture during the MT_V period was normalized to 100 standard ‘percent bins’, and grip aperture during the MT_D period was normalized to 100 standard ‘percent bins’.

The principal 'landmark' dependent measures, RT, t_D, PGA, tPGA, MT_V, and MT_D were analyzed separately using a one-way repeated measures Analysis of Variance (rmANOVA) with disk size as the main factor with four levels – one for each disk diameter. Mauchley's Test of Sphericity was used to detect departures from sphericity that can inflate type I and type II errors. A liberal alpha criterion (0.25) was adopted for these tests. As such, Greenhouse-Geisser epsilon multipliers were applied to the degrees of freedom for any of the rmANOVAs in which Mauchley's test yielded an alpha at or below 0.25. The result of applying the Epsilon multipliers is reflected in the reported degrees of freedom for the effect in Section 2.2.4 (Results). Note that the base (i.e. sphericity assumed) degrees of freedom are 3 for the effect term (numerator) and 27 for the error term (denominator). All significant effects of disk size were followed with bivariate linear regressions of the respective dependent measure (in that measure's units) on disk diameter (in mm) to yield unstandardized regression coefficients for each participant (b_i) and to test if the group mean coefficient, $\bar{b}$, for that measure, differed significantly from zero using a paired t-test (per-contrast alpha set to 0.05). The b for a given participant, i, therefore, reflects the average change in the dependent measure (in its respective units) per incremental millimeter increase in disk size.

Additional rmANOVAs were conducted on time-normalized (i.e. resampled) grip aperture at each of 100 standardized percent bins (i.e. the interpolated points). To test for specific predicted linear effects of disk size on these profiles, a bivariate linear regression was performed at each normalized time-bin, *j*, for each participant separately and each $\bar{b}_j$ was tested against zero using a paired-samples t-test. The rmANOVA on the time-normalized grip aperture and tests of $\bar{b}$ across the percent time bins were treated as separate families of tests, and we applied Holm's step-down Bonferroni correction (Holm, 1979) to keep the per-family type I error at 0.05.

No effect of object size was expected for RT, t_D, or PGA for three reasons. First, these measures reflect what happens at or well before PGA has been reached. Thus, they would not be affected at all by the differences in the size of the target disks. Second, these measures are not normalized to movement time. Third, the participants were completely 'blind' with respect to disk size throughout all the experimental trials. In contrast, an effect of disk size was predicted for MT_V and MT_D because the participants were expected to adopt the strategy outlined in Section 2.1 (Introduction), in which they reached out in the same way from trial to trial until their thumb and index-finger contacted the target. As such, participants were expected to take longer to complete a grasp to the smaller disks than the larger ones. Furthermore, an effect of disk size was expected to emerge in the normalized grip aperture profiles when those profiles were standardized to these temporal measures (i.e. MT_V and MT_D).

2.2.4 Results

There was no effect of disk size on reaction time (RT: see Fig 2-3A) [$F(3,27) = 1.81$, $p = 0.17$], peak grip aperture [$F(2,16) = 1.56$, $p = 0.24$], time to peak grip aperture (tPGA: see Fig. 2-3A) [$F(3,27) = 0.12$, $p = 0.95$], or the time it took for the thumb IRED to reach the frontoplanar boundary 7 cm from the disk (t_D: see Fig 2-3B) [$F(1,10) = 1.17$, $p = 0.31$]. Disk size did, however, affect the velocity-based

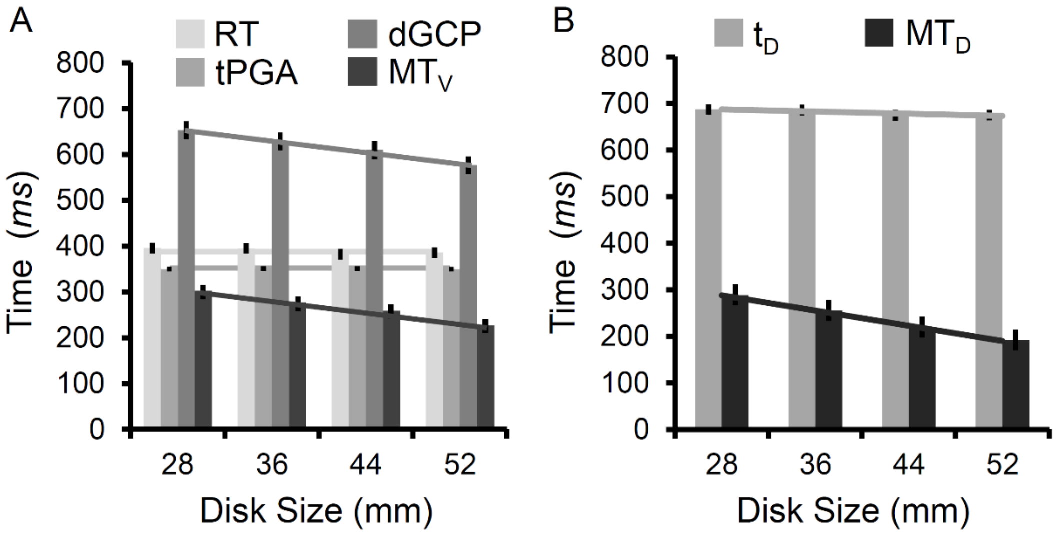

Figure 2-3. Experiment 1 results on the temporal measures. Panel A: Reaction time (RT), time to peak grip aperture (tPGA), and the time from PGA to the velocity-defined end of the movement (dGCP) and the velocity-defined movement time (MT_V) as a function of the diameter (size) of the target disk. Target size has no effect on RT and tPGA. In contrast, MT_V decreased linearly with increased target size. Panel B: The time from movement onset to the point at which the thumb crossed the fronto-parallel plane 7 cm from the target disk (t_D), and the time it took for the thumb or index-finger to travel from the fronto-parallel plane at 7 cm to a boundary 1 cm from the surface of the target disk (MT_D). Disk size had no effect on the t_D. Like MT_V, however, the MT_D decreased with increased disk size. Overall, the data suggest that the differences in movement times occurred after the hand achieved peak grip aperture, during the grip-closing phase of the grasp.

movement time (MT_V: see Fig. 2-3A) [$F(2,19) = 20.48$, $p < 2 \times 10^{-5}$; $\bar{b} = -3.1$ ms/mm increase in disk size, $p < 2 \times 10^{-4}$]. Not surprisingly, therefore, the time from tPGA to MT_V (the duration of the grip closing phase – dGCP) showed a significant effect of disk size [$F(2,19) = 21.62$, $p < 2 \times 10^{-5}$] (see Fig. 2-3A). Similarly, the time frame from the point at which the thumb reached the 7 cm mark to the point at which either the index-finger or thumb came within 10-mm of the side or top surface of the disk (MT_D: see Fig. 2-3B) showed an effect of object size [$F(1,10) = 48.92$, $p < 4 \times 10^{-5}$; $\bar{b} = -4.1$ ms/mm increase in disk size, $p < 5 \times 10^{-5}$]. Overall, MT_V, the dGCP, and the MT_D, increased linearly as a function of disk size.

When normalized for the entire velocity-defined movement time (MT_V), grip aperture was clearly affected by disk size (see Fig. 2-4A). Robust (above-

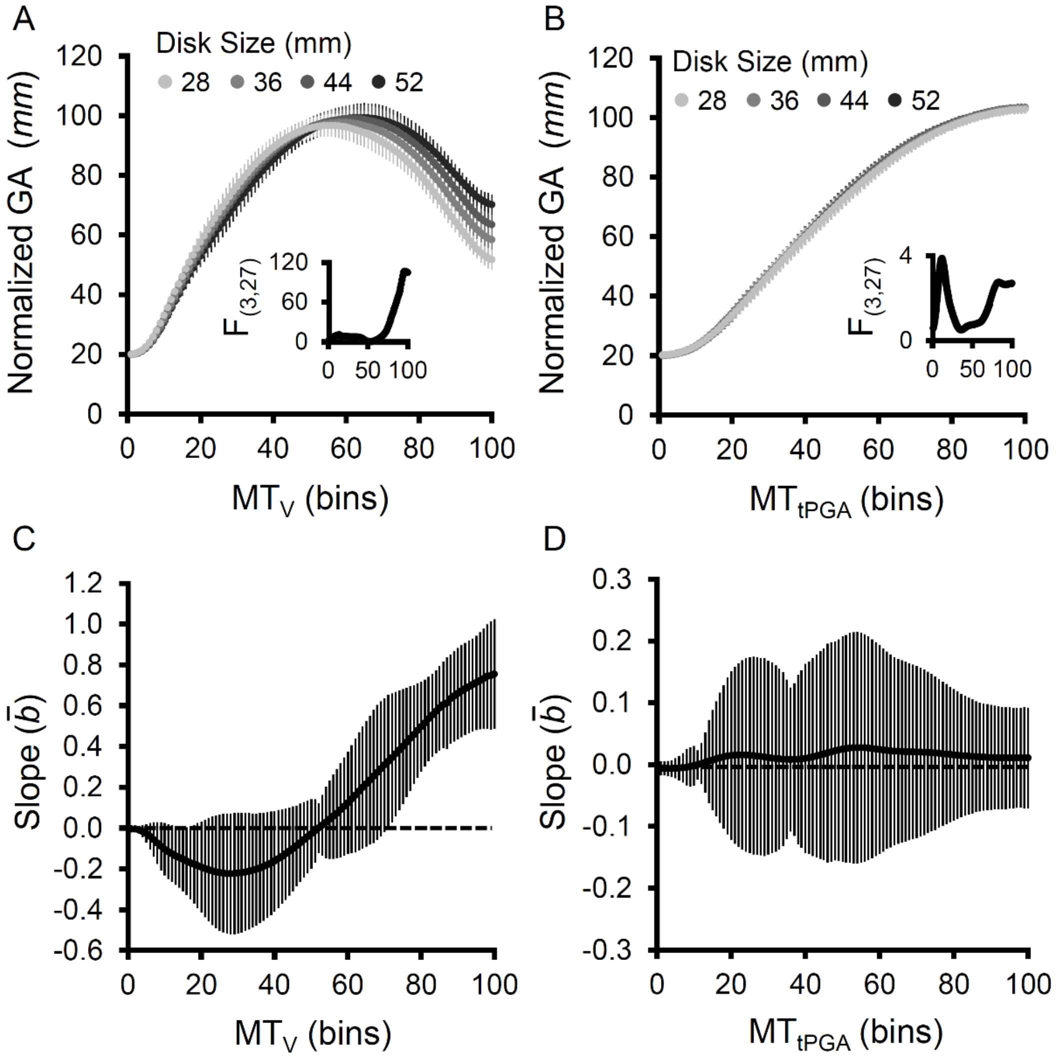

Figure 2-4. Experiment 1 results on normalized grip aperture and the slopes relating grip aperture to the unseen size of the cylinder when a velocity-defined movement time is used. Panel A: Normalized grip aperture (GA) as function of the

velocity-defined movement time (MT_{V}). These profiles are clearly positively correlated with the size of the target disk during the grip-closing phase of the grasp. The inset shows the F-statistic at each time bin from the repeated measures ANOVAs. Panel B: Grip aperture normalized over the time period from the beginning of the movement to the point at which PGA (tPGA) is achieved (MT_{tPGA}). Clearly, the normalized profiles sit on top of one another throughout this portion of the grasp (the grip-opening phase). No above-threshold differences were observed throughout this period. Panel C: This graph shows the mean regression coefficient ($\bar{b}$) relating MT_{V}-normalized GA to disk size at each percent-time bin. The closer fingers get to the disk, the sharper the relationship between grip aperture and disk size. Panel D: Not surprisingly, no linear relationships ($\bar{b}$, all $p > 0.05$) were observed over any of the percent time-bins when GA is normalized from the beginning of the movement up until tPGA. Note: All error bars reflect 95% confidence intervals extracted from the mean square error term from the rmANOVAs and have been corrected for 100 post-hoc comparisons.

threshold) effects of disk size occur from percent bins 7–39 and again from percent bins 66 onwards. As can be seen in Figure 2-4C, the $\bar{b}$ describing the linear relationship between normalized grip aperture and disk size are negative during the grip-opening phase of the grasp, approach zero as grip aperture peaks, and then becomes positively related to disk size throughout increases throughout the remainder of the grasp. Robust positive linear relationships between normalized grip aperture and disk size were found from percent bins 71 and onwards. Interestingly, these effects were not unique to the velocity-defined movement time that used a movement termination threshold of 50 mm/s. An identical analysis performed on normalized grip aperture over a time frame beginning at the start of the movement and ending when the thumb IRED fell below 100 mm/s yielded results that were remarkably similar to those found using the 50 mm/s velocity threshold. This additional analysis showed robust effects of disk size from percent bins 75 onwards and robust positive linear effects of disk size on grip aperture from bins 82 and onwards. In short, an effect of time-normalization on grip aperture was apparent for two commonly used thresholds for velocity-defined end of movement.

To help determine whether these spurious relationships between normalized grip aperture and disk size are driven entirely by differences in the duration of the grip-closing phase, we time-normalized grip aperture from the start of the movement to the point at which peak grip aperture (PGA) was achieved (tPGA). Since tPGA theoretically would have no relationship to disk size, the tPGA time frame itself should not introduce a spurious relationship between grip aperture and disk size during this part of the movement. As Fig 2-4C 4B indicates, this is exactly what happened: the grip aperture profiles clearly sit atop one another throughout this period of time. Not surprisingly, there was no evidence for a relationship between normalized grip aperture and disk size throughout this period of the grasp, including any linear effects (see Fig. 2-4C 4D).

Interestingly, time-normalizing grip aperture over the distance-based movement time (MT_D: see Fig. 2-5A) strengthens the effects of disk size on grip aperture. The rmANOVAs over this time frame yielded robust effects of disk size on normalized grip aperture from percent bin 43 and onwards and a specific positive linear effect on normalized grip aperture from percent time bin 50 and

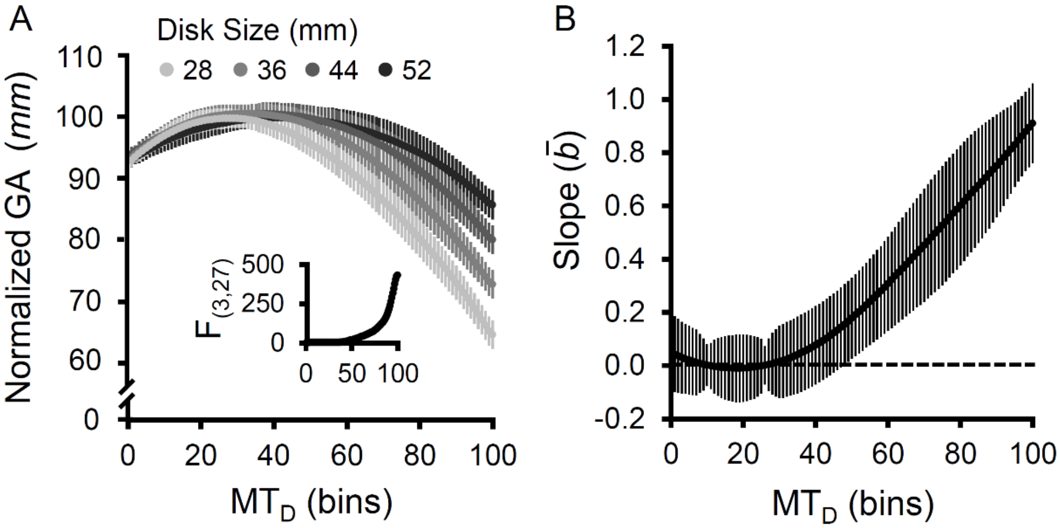

Figure 2-5. Experiment 1 results on normalized grip aperture and the slopes relating grip aperture to the unseen size of the cylinder when a distance-defined movement time is used. Panel A: Normalized GA as a function of the distance-based movement time (MT_D). Specifically, the MT_D spanned the time from the point at which the thumb crossed the fronto-parallel plane 7 cm from the target disk (t_D) to the point at which the thumb or index-finger fell within a boundary extending 10 mm out from the surface of the target disk. Again, grip aperture scales to the size of the target disk from 43% of this time window onwards. The inset shows the F-statistic at each time bin from the repeated measures ANOVAs. Panel B: The $\bar{b}$ reflects the average linear relationship between MT_D-normalized grip aperture and the size of the disk during the closing phase of the response.

onwards. As we argue later on, these effects of disk size on grip aperture are a product of time-normalization. Before this, however, we report the results of a second experiment in which previewed blocks, on some trials, are swapped for new ones of different sizes. The aim of this second experiment was to determine whether or not spurious grip scaling to unseen changes in target size would emerge following normalization even when participants were provided a visual preview of the initial target.

2.3 Experiment 2

2.3.1 Methods

2.3.1.1 Participants

Eight self-reported right-handed individuals (M = 29.6 years, SD = ±3.2 years) provided their informed consent and were compensated $10 for their participation.

2.3.1.2 Equipment, Procedures, and Design

The equipment, procedures, and design were similar to those used for Experiment 1. Thus, only those aspects that were modified are noted. Participants began and ended each trial with the tips of the thumb and index-finger of their right hand pinched together resting on the start button (rather than a Felt pad). The IREDs were attached in the same manner as experiment 1 but sampled at 300 Hz (rather than 400 Hz). The target objects were 6 cm in length, 1.5 cm in height, and varied only in their widths (1.5 cm to 6 cm in 1.5 cm increments). The targets were always positioned 16 cm along the frontoparallel plane directly to the left of the participant's start position (see Fig. 2-6A). Furthermore, the targets were

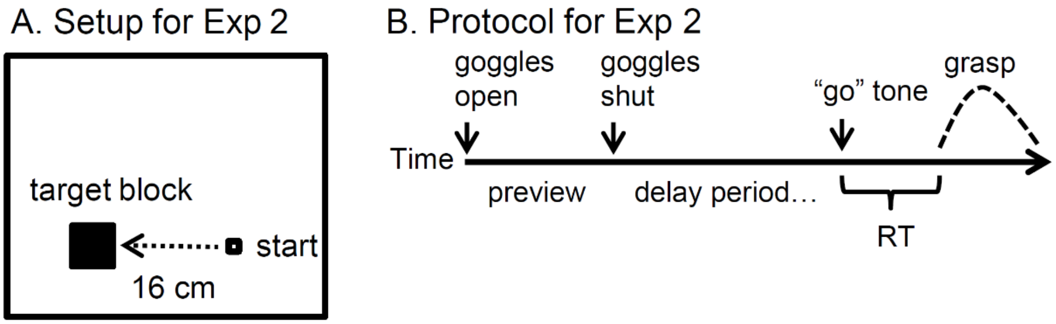

Figure 2-6. Setup and Protocol for Experiment 1. Panel A: Setup and trial protocol for Experiment 2. The dashed arrow indicates the direction in which the participant reached out to pick up the target. At the start of the trial, the goggles opened to permit a preview of the target and then closed for the remainder of the trial. Following a 3-s delay period at the end of the preview, an auditory "go" tone cued the participant to reach out blindly to grasp the target. On some trials, however, the experimenter replaced the previewed target for a new one, unbeknownst to the participant.

instrumented such that the time points at which the targets were touched were included in the kinematic data set. On a given trial, the lenses of the goggles were switched from their translucent state to their transparent one for 2 s. During this period, the participant could see the workspace which included their hand and one of four targets. Three seconds after the lenses returned to their translucent state, an auditory tone cued participants to reach out to pick up the target using a precision pincer grasp with the thumb and index-finger (see Fig. 2-6B). Before the experiment began, the experimenter explained the nature of the conditions to the participant. Specifically, participants were made aware of the fact that the smallest and largest targets (previewed on 15 trials each), would remain for the duration of the trial but that the two middle-sized targets (previewed on 45 trials each) could be swapped out for either the largest target (30 trials total, 15 trials each) or the smallest one (30 trials total, 15 trials each) during the 3-sec delay period or remain untouched for the duration of the trial (30 trials total, 15 trials each). The trial order, therefore, comprised of 120 trials which were pseudo-randomized. No condition occurred more than two times in succession, and no particular object was grasped more than three times successively. During the experiment, trials in which the experimenter noticed that the participant missed or fumbled the object were repeated at the end of the experiment.

Before the practice and experimental trials were administered, a series of calibration trials were administered to compute the thumb- and finger-contact planes of the blocks in 3 dimensional Cartesian coordinates. For these trials, the participants had a full view of the workspace and target. The participants were asked to place the tips of their thumb and index-finger on opposing sides of a given target such that their grip opposition axis spanned the width of the target at one end. They did not lift the block during these trials and were asked to keep their fingers as stable as possible for a 2-sec period of data collection. This procedure was repeated several times at the two ends of the smallest and largest targets. Finally, the participants were given five practice trials to familiarize them with the experimental protocol after which the experimental trials were administered. On two of these practice trials, the smallest and largest targets were presented – the conditions in which the target remained the same. The remaining three trials were a pseudo-random subset of the conditions in which the previewed target was swapped out for the largest or smallest object. Note that the participants in this experiment needed fewer practice trials because, unlike what happened in Experiment 1, they always saw the object at the beginning of the trial.

2.3.1.3 Data and Statistical Analysis

The raw positional data for each IRED was processed and analyzed offline using the same custom in-house software as described in Experiment 1. All dependent measures were computed in the same way as reported in Experiment 1, except the homologs of t_D and MT_D from Experiment 1. In Experiment 2 (and similar to Himmelbach et al. 2006) the t_D was the point at which the thumb reached a sagittal plane 7 cm from the target along the participant's frontal plane (see Fig 2B). Since the targets used in Experiment 2 were blocks rather than disks, the target boundaries used to define the end of the grasp for the MT_D differed from those used to define the MT_D in Experiment 1. For Experiment 2, the MT_D was based on participant-specific target-contact plane and height measurements that were derived from the calibration trials. These target-contact planes and height measurements were used to determine a boundary that extended 10-mm outward from the measured top and finger-contact sides of the targets. Thus, the MT_D was defined as the time from t_D to the point in time at which the target boundary was reached by the thumb or index-finger IRED. Using the time of finger-contact data recorded from the targets, the MT_D was confirmed to have successfully removed sample frames in which the fingers made contact with the target.

The statistical analysis of the results of Experiment 2 was broken down into two parts: In the first part of the analysis, we examined the conditions in which the participants knew that the previewed target would remain the same throughout the trial (the 15-mm and 60-mm previewed targets) and the conditions in which the participants knew that the previewed target (the 30-mm and 45-mm targets) could remain the same or be swapped out for either the smallest (15 mm) or largest target (60 mm). The principal landmark dependent measures, RT, t_D, PGA, tPGA, MT_V, and MT_D were analyzed separately with planned t-tests that we report in Section 2.3.2 (Results). We present the figures for some of these measures, in case the reader wishes to compare any pair of conditions by visual inspection. Thus, the error bars in these figures contain 95% confidence intervals that reflect this multiple-comparison post-hoc approach. To calculate these error bars, we ran a one-way rmANOVA for the conditions displayed and used the Greenhouse-Geisser corrected mean-square error term and a t-critical value with a per-contrast alpha criterion set at 0.003 (0.05/15) to reflect the maximum number of paired comparisons one can make with the displayed condition means of any given measure.

The second part of the analysis was focused on the normalized grip aperture profiles. Two one-way rmANOVAs were conducted on the time-normalized grip aperture at each of 100 standardized ‘percent’ bins (i.e. the interpolated points) for the conditions in which the two middle-sized targets were previewed. For these conditions, the participants were thought to adopt a strategy by which they opened their hand widely during their reach to accommodate the full range of possible target-size outcomes for these trials. That is, we predicted that they would opt for a more cautious grasp akin to what was observed in Experiment 1. Thus, for the same reasons we outlined in Section 2.1 (Introduction), linear effects of final target size were expected to emerge during the closing phase of the grasp. To test this prediction, a bivariate linear regression was performed at each normalized time-bin for each participant separately and the $\bar{b}$ for each bin was tested against zero using a paired-samples *t*-test. As in Experiment 1, the rmANOVA on the time-normalized grip aperture and the tests of $\bar{b}$ across the percent time bins were treated as separate families of tests, and we applied Holm's step-down Bonferroni correction (Holm, 1979) to keep the per-family type I error at 0.05.

2.3.2 Results

Reaction time did not differ significantly when either the 15-mm (M = 354 ms, SD = 104 ms) or the 60-mm targets (M = 349 ms, SD 114 ms) were previewed, [$t(7) = 0.41$, $p = 0.69$]. Similarly, RT did not significantly differ when either the 30-mm (M = 419 ms, SD = 107 ms) or the 45-mm (M = 413 ms, SD = 113 ms) targets (the two middle-sized targets) were previewed [$t(7) = .56$, $p = 0.59$]. Furthermore, as one would expect, the size of the substitute target had no influence on the RTs [30-mm target previewed: 15-mm target grasped (M = 428 ms, SD = 110 ms) vs. 60-mm target grasped (M = 433 ms, SD = 112 ms), $t(7) = 0.38$, $p = 0.72$; 45-mm target previewed: 15-mm target grasped (M = 414 ms, SD = 121 ms) vs. 60-mm target grasped (M = 418 ms, SD = 116 ms), t(7) = 0.38, p = 0.71]. Finally, because the participants knew that the two middle-sized blocks, when previewed, could be swapped out for the largest or the smallest target, it was not surprising to find that the pooled RT for these conditions was slightly but significantly longer than the pooled RTs for the large and small object [$t(7) = 3.1$, $p < 0.02$].

As expected, peak grip aperture (PGA: see Fig. 2-7A) was significantly greater when the 60-mm object was previewed than when the 15-mm object was previewed [$t(7) = 8.79$, $p < 5\times10^{-5}$]. Critically, the size of the substitute target had no effect on PGA when either the 30-mm target [$t(7) = 0.22$, $p = 0.83$] or 45-mm target [$t(7) = 1.43$, $p = 0.2$] was previewed. Curiously, however, even though

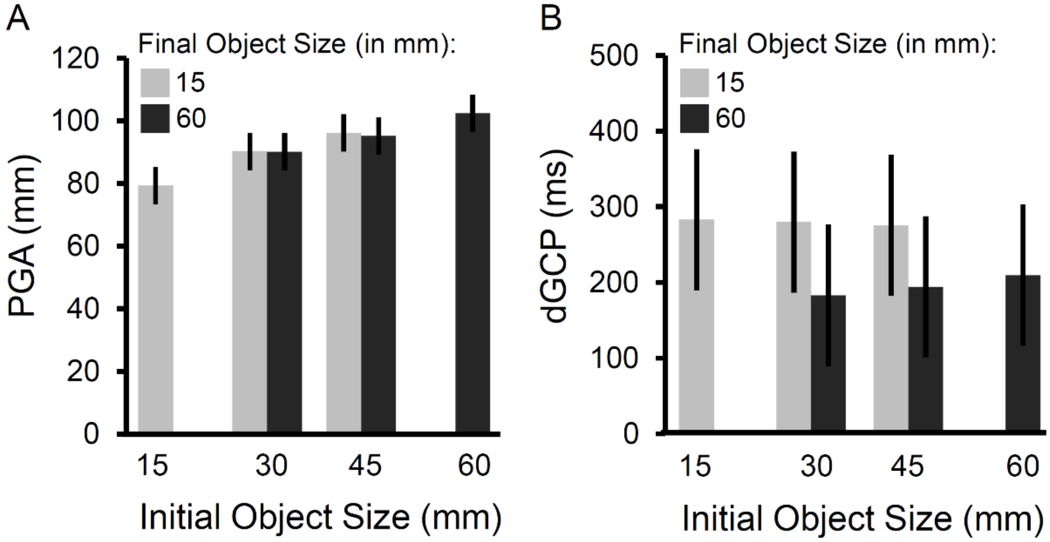

Figure 2-7. Peak grip aperture and the duration of the grip-closing phase as functions of the width (size) of the previewed (initial) and substitute (final) target. Panel A: Peak grip aperture (PGA) increased with the initial size of the target, but not with the size of the substitute target. Panel B: The duration of the grip-closing phase (dGCP) was shorter for the 15-mm target than for the 60-mm target when they were previewed and when they served as substitute targets. Note: For each dependent measure, all error bars reflect 95% confidence intervals extracted from the Greenhouse-Geisser adjusted (where warranted) mean square error term from the rmANOVA and are corrected for all post-hoc comparisons among the conditions.

participants knew that the 30-mm and 45-mm targets, when previewed, could be swapped out for the smallest or largest target or remain the same throughout the trial, PGA was larger when the 45-mm target was previewed than when the 30-mm target was previewed [$t(7) = 5.23$, $p < 2\times10^{-3}$]. This result is interesting, because it does not conform to what one would expect to observe if participants simply used an overarching ‘fail-safe’ strategy in which they opened their hand very wide for all trials in which they could not anticipate the size of the grasped target. Two possible explanations can accommodate this unexpected result. First, PGA (on these trials) could reflect a combination of both a visual memory (or visual ‘prime’) of the size of the previewed target and a ‘fail-safe’ strategy, because the strategic response included a margin of error that could accommodate a reduction in grip aperture for the size of the two previewed targets. Alternatively, this result could be due to the fact that the average size of the object grasped when the 45-mm object was previewed (M = 40 mm) was larger than the average size of the object grasped when the 30-mm object was previewed (M = 35 mm). This latter account suggests that participants specified their responses using a statistically optimal strategy. Overall, the PGA results are consistent with the view that PGA is a reliable indicator of the anticipated size of the goal object when information about the size of that object is available.

The participants took longer to achieve peak grip aperture (tPGA) when reaching out to pick up the previewed 60-mm target (M = 357 ms, SD = 45 ms) than when reaching out to pick up the previewed 15-mm target (M = 330 ms, SD = 41 ms) [$t(7) = 3.1$, $p < 0.02$], but again (and not surprisingly) the size of the substitute target did not influence tPGA when either the 30-mm target was previewed [15-mm target grasped (M = 347 ms, SD = 48 ms) vs. 60-mm target grasped (M = 340 ms, SD = 42 ms), t(7) = 1.11, *p* = 0.30] or the 45-mm target was previewed [15-mm target grasped (M = 350 ms, SD = 56 ms) vs. 60-mm target grasped (M = 357 ms, SD = 55 ms), *t*(7) = 2.0, *p* = 0.09]. Furthermore, the tPGA did not differ when either the 30-mm (M = 341 ms, SD = 45 ms) or the 45-mm target (M = 346 ms, SD = 49 ms) was previewed [*t*(7) = 1.08, *p* = 0.32].

The time from PGA to the velocity-based end of the movement (dGCP: see Fig. 2-7B) was longer when the 15-mm target was previewed than when the 60-mm target was previewed [$t(7) = 4.76$, $p < 3\times10^{-3}$]. In contrast, because the participants knew that the 30 and 45-mm targets, when previewed, could either be swapped out for different target or remain the same, the size of these previewed targets did not influence the dGCP [*t*(7) = 0.54, *p* = 0.61]. As predicted, however, the dGCP was significantly longer when the substitute target was 15 mm than when it was 60 mm when either the 30-mm target [$t(7) = 7.33$, $p < 2\times10^{-4}$] or the 45-mm target was previewed [$t(7) = 5.35$, $p < 2\times10^{-3}$].

The participants' velocity-defined movement times (MT_V: see Fig. 2-8A) were longer when the 15-mm target was previewed than when the 60-mm target was previewed [*t*(7) = 2.79, *p* < 0.03]. In contrast, the size of the previewed 30-

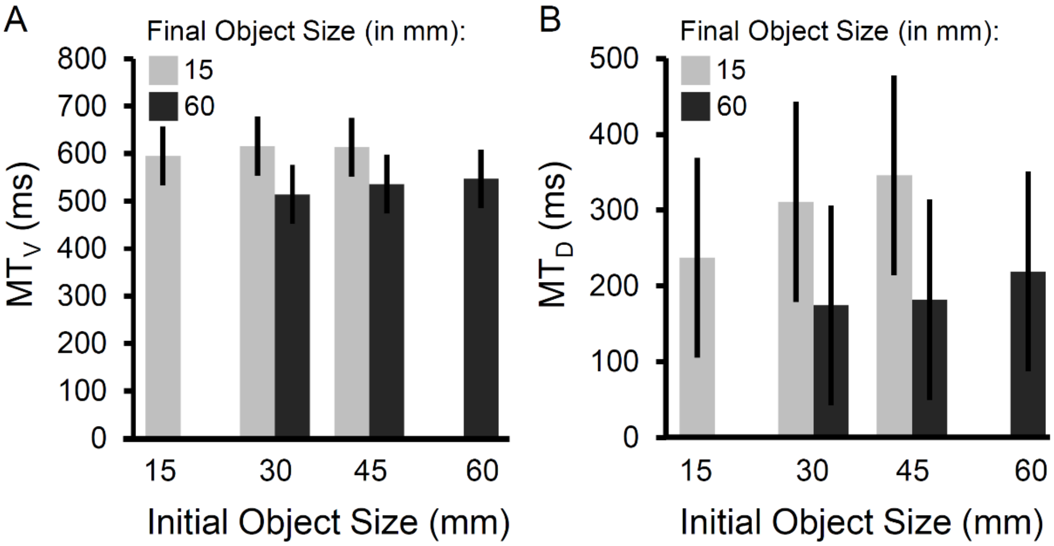

Figure 2-8. Movement times defined using velocity and distance. Panel A: The velocity-defined movement time (MT_V). MT_V was driven by the width (size) of the target that was ultimately grasped, rather than the previewed size of the target. The smaller the target, the longer the grasp movement lasted. Panel B: The time it took for the thumb or index-finger to travel from the fronto-parallel plane 7 cm from the target to a boundary 10 mm from the surface of the target (MT_D). As was seen with MT_V, the MT_D, was influenced by the size of the target that was grasped and not the size of the previewed middle-sized targets. Note: For each dependent measure, all error bars reflect 95% confidence intervals extracted from the Greenhouse-Geisser adjusted (where warranted) mean square error term from the rmANOVA and are corrected for all post-hoc comparisons among the conditions.

mm or 45-mm target did not influence MT_V, [$t(7) = 0.28$, $p = 0.78$]. However, as predicted, MT_V was shorter for the 60-mm substitute target than the 15-mm substitute target following a preview of either the 30-mm target [$t(7) = 5.95$, $p < 6\times10^{-4}$] or the 45-mm target [$t(7) = 6.07$, $p < 6\times10^{-4}$]. Overall, MT_V was driven largely by the size of the target that was ultimately grasped – even when they did not know how large that target would be. Furthermore, given the null findings for tPGA and the positive findings for dGCP, much (if not all) of the effect of the size of the substitute target on MT_V seems to be a direct result of the effect on dGCP. In short, differences in the time taken for the thumb and pointer finger to close down on the opposing sides of unseen small and large substitute targets translated into similar differences in the overall MT_V.

The time it took for the thumb to come within 7 cm of the target (t_D) did not depend on the size of the previewed 15-mm (M = 227 ms, SD = 30 ms) or 60-mm target (M = 228 ms, SD = 32 ms) [$t(7) = 0.14$, $p = 0.89$] or the size of the previewed middle-sized targets [30-mm target previewed (M = 225 ms, SD = 31 ms) vs. 45-mm target previewed (M = 217 ms, SD = 32 ms), $t(7) = 0.40$, $p = 0.7$]. Not surprisingly, the size of the substitute target had no effect on the t_D when either the 30-mm [15-mm substitute target (M = 231 ms, SD = 34 ms) vs. 60-mm substitute target (M = 226 ms, SD = 34 ms), $t(7) = 1.49$, $p = 0.18$] or the 45-mm target [15-mm substitute target (M = 230 ms, SD = 40 ms) vs. 60-mm substitute target (M = 231 ms, SD = 39 ms), $t(7) = 0.02$, $p = 0.98$] were previewed.

The time from the point at which the thumb IRED reached 7 cm from the target to the point at which either thumb or index-finger IRED crossed a boundary 10 mm from the target's surface (MT_D: see Fig. 2-8B) did not differ between the 15-mm or 60-mm target when they were previewed [$t(7) = 1.31$, $p = 0.23$]. As predicted, however, the MT_D was longer for the 15-mm substitute target than it was for the 60-mm substitute target when either the 30-mm target [$t(7) = 5.31$, $p < 2\times10^{-3}$] or the 45-mm target [$t(7) = 4.72$, $p < 3\times10^{-3}$] was previewed. The size of the previewed 30- or 45-mm target did not influence the MT_D [$t(7) = 0.38$, $p = 0.71$]. Thus, like MT_V, the MT_D was driven largely by the size of the target that was grasped – even when the size of the target was unknown.

When normalized throughout the velocity-defined movement time ($\mathrm{MT_V}$), grip aperture is clearly affected by the size of the substitute target when either the 30-mm target is previewed (see Fig. 2-9A) or the 45-mm target is previewed (see Fig. 2-9B). When the 30-mm target was previewed, robust (above-threshold) effects

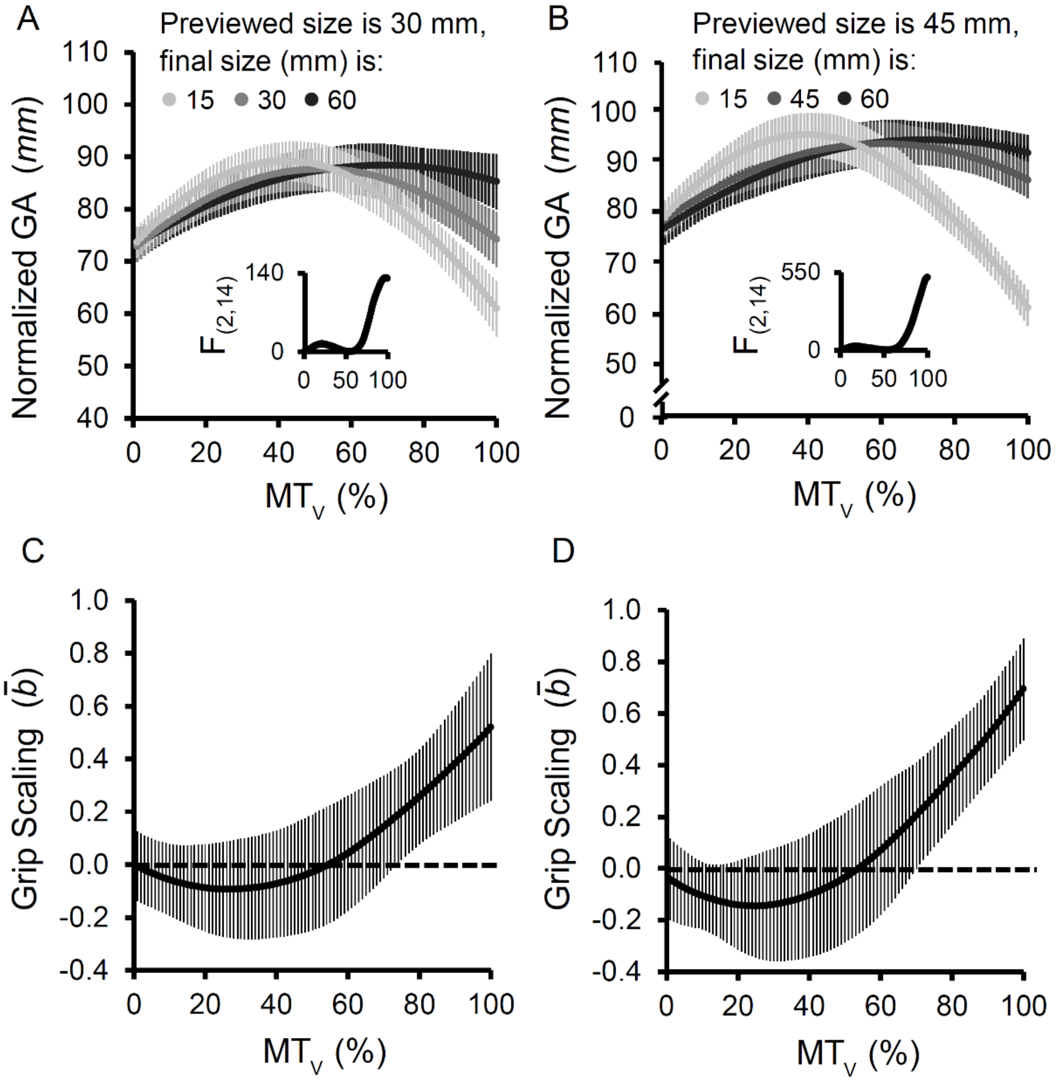

Figure 2-9. Experiment 2 results on normalized grip aperture and the slopes relating grip aperture to the unseen size of the cylinder when a velocity-defined movement time is used. Panel A: Normalized grip aperture (GA) as function of the velocity-defined movement time ($\mathrm{MT_V}$) for the conditions in which the 30-mm target was previewed. Similar to Experiment 1, the profiles are clearly correlated

with the width (size) of the grasped target during the grip-closing phase of the grasp. The inset shows the F-statistic at each time bin from the repeated measures ANOVAs. Panel B: Normalized GA as a function of MT_V for the conditions in which the 45-mm target was previewed. Again, during the grip closing phase of the response, grip aperture scaled to the size of the target. The inset shows the F-statistic at each time bin from the repeated measures ANOVAs. Panels C and D: These graphs shows the mean regression coefficient ($\bar{b}$) relating MT_V-normalized GA to final target size at each percent-time bin when the 30-mm target (Panel C) and when the 45-mm target (Panel D) was previewed. The closer fingers get to the target, the sharper the relationship between grip aperture and the size of the substitute target. Note: All error bars reflect 95% confidence intervals extracted from the mean square error term from the rmANOVAs and have been corrected for 100 post-hoc comparisons.

of the unseen size of the substitute (i.e. grasped) target occur from percent-time bins 16–43 and again from bins 70 onwards. When the 45-mm target was previewed, robust effects of the substitute target occur from bins 31–51 and again from 74 onwards. The average linear relationship between normalized grip aperture and target size, $\bar{b}$, yielded a pattern of results similar to those observed in Experiment 1. Specifically, the relationship is negative during the grip-opening phase of the grasp, approaches zero as grip aperture peaks, and then becomes positively related to target size throughout the remainder of the grasp. During the grip-opening phase of the grasp, robust negative linear relationships between normalized grip aperture and target size were found from percent bins 24–36 when the 30-mm target was previewed and from bins 25–39 when the 45-mm target was previewed. In contrast, robust positive linear relationships between normalized grip aperture and target size were found from percent bins 4 and onwards when the 30-mm target was previewed and from bins 80 and onwards when the 45-mm target was previewed.

Again, these spurious effects of target size were not unique to the 50 mm/s velocity-defined movement time. An identical test of target size performed on normalized grip aperture over a time frame beginning at the start of the movement and ending when the thumb IRED fell below 100 mm/s yielded results that were remarkably similar to those found using the 50 mm/s velocity threshold to end the movement. This additional analysis showed robust effects of the size of the unseen substitute target from percent time-bins 75 and onwards when the 30-mm target was previewed. When the 45-mm target was previewed, robust effects of the size of the unseen substitute target were observed from bins 9–65 and again from bins 75 and onwards.

Similar to Experiment 1, we normalized grip aperture over a time frame beginning at the start of the movement and ending at the point at which peak grip aperture (PGA) was achieved (tPGA). Again, as was the case in Experiment 1, the grip aperture profiles sit atop one another throughout this period of time, and, not surprisingly, there was no evidence for a relationship between normalized grip aperture and target size throughout this period of the grasp, including any linear effects.

Time-normalizing grip aperture over the distance-based movement time (MT_D: see Fig. 2-9A and C) strengthened the spurious effects of target size on grip

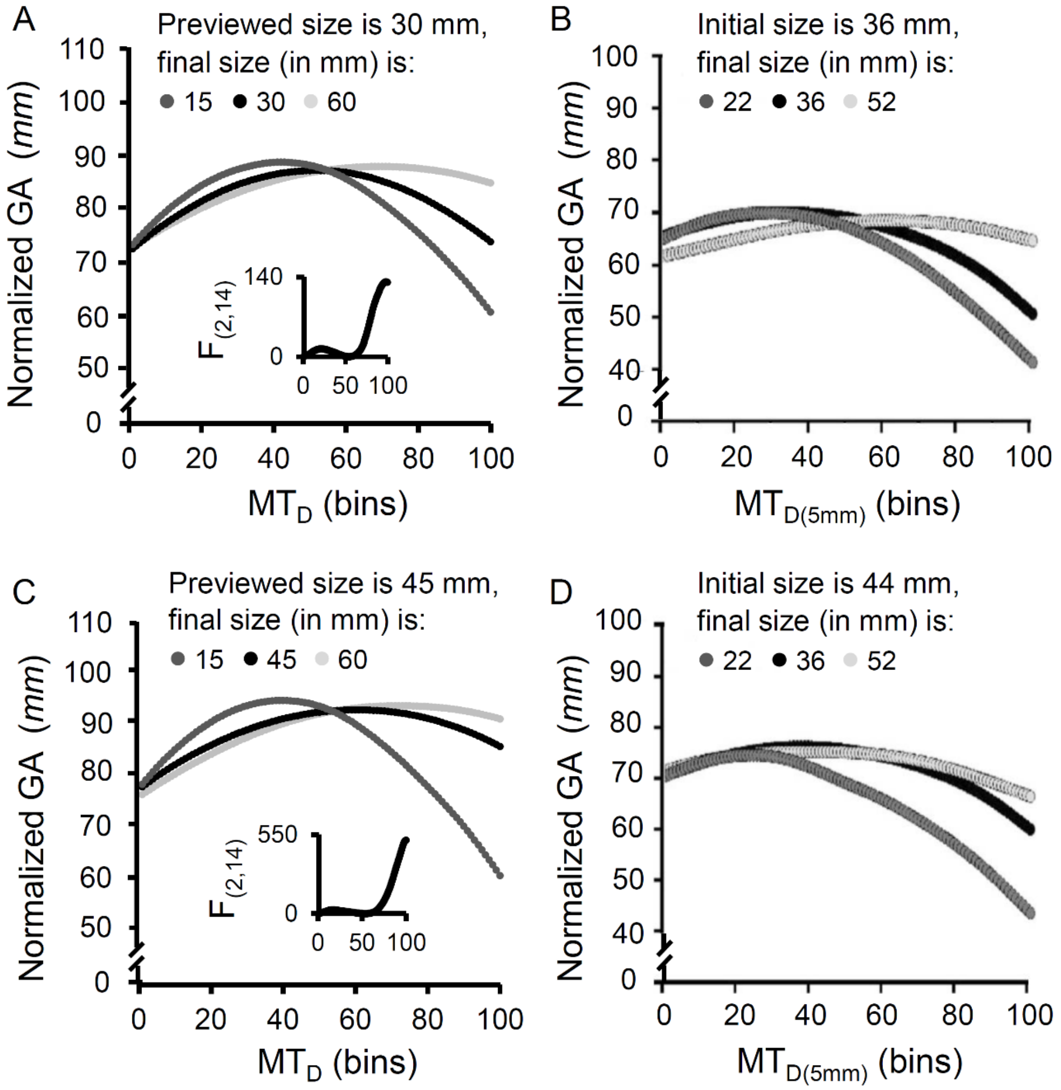

Figure 2-10. Experiment 2 results on normalized grip aperture and the slopes relating grip aperture to the unseen size of the cylinder when a distance-defined movement time is used. Panel A: Normalized grip aperture (GA) as function of the distance-based movement time (MT$_D$) for the conditions in which the 30-mm target was previewed. Similar to Experiment 1, the profiles are clearly correlated with the final width (size) of the target during the grip-closing phase of the grasp. The inset shows the F-statistic at each time bin from the repeated measures ANOVAs. Panel B: For comparison, the normalized GA profiles from Himmelbach et al. (2006). Note that Himmelbach used a distance-based movement time cut-off that was 5-mm closer to their target disks than ours was to the target blocks. Panel C: Normalized grip aperture (GA) as function of the

distance-based movement time (MT_D) for the conditions in which the 45-mm target was previewed. Again, during the grip closing phase of the response, grip aperture scaled to the size of the target. The inset shows the F-statistic at each time bin from the repeated measures ANOVAs. Panel D: For comparison, the normalized GA profiles from Himmelbach et al.

aperture observed when the velocity-based movement time was used. Note the similarity of these profiles to those obtained by Himmelbach et al. (2006) (see Fig. 2-9B and C). When the 30-mm target was previewed, the rmANOVAs over this time frame yielded robust effects of the size of the grasped target on normalized grip aperture from percent time bins 17–22 and again from bin 69 onwards. Tests of the $\bar{b}$ over this time frame yielded positive linear effects from bin 71 onwards. When the 45-mm target was previewed, robust effects of the size of the grasped target were observed from bins 7–36 and again from bin 64 onwards. Tests of the $\bar{b}$ over this time frame yielded negative linear effects from bins 6–38 and positive linear effects again from bin 69 onwards.

2.4 Discussion and Conclusions

Here, we report two experiments which illustrate how time-normalizing visuomotor data can lead to spurious conclusions. In Experiment 1, we asked ten blindfolded individuals to reach out to lift target disks of different sizes. Thus, motor output could not be influenced by online visual input about the target in this experiment. In Experiment 2, we asked eight blindfolded individuals to reach out to lift target blocks of different sizes following a brief preview of the target that was terminated 3 s before the participants were cued to respond. Thus, in this experiment, visual input about the target was available on each trial but this information had to be maintained for 3 s (or stored for subsequent retrieval 3 s later) when the response was cued. Moreover, in this experiment the two middle-sized targets could be swapped out for the largest or the smallest target size unbeknownst to the participant. Thus, for these particular conditions (and all of the conditions of Experiment 1), motor control could not exploit real-time visual information in either a feedforward or feedback manner. Rather, participants had to plan their grasp to deal with the possibility that they could encounter any one of a number of different target sizes at the end of the movement.

In our experiments, blindfolded participants took longer to complete their movements to small targets than for larger ones. In fact, because the participants could not predict which target would be present at the end of the grasp, the movement time on a particular trial was a function of the size of the target encountered on that trial. In short, they took longer to complete a movement to a small target than to a large one. This relationship between movement time and target size was reflected in the normalized measures of grip aperture, which showed apparent target-size dependent changes in grip aperture early on in the movement and later on during the grip-closing phase of the grasp. In other words, the differences in movement time across different sized-targets when combined with the normalization procedure led to a spurious correlation between grip scaling and target size that strengthened as the differences in movement time increased. Not surprisingly, a classic measure of grip scaling, the peak amplitude of the grip aperture before contact with the target, was completely uncorrelated with the size of the target that was ultimately grasped both in Experiment 1 and in those trials of Experiment 2 in which the targets were switched. Finally, it should be noted that time-normalization of the grip aperture profile over the entire movement can also result in significant but entirely spurious differences in the early phases of the grasp. Time-normalization creates a situation in which events that unfold towards the end of the movement will come to influence measures at the beginning of the movement. These early differences in the grasp profile that emerge following a movement-time normalization could be as prone to misinterpretation as the later differences in the grasp profile.

The demonstration of apparent grip scaling in blindfolded individuals calls into question the conclusions of previous investigations that made use of time-normalized data to extract the measurements of interest – particularly when these conclusions rest on the emergence of various effects or relationships towards the later stages of the movement. Take the case of Himmelbach et al. (2006), which we discussed in Section 2.1 (Introduction). The findings of their experiment appeared to challenge the interpretation of optic ataxia as a deficit in the ‘online’ control of target-directed movements (e.g., Glover, 2003; Pisella et al., 2000; Rossetti, Pisella, & Vighetto, 2003). Himmelbach et al. duly noted that although misreaching to stationary (Jakobson, Archibald, Carey, & Goodale, 1991) and ‘jumping’ targets in pointing (Pisella et al., 2000) and grasping (Gréa et al., 2002) tasks are well-documented deficits of optic ataxia, adjustments in grip aperture following changes in target size during grasping have not been investigated.

Himmelbach et al. further recognized that one could not be certain whether deficits in online adjustments in reach trajectories would generalize to deficits in adjusting grip aperture following changes in target size. Thus, they devised a novel experiment in which the size of some of the targets was increased or decreased when optic ataxic patient IG's thumb was 7 cm from the target. Their results seemed to indicate that IG, who is demonstrably compromised in target-directed pointing tasks, was nevertheless capable of adjusting her grip aperture to changes in target size in their experiment. Himmelbach et al. based their conclusion on the fact that IG's normalized grip aperture during the later phase of the movement reflected the new target size rather than its initial size. However, because it took longer to complete the movement to small targets than to large ones, the time-normalization procedure could have created the same spurious relationship between grip aperture and object size that we found in our blindfolded participants. It is not clear, therefore, whether Himmelbach et al., (2006) have sufficient evidence to conclude that posterior parietal lesions that lead to optic ataxia spare the grasp components of prehension while affecting the reaching and pointing aspects of limb control. Indeed, the remarkably similarity between the time-normalized grip profiles we observed in Experiment 2 and those of IG suggest that she was using the same sort of strategy as the blind-folded participants. Of course, it might be the case that IG does show some residual ability to scale her grasp in central vision – but the results of Himmelbach et al. cannot be used to support this conjecture.

Despite the wide use of normalizing procedures on movement trajectories in kinematic investigations of motor control, there is little discussion in the literature about what these procedures entail and what effects normalizing might have on variables of interest. The present experiments clearly highlight a deceptively simple problem: when time varies with an independent variable and is used to standardize a dependent measure of spatial position, comparisons of those measures at equivalent points in standardized time are comparisons of spatial position at different points in raw time. The same can be said for phase planes, if distance or displacement is correlated with grip size, for example. At the very least, investigators should pause before time-normalizing their data, particularly when the variable of interest is correlated with time.

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Chapter 3

3 DF's visual brain in action: The role of tactile cues

Patient DF, an extensively-tested woman with visual form agnosia from ventral-stream damage, is able to scale her grip aperture to match a goal object's geometry when reaching out to pick it up, despite being unable to explicitly distinguish amongst objects on the basis of their different geometry. Using evidence from a range of sources, including functional MRI, we have proposed that she does this through a functionally intact visuomotor system housed within the dorsal stream of the posterior parietal lobe. More recently, however, Schenk (2012a,b) has argued that DF performs well in visually guided grasping, not through spared and functioning visuomotor networks in the dorsal stream, but because haptic feedback about the locations of the edges of the target is available to calibrate her grasps in such tasks, whereas it is not available in standard visual perceptual tasks. We have tested this 'calibration hypothesis' directly, by presenting DF with a grasping task in which the visible width of a target varied from trial to trial while its actual width remained the same. According to the calibration hypothesis, because haptic feedback was completely uninformative, DF should be unable to calibrate her grip aperture in this task. Contrary to this prediction, we found that DF continued to scale her grip aperture to the visual width of the targets and did so well within the range of healthy controls. We also found that DF's inability to distinguish shapes perceptually is not improved by providing haptic feedback. These findings strengthen the notion that DF's spared visuomotor abilities are largely driven by visual feedforward processing of the geometric properties of the target. Crucially, these findings also indicate that simple terminal tactile contact with an object is needed for the visuomotor dorsal stream to be engaged, and accordingly enables DF to execute visually guided grasping successfully. This need for actions to have a tangible endpoint provides an important new modification of the Two Visual Systems theory.

3.1 Introduction

3.1.1 The Two Visual Systems Hypothesis and Patient DF

Human beings and other primates are capable of reaching out and grasping objects with great skill and precision, and vision plays an indispensable role in this ability. Marc Jeannerod and his colleagues in Lyon pioneered the study of visuomotor control in both humans and non-human primates, and he wrote the first comprehensive account of visuomotor neuroscience (Jeannerod, 1988). Subsequently, Jeannerod was one of the first to argue that “visuomotor coordination relies on a specific mode of visual input processing which is different from that giving rise to visual perception” (Jeannerod & Rossetti, 1993). At about the same time, Goodale and Milner (1992) had independently proposed a similar thesis, identifying the specific cortical visual pathways in the cerebral cortex that might underlie these separable visual functions. According to their account, the visual control of action is mediated by pathways that arise in early visual areas and project to the posterior parietal cortex, whereas visual perception is mediated by pathways that also arise in early visual areas but project to the inferotemporal cortex. Although the “two-visual systems” (TVS) hypothesis is strongly supported by a range of evidence from neurobehavioural and neurophysiological studies of human and non-human primates as well as neuroimaging (for reviews, see Goodale, 2011; Milner & Goodale, 2006, 2008), the key observation that led to the genesis of the core concepts of the TVS hypothesis was the striking dissociation between perception and action observed in patient DF (Goodale, Milner, Jakobson, & Carey, 1991).

DF, who was a young woman at the time that the first studies were carried out, had developed a profound visual form agnosia as a consequence of carbon monoxide poisoning. She could no longer recognize objects on the basis of their form, and could not discriminate between even simple geometric shapes, such as a triangle and circle. In addition, she had great difficulty reporting the orientation of objects. Remarkably, however, she was still able to recognize objects on the basis of their diagnostic colour and other surface features (Humphrey, Goodale, Jakobson, & Servos, 1994; Milner et al., 1991; Cavina-Pratesi, Kentridge, Heywood, & Milner, 2010a,b). She could also recognize objects from touch. In short, DF appeared to have a specific deficit in form vision.

Those who were aware of the severity of her visual disorder, however, were struck by how well she was able to interact with objects, both familiar and unfamiliar, and to navigate through cluttered rooms and environments in her daily life. For example, even though she could not report the orientation of a pencil held in front of her by the examiner, when she reached out to grasp the pencil, she smoothly oriented her open hand in flight so that she grasped it properly (Goodale

& Milner, 2013). It was these informal observations that led to more formal testing of her visuomotor abilities.

3.1.2 Patient DF’s Action-Perception Dissociations in Orientation and Form

Despite her gross deficits in visual form perception, DF could ‘post’ a hand-held wooden card into a rectangular slot that varied in orientation from trial to trial. Not surprisingly, however, given her demonstrated deficit in form vision, DF could not report the orientation of the slot by rotating the card in place without posting (Goodale et al., 1991; Milner et al., 1991). It has also been demonstrated many times that DF is able to reliably scale her grip aperture in anticipation of the dimensions of a goal object she is trying to pick up with her forefinger and thumb, even though she is unable to indicate the width of the object by opening her forefinger and thumb a matching amount (for review, see Milner & Goodale, 2006). Finally, when DF was asked to pick up irregular smooth-shaped objects (that resemble flattened pebbles), she selected finger-contact points on the surface of the object that minimized the likelihood that the object would slip from her fingertips when she applied the requisite grip and lift forces. In contrast, when she was asked to indicate whether pairs of these stimuli were the same or different, she performed at chance levels (Goodale et al., 1994b). Thus, these early studies indicated that DF retained the ability to process object orientation, width, and overall form when the task involved skilled goal-directed action, but not when the task required an explicit declarative judgment that reflected her visual perception of those object features.

Structural MR imaging of DF`s brain at the time of the initial testing revealed diffuse damage throughout her brain, as is often the case with carbon monoxide poisoning. In addition, however, there was clear evidence of bilateral lesions in the ventrolateral regions of the occipital lobe in areas that are part of the human ventral stream (Milner et al., 1991). More recent structural and functional MRI evidence points clearly to a destroyed shape perception system within the ventral stream of her occipitotemporal cortex (Bridge et al., 2013; James, Culham, Humphrey, Milner, & Goodale, 2003). Although there was some indication of damage and bilateral atrophy in the region of the occipitoparietal sulcus, her dorsal stream appeared to be largely intact.

Just prior to some of the early experiments performed with DF, Marc Jeannerod and his colleagues had been carrying out pioneering studies revealing visuomotor deficits of patients following unilateral and bilateral damage to the posterior parietal cortex (Jeannerod, 1986; Perenin & Vighetto, 1988). This work was replicated by Jakobson, Archibald, Carey, and Goodale (1991), whose patient with bilateral lesions to the posterior parietal cortex showed reaching and hand pre-shaping impairments when asked to pick up centrally located targets. These findings, along with new discoveries on the single-unit physiology of primate parietal cortex (Taira et al., 1990) led Goodale and Milner (1992) to suggest that DF’s form vision deficits arose because of damage to the ventral stream and that her intact visually guided grasping was mediated by the intact circuitry in the dorsal stream. Since then, this formulation of the division of labour between the ventral and dorsal streams of visual processing has continued to provide a parsimonious and overarching theoretical framework for understanding the processing of visual signals in the primate cerebral cortex (for review, see Westwood & Goodale, 2011; Goodale, 2011).

3.1.3 DF’s Delayed and Pantomimed Grasps

Although DF’s ability to scale her grasp to the size and shape of a goal object is remarkable, it does have some revealing limitations. For example, if a 2-s delay is interposed between showing an object to DF and instructing her to reach out to grasp it in the dark, all evidence of grip scaling disappears (see Goodale, Jakobson, & Keillor, 1994b). In normal subjects, grip size still correlates well with object width, even for delays as long as 30 s. This failure in DF cannot be attributed to a general impairment in short-term memory since DF has only a mild impairment when tested on more 'cognitive' (auditory-verbal) tasks (Milner et al. 1991). It is important to note that even the grasping movements made by normal subjects in the delay condition look quite different from those directed at objects that are physically present. In short, the normal subjects appear to be 'pantomiming' their grasps in the delay conditions, and in doing so rely upon a stored perceptual representation of the object they have just seen. It has been argued that DF's problem in the delay condition arises from the fact that she cannot use a stored percept of the object to drive a pantomimed grasping movement because she never 'perceived' the goal object in the first place (Goodale et al., 1994b).

Interestingly, when DF pantomimes a grasp by reaching beside an object, her grip scaling is much better than it is following a delay, although it does appear to be more variable than her grip-scaling during object-directed grasping (Goodale et al., 1994b). Also, like normal subjects, she does not open her hand as wide in this condition as she does in object-directed grasping. It seems that for DF to show grasping that is most comparable to that shown by neurologically intact individuals, she has to direct her hand towards a visible object.

3.1.4 Tactile Contributions to Grasping in DF

In an interesting recent study, Schenk (2012a) has challenged Goodale and Milner's (1992) interpretation of DF's spared visuomotor abilities. Schenk (2012a) argues that DF's intact visually guided grasping depends on additional haptic sensory information from grasping the goal object – information not available to her when she gives verbal reports or manual estimations of object size. In short, DF's spared grip scaling to target size may not be primarily attributable to intact visual coding of object width within her visuomotor dorsal stream, as Goodale and Milner have supposed. To examine this hypothesis, Schenk re-tested DF on a series of grasping tasks in which three cylinders of different diameters were presented by means of an ingenious mirror arrangement modified from a similar setup used by Bingham, Coats, and Mon-Williams (2007), so that the cylinder visible to DF could be dissociated from the one that she grasped. In different tasks, the cylinder that she grasped either coincided spatially with the one she viewed in the mirror, was present at a different location altogether, or was completely absent. Schenk found that although DF performed well on a ‘standard’ task of grasping (i.e. when the viewed and grasped objects coincided in space) – confirming Goodale et al.’s (1991) original observation – she performed very poorly on a comparable task where there was no actual hand contact with the target cylinder. In this latter task, there was no cylinder present in the apparent location of the cylinder viewed in the mirror. Schenk (2012a) argued that DF’s apparent ability to calibrate her grip in the standard condition does not reflect intact visuomotor control but instead is due to haptic feedback, which she uses “to compensate for her deficit in size-perception” (p. 2013).

It could be the case that haptic feedback about object size influences grip scaling by means of an error signal that reflects the difference between the “expected” and the “observed” outcome of the grasp, in a manner similar to what has been proposed for the calibration of grip and load forces (Johansson & Flanagan, 2009). In the case of grasping, such a signal could be used to calibrate the relationship between vision and motor output over a series of trials. A small error would maintain the status quo, whereas a larger error signal would result in a recalibration of the grasp. The signal itself could be derived from time-to-contact. In other words, the visuomotor system may compare the anticipated time of finger contact with the target with the actual time of contact, and then use the resultant discrepancy to update the programming of subsequent grasps. Indeed, Safstrom and Edin (2008) have argued that such updating is part of normal visuomotor control. Alternatively, as Schenk (2012a,b) suggests, the effects might depend on grasp-point updating. He argues that DF’s grip scaling relies on the integration of visual and haptic feedback about the finger and thumb endpoints that are, presumably, applied in a predictive (i.e. feedforward) manner on subsequent trials (for a discussion of Schenk's interpretation and related issues, see Milner, Ganel, & Goodale, 2012; Whitwell & Buckingham, 2013).

Although haptic feedback is almost certainly important, there may be a simpler explanation for why DF fails in the task in which she is required to reach out and grasp an object that is never tangibly present. We propose that visuomotor systems in the dorsal stream become properly engaged only when the hand can make tactile contact with the goal object (or a proxy for the goal object such as another object of different size) at the end of each grasping movement. In Schenk's (2012a) 'no haptic feedback' task, DF's fingers would simply have closed on thin air when they reached the apparent location of the object. The movement, therefore, would have become a kind of 'pantomimed' act, for which perceptual mechanisms in the ventral stream would need to be engaged along with visuomotor mechanisms in the dorsal stream (Milner et al., 2012). Because of her ventral stream damage, DF is unable to pantomime in delayed grasping tasks (Goodale et al., 1994a) or give explicit manual estimations of the width of an object in plain view (Goodale et al., 1991; Goodale et al. 1994a). But as we discussed earlier, if DF is required to reach out to a location just beside the goal object, she continues to show partial grip scaling (Goodale et al. 1994). In that task, of course, her fingers would have made contact with the table – and, as we know from work by Westwood, Danckert, Servos, and Goodale (2002), DF shows good evidence for grip scaling when she reaches out to 'grasp' 2-D objects presented on a flat display on a table. Although the tactile information in these tasks was derived simply from touching the surface of the table, it appeared to be enough for her dorsal stream to keep her grip tuned to the size of the goal objects. In other words, although tactile feedback might be critical for DF to show accurate grasping, we propose that the feedback need not be “haptic” and indeed need carry no information other than of the termination of the action.

3.1.5 The Present Experiment With DF

In the present experiment, we explored this possibility by re-testing DF in a version of Schenk’s (2012a) mirror apparatus in which the cylinder that she grasped remained the same size from trial to trial – even though the cylinders viewed in the mirror varied in width. We reasoned that in this situation haptic feedback would certainly be available, but, crucially, that feedback would not differ from trial to trial – that is, it would be totally uninformative. If DF’s grip scaling relies on visuohaptic calibration as Schenk proposed, then irrespective of trial-to-trial changes in the visual appearance of the goal objects, the absence of veridical haptic feedback should derail DF’s performance, and she should show poor grip scaling. We predicted, however, that DF should scale her grip to the visual appearance of the target just as well as controls.

Schenk’s haptic feedback hypothesis also makes an important prediction concerning DF’s ability to make perceptual size estimates. According to this hypothesis, haptic feedback is what allows DF to perform well on visually guided grasping despite performing poorly on size estimation. It should follow that allowing DF to handle each object after making a size estimate should render her able to make accurate size estimates. We have tested this prediction directly.

Finally, another issue we address in the present paper is DF's relatively good performance at making size estimates in Schenk's (2012a) study. In the original report describing the dissociation between perception and action in DF, Goodale et al. (1991) used so-called "Efron" blocks, in which the dimensions of the rectangular goal objects varied but the overall surface area – and therefore the brightness and weight – remained the same (Efron, 1969). This prevented DF from performing well through a strategy of discriminating on the basis of non-shape cues. Because of her profound deficit in form vision, DF could not discriminate between the objects on the basis of their differences in width (Goodale et al. 1991). Although Schenk used Efron shapes in earlier experiments (see Schenk and Milner, 2006), in his 2012 study his cylinder stimuli varied in overall size and weight. This may explain why in at least one of the perceptual tasks that he used, DF was able to discriminate between some of the cylinders. In the present experiments, we explicitly compared DF's discrimination performance when presented with a set of cylinders similar to those used by Schenk, against her discrimination performance with Efron blocks.

3.2 Methods

3.2.1 Participants

Patient DF (57 years of age at the time of testing), suffers from a profound visual form agnosia, which followed accidental carbon monoxide intoxication in 1988 that resulted in large bilateral lesions to her lateral occipital cortex (Milner et al, 1991) and small bilateral lesions to her superior parietal occipital cortex (James et al., 2003). Initial testing revealed that her visual acuity, colour, intelligence, and haptic recognition, were intact, though there was a log-unit reduction in her sensitivity to spatial frequencies under 5 cycles/deg. Her visual fields were also intact up to approximately 30°. In addition to testing patient DF we tested 24 normally-sighted gender-matched and age-appropriate controls (*M* = 49 years of age, *SD* = 10.3 years).

The experimental procedures were approved by the local Ethics committee, and informed consent was obtained from all of the participants before the experimental session began. The controls were compensated $40 for their time.

3.2.2 Experimental Apparatus, Protocol, and Design

All the participants, including DF, were seated comfortably in front of a table for the duration of the experiment. DF was tested in Durham, UK, whereas the control participants were tested in London, Canada. An Optotrak 3020 optoelectronic recording system (Waterloo, ON, Canada) was used to capture the control participants' hand movements, whereas a miniBIRD (Ascension Technologies) motion capture system recorded DF's hand movements. Both motion-capture systems tracked the positions of their respective markers at 80 Hz. The Optotrak 3020 was configured to record for 3 s at the beginning of the trial, whereas the miniBIRD was configured to record for 4 s. For both the control participants and DF, one motion-tracking marker was attached to the distal interphalangeal joint of the thumb and a second marker was attached to the distal interphalangeal joint of the forefinger. For the practice and experimental trials, the participants wore PLATO LCD goggles (Translucent Technologies Inc., Toronto, ON, Canada) to occlude the participants' view between trials. The lenses of these goggles switch from a translucent default state that blocks the wearer's view to a transparent one in less than 6 ms.

Target objects for the first four tasks were cylinders (three grasping tasks and one manual estimation task). Each of the cylinders was 7-cm tall but varied in their diameter (3.5 cm, 4.8 cm, and 6 cm) and, therefore, in their overall size. The cylinders were painted matt black and presented against a white background under normal room illumination. For the remaining tasks (again, grasping and manual estimation tasks), the target objects were Efron blocks. The blocks were 1.5 cm tall and varied in both their width and length to match one another for overall surface area (*w*×*l*: 2 cm × 12.5 cm; 3.5 cm × 7 cm; 5 cm × 5 cm). These Efron blocks were presented in a darkened room on a black background but were covered with phosphorescent paint, which glowed in the dark. This was done in order to remove additional environmental cues that are normally available in laboratory grasping tasks under standard room illumination. These Efron blocks were randomly presented at three different distances from the participant's starting hand position (10, 20, and 30cm) along their midline and and were not used in conjunction with the mirror arrangement. In a subsequent test session approximately one year after the first, a second set of Efron blocks was included.

These blocks were 1 cm tall and varied in both their width and length to match one another for overall surface area (*w*×*l*: 3 cm × 8.3 cm; 5 cm × 5 cm; 6.25 cm × 4 cm).

In the first two grasping tasks, the cylinders were viewed in a mirror apparatus (see Fig. 3-1). To accommodate the mirror, the participants' start position was located to the right of their midline. The mirror itself was aligned 45° clockwise from the edge of the table facing the participants (see Fig. 3-1). To

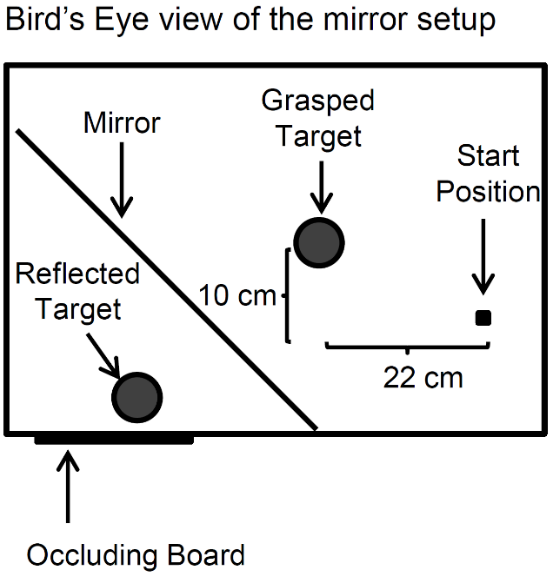

Figure 3-1. The experimental setup for the grasping and manual estimation tasks. The experimental setup for the grasping and manual estimation tasks. For the mirror tasks, a direct view of the mirror-reflected cylinder was blocked by a white board. When the goggles cleared, the participants reached out behind the mirror to grasp a second cylinder that was positioned to match the apparent position of the one viewed in the mirror. In the veridical mirror (VM) task, the cylinder behind the mirror always matched the diameter of the one viewed in the mirror. All aspects of the non-veridical mirror (NVM) task were the same as those in the VM task, except that the cylinder positioned behind the mirror remained the same from trial to trial. In the normal grasping (NG) task (and all of the manual estimation tasks except for one), the mirror was removed altogether to reveal the goal object for a direct view. In the NG task, the hand's starting position was moved towards the participants' midline – approximately 20 cm directly in front of the goal object (not shown).

block the participants from seeing the reflected cylinder directly, an occluding board with a white background was attached to this same table edge just left of their midline. When the mirror was present, a second cylinder was positioned behind the mirror to precisely match the apparent position of the one viewed in the mirror. In tasks without the mirror, the cylinders (and later the Efrons) were viewed directly, and the start position was located 5 cm from the table edge along the same frontal plane as the target.

At the beginning of all trials in all the tasks, the lenses of the goggles cleared to permit the participants a full view of the workspace, including the target, and remained open for the duration of data collection. For both the grasping and perceptual estimation tasks, the “go” signal was the opening of the goggles. For the grasping tasks, the participants were asked to reach out to pick up the target as quickly and as accurately as they could and to place it back down on the table. Note that for the two grasping tasks in which the mirror was in place, the participants had to reach behind the mirror to pick up the target cylinder. This meant that the participants lost sight of their hand and limb during the reach and that the object they viewed in the mirror did not move when they lifted the spatially matched object behind mirror.

For the perceptual estimation tasks, no mirror was used, and the participants were asked to keep the base of their hand on the starting position and to displace their thumb and forefinger an amount that matched the target dimension of the object. The task-relevant dimension for the cylinders was diameter, whereas the relevant dimension for the Efron blocks was width, which was explained to the participants as the distance between the nearest and farthest edge of the blocks. In the perceptual estimation tasks, the participants were asked to be as accurate as possible. To this end, the participants were permitted to look freely between the target and their hand until they were satisfied with their estimate. Finally, the participants were asked to keep their fingers as still as possible once they were satisfied with their estimate, so that their manual estimate aperture (MEA) could be determined offline using grip stability.

The trial sequences ensured that each object had an equivalent probability of being immediately preceded by itself or by any of the other cylinders. We did this for two reasons. First, we wanted to guard against the possibility that participants used haptic feedback about target width on one trial to scale their grip aperture on a subsequent trial. The trial order we used would have resulted in zero grip scaling if a participant relied on such a strategy. Second, this trial order minimized any bias in our measures attributable to autocorrelation – a problem that is inherent in repeated measurements. This is a particularly prudent precaution to take when single-subject analyses are used. Removing the variation in DF’s responses that is attributable to her response on the immediately preceding trial (i.e. a lag-1 trial autoregression) yielded no evidence to suggest that her measurements were correlated from one trial to the next. The trial sequences for each task included one additional repeat for one of the sizes, since the first trial of a given block of administered trials has no immediate trial history.

The testing order was as follows. All participants first received 10 practice grasping trials with the mirror in which the cylinder hidden behind the mirror was identical to the cylinder viewed in the mirror (three repeats per cylinder size with one additional repeat for one of the cylinder sizes). Following a brief break, the participants then executed 28 more grasps using this Veridical Mirror (VM) setup. In this VM task, we included 9 repeats of each cylinder (plus one additional repeat for one of the cylinders). Immediately following the VM task, and without any delay, 27 additional trials were administered in which the target behind the mirror remained the same size (4.8 cm) but the cylinder viewed in the mirror was allowed to vary. There was no additional repeat for any of the cylinder sizes, because the first trial in this task was preceded by the last trial in the preceding task. In this Non-Veridical Mirror (NVM) task, the participants were not informed of this manipulation. To keep the same sequence and timing as the VM task, the experimenter removed the hidden cylinder at the end of each trial, returning it to the ‘pool’ of cylinders, then reselected the same hidden cylinder to put it back in place behind the mirror for the next trial.

The mirror was removed for the next two tasks. The participants were first asked to render manual (perceptual) judgements of cylinder diameter. Again, 28 trials were administered (9 replicates for each cylinder, with one additional repeat for one of the cylinders). Following this, they were asked to perform a Normal Grasping (NG) task, in which they reached out and picked up the cylinder that was now in direct view. Due to limited testing time and the fact that DF has been shown to scale her grip aperture to target size in ‘normal’ laboratory grasping tasks a number of times, only 19 trials were administered in this condition.

After a break, the cylinders were exchanged for the Efron blocks, and the participants put on a glove covered in phosphorescent paint to provide visual feedback of their hand in the darkened room. Twenty-eight grasping trials were administered in which there were nine per Efron block (three trials at each of three positions, plus one additional trial to balance the trial order as before, each presented in the dark). Following this, only 9 manual estimation trials were administered using the same trial arrangement, again due to limited testing time. Before each trial was initiated the room lights were turned off, and then after the trial was completed they were turned on to ‘recharge’ the phosphorescent paint on the glove and the objects.

Approximately one year later, we tested DF on three additional manual estimation tasks with the Efron blocks. All aspects of the experimental apparatus were identical to those used in the first experimental session. Furthermore, the position of the Efrons did not vary from trial to trial in any of these additional estimation tasks. In the first manual estimation task, DF was permitted haptic feedback after each of her estimates. Specifically, she reached out to pick up the target right after providing an estimate of the target’s width. In the second and third estimation tasks, DF was asked to estimate the widths of a set of grey Efron blocks presented on a white background. In one variant, she viewed the targets in the mirror. In a second variant, she viewed them directly. These final manual estimation tasks allowed us to perform a control test for an effect of the mirror on her estimations. In all three additional estimation tasks, we predicted her estimates would show no relationship to Efron width.

3.2.3 Data preprocessing and analysis

The data were processed offline with custom software written in Matlab (Mathworks Inc., Natick, MA, USA). The positional data from the markers was low-pass filtered at 20Hz using a 2nd order Butterworth digital filter. Grip aperture was computed as the Euclidean distance between the marker placed on the thumb and the marker placed on the forefinger, and the instantaneous velocities were computed for each of the three markers and for grip aperture.

The principal measure we examined for grasping was peak grip aperture (PGA), the maximum extent that the thumb and forefinger opens as the hand approaches the object. Thus, on a given grasp trial, the approach phase of the grasp was first isolated and the PGA then extracted from it. The onset of the approach phase was defined as the first of 20 consecutive sample frames (250 ms) during which the instantaneous speed of the forefinger marker exceeded 20 mm/s. The duration requirement was used to avoid incorporating incidental finger movements into the analysis. The same threshold was used for the manual estimations but because these movements are typically shorter than grasping movements, the duration criterion for the onset was relaxed to 10 consecutive frames for this perceptual task.

The end of the approach phase of the grasp was defined as the first sample frame in which the speed of the forefinger marker fell below 100 mm/s. For the manual estimates, the manual estimate aperture (MEA) was defined as the first of 10 consecutive frames during which the rate at which the aperture changed fell below 10 mm/s. Because the participants were asked to keep their thumb and forefinger stable once they were satisfied that their aperture reflected the target’s size, this definition was designed to capture the point at which the estimate aperture plateaus. Finally, each trial was visually inspected for gross errors. Corrections for such errors were made by increasing or decreasing the duration criterion.

3.2.4 Statistical analysis

We focused largely on two principal dependent measures, the unstandardized bivariate regression coefficient (slope, *b*), and the standardized one (i.e. the Pearson’s product-moment correlation, *r*). For each task, ordinary least-squares bivariate linear regression modelled the dependent measure (PGA or MEA, in mm) from each trial as a function of the task-relevant dimension of the target (also in mm) for each task separately. Thus, the resultant slopes reflect the predicted change in the dependent measure, in mm, following a 1 mm increase in target width. In contrast, *r* reflects the linear slope relating the Z-transformed measures. As such, *r* reflects how tightly the data points are clustered around any non-zero regression slope. In short, both the slopes and the correlations can be viewed in this context as meaningful indicators of grip scaling that reflect related but different aspects of the response. Thus, each was submitted to the same series of analyses.

The control subjects’ slopes (*b*) and the Fisher-transformed correlations (*r*') for the VM, NG, and NVM tasks were subjected to repeated-measures

Analysis of Variance (rmANOVA) and appropriate t-tests. No violations of sphericity were detected ($p_{\text{min}} = 0.47$). Paired-samples t-tests were employed for the targeted comparisons among the controls. Independent samples t-tests were employed for the comparisons between the controls and DF (Crawford, Garthwaite, Howell, & Venneri, 2003b; Crawford & Garthwaite, 2004; Crawford and Howell, 1998). When DF's grip scaling was compared to those of the control participants, the tests were one-tailed since any difference was predicted to be uni-directional (towards impairment). These tests, therefore, had the benefit of providing more power than their two-tailed counterparts to detect a visuomotor impairment in DF should one be present. Finally, in comparing the performance of DF across pairs of tasks to that of the controls, we used Crawford's 'unstandardized difference test' to test for 'classical' or 'strong/differential' dissociations. This test relies on the variance of the control sampling distribution of paired *task-difference scores* to evaluate the abnormality of the patient's task difference score (Crawford & Garthwaite, 2005; Crawford, Garthwaite, & Gray, 2003a; Crawford, Howell, Garthwaite, 1998). Unlike the Crawford et al. (1998) formulation, the patient's scores are not Z-score transformed. In fact, since sample variance naturally varies from sample to sample, incorporating superficial differences in sample variance into patient measures when there is no significant justification to do so risks distorting the resultant transformed measures with sampling error. Moreover, sampling error is reduced with larger sample sizes. Taken together, this probably explains why the inflation of type I error that occurs when using the original Crawford, Howell & Garthwaite (1998) test is mitigated as the sample size increases from 5 to 50 (see Crawford and Garthwaite, 2005). In short, the SD is naturally more susceptible to sample variance at smaller sample sizes, and is, therefore, more likely to exaggerate the patient's Z-score difference across tasks for smaller sample sizes. Note that the unstandardized measures (e.g., regression slopes) are quite meaningful as they stand: they are in the same units across all tasks and were taken from the same hand and fingers. Furthermore, there were no significant violations of homogeneity of variance between any pair of contrasted tasks. The unstandardized difference tests were two-tailed. The alpha criterion was set to 0.05 for each of the tests we employed.

The comparisons of DF's grip scaling between tasks were implemented using a fixed-effects 'heterogeneous slopes' Analysis of Covariance (ANCOVA), in which DF's PGA for each trial was treated as an independent observation. As we have already noted, the lag-1 trial autoregression was not significant for any of the tasks. In other words, neither DF's PGA nor her MEAs were reliably correlated from one trial to the next. Thus, we compared the 'full' and 'restricted' model of DF's PGAs regressed on the cylinder diameter (the covariate), an effect of task, and the interaction between the covariate (target diameter or width) and the task factor (i.e. the product of the covariate and task factor). This residual error for this full model was compared to the residual error for a restricted model that lacked the interaction term (see e.g., Rutherford, 2011).

3.3 Results

3.3.1 Comparing performance across all three grasping tasks in the control participants

Two one-way repeated measures ANOVAs revealed that the slopes [$F(2,46) = 14.87$, $p < 2\times10^{-5}$] and the (transformed) correlations [$F(2,46) = 21.81$, $p < 3\times10^{-7}$] describing the relationship between PGA and viewed cylinder diameter for the control participants differed across the three grasping tasks included in the analyses: VM task (viewed and hidden cylinder varied together), NVM task (viewed cylinder varied but hidden cylinder stayed the same), and the NG task (direct view of the cylinders). These differences can be seen in Figs. 3-2 and 3-3. In the following sections, the sources of the differences driving these task effects on grip scaling in the control participants are explored, and DF's grip scaling is compared to that of the control participants across all three tasks.

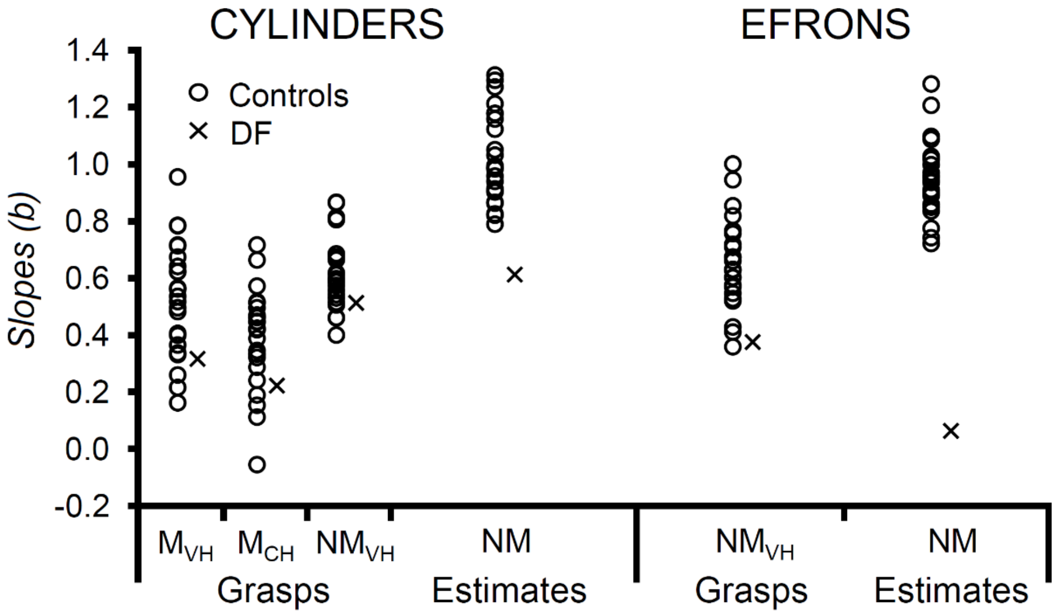

Figure 3-2. Grip aperture scaling (as measured by slopes) for the grasping and manual estimation tasks for the controls (open circles) and DF (crosses). Grip aperture scaling (as measured by slopes) for the grasping and manual estimation tasks for the controls (open circles) and DF (crosses). Control participants showed less grip-scaling in the non-veridical mirror (NVM) task than they did in the veridical mirror (VM) task, and less grip-scaling in the VM task than they did in the normal grasping (NG) task. Overall, DF's grip scaling was not significantly different from the control participants. Although her manual estimations of cylinder diameter were not as good as those of the control participants, DF did show some sensitivity to cylinder diameter when manually estimating this feature. In contrast, when the Efron blocks were used, DF showed no sensitivity to their widths when manually estimating them. Not surprisingly, when she reached out to pick them up, DF showed significant grip scaling to Efron width that did not differ significantly from the controls, although there was a trend (one tailed) towards a deficit.

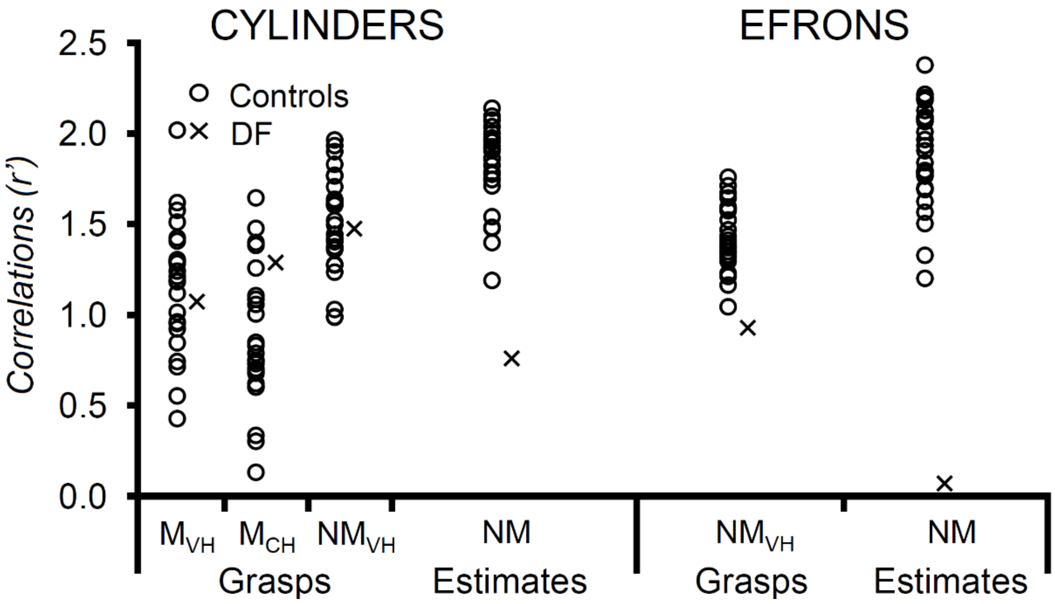

Figure 3-3. Grip aperture scaling (as measured by Fisher-transformed correlation coefficients) for the grasping and manual estimation tasks for the controls (open circles) and DF (crosses). Similar to the results when slopes were taken as a measure of grip scaling, the controls showed weaker grip scaling in the non-veridical mirror (NVM) task than they did in the veridical mirror (VM) task, and they showed weaker grip aperture scaling in the VM task than they did in the normal grasping (NG) task. DF's grip scaling (as measured by correlations) was not significantly different from that of the control participants on any of these grasping tasks. Although her manual estimations of cylinder diameter were not as good as those of the control participants, the correlation was nevertheless reliable. When Efron blocks were used as targets, DF's grip scaling to Efron width was very reliable but significantly weaker than that of the controls. Critically, DF showed absolutely no evidence of any sensitivity to Efron width when rendering manual estimates and her correlations fell well outside of the normal range. Thus, for the Efrons, DF showed a strong dissociation when the correlations were used as a measure of grip scaling.

3.3.2 Effects of mirror viewing on grip-scaling when haptic and visual target sizes were matched

In the VM task (in which the cylinder grasped behind the mirror was identical in diameter and position to the one observed in the mirror), all of the control participants scaled their PGA to the diameter of the observed cylinder as indicated by their slopes and correlations [$p_{max} < 0.03$; $\bar{b} = 0.55$ mm/mm, $SD = 0.20$

mm/mm; $\overline{r'} = 1.23$, $SD = 0.39$]. Not surprisingly, when the mirror was removed to reveal the target cylinder for a direct view (NG task), all the control participants continued to scale their grasps reliably to the diameter of the cylinders [$p_{max} < 0.03$; $\bar{b} = 0.60$ mm/mm ($SD = 0.16$ mm/mm); $\overline{r'} = 1.59$ ($SD = 0.38$) (see Figs. 3-2 and 3-3)]. Patient DF also reliably scaled her grasp to the diameter of the cylinders in both the VM task [$b = 0.33$ mm/mm, $r' = 1.15$, $t(26) = 7.23$, $p < 2\times10^{-7}$] and in the NG task, $b = 0.52$ mm/mm, $r' = 1.52$, $t(17) = 8.98$, $p < 8\times10^{-8}$. In both cases, DF's grip scaling did not differ significantly from that of the controls as measured by slopes [VM task: $t(23) = -1.08$, $p = 0.15$; NG task: $t(23) = -0.46$, $p = 0.32$] or correlations [VM task: $t(23) = -0.21$, $p = 0.42$; NG task: $t(23) = -0.19$, $p = 0.43$] (see Fig. 3-2).

Interestingly, the use of the mirror reduced the magnitude of patient DF's grip scaling compared to that observed in the NG task [$F(1,43) = 6.85$, $p < 0.02$]. Similarly, the control participants showed a significant reduction in grip scaling in the VM task compared to the NG task, as measured by either the slopes [$\bar{b} = 0.08$ (SD = 0.17 mm/mm), $t(23) = 1.85$, $p = 0.05$] or the correlations between grip aperture and cylinder diameter [$\overline{r'} = 0.36$ (SD = 0.47), $t(23) = 3.75$, $p < 2\times10^{-3}$]. Notably, the reduction in DF's grip scaling due to the mirror did not differ significantly from the mean reduction in the grip scaling of the control participants as measured by their slopes [$t(23) = -0.62$, $p = 0.54$] or correlations [$t(23) = -0.02$, $p = 0.98$]. Thus, there was evidence for a detrimental effect of the mirror on grip scaling in both the controls and DF, but the effect of the mirror on

DF’s scaling was not beyond what can reasonably be expected to occur in the gender-matched and age-appropriate population.

3.3.3 Tests of the effect of non-veridical haptic feedback on grip sensitivity and reliability

In the NVM task, in which the diameter of the viewed cylinder varied from trial to trial, but the diameter of the target cylinder behind the mirror was kept constant (4.8 cm), three of the 24 controls failed to reliably scale their grasps to cylinder diameter [$p_{max} = 0.59$; $\bar{b} = 0.40$ mm/mm ($SD = 0.18$ mm/mm); $\overline{r'} = 0.89$ ($SD = 0.40$)]. DF, however, continued to scale her grasp reliably to the diameter of the cylinder viewed in the mirror as measured by the slope or correlation [$b = 0.22$ mm/mm, $r' = 1.27$, $t(25) = 8.17$, $p < 2\times10^{-8}$]. Furthermore, neither of these measures of DF’s performance differed significantly from those of the control participants [slope: $t(23) = -0.97$, $p = 0.17$; correlation: $t(23) = 0.92$, $p = 0.18$].

Anticipatory grip scaling in NVM task was significantly below that in the VM task in the controls [reduction in slope: $\bar{b} = 0.15$ mm/mm ($SD = 0.20$ mm/mm), $t(23) = 3.61$, $p < 2\times10^{-3}$; correlations: $\overline{r'} = 0.34$ ($SD = 0.53$), $t(23) = 3.18$, $p < 5\times10^{-3}$]. A similar comparison of DF’s grip scaling on these two tasks indicated a marginally significant reduction in her slope [$b = 0.09$ mm/mm, $F(1,51) = 3.85$, $p = 0.055$]. Critically, however, any reduction in DF’s grip scaling between the VM and NVM grasping tasks did not differ from the mean reduction in the controls, as measured by the slopes [$t(23) = -0.21$, $p = 0.83$] or the correlations [$t(23) = 0.86$, $p = 0.40$]. In short, the effect of constant haptic feedback from repeatedly grasping the same cylinder behind the mirror did not abolish DF's grip-scaling with respect to the cylinder that she viewed in the mirror, but rather reduced it by the small amount one would expect to observe in controls.

As expected, the reduction in the controls' grip scaling to the viewed diameter of the cylinder was driven by motor adaptation to the unchanged diameter of the grasped cylinder that was hidden behind the mirror. In other words, the mean PGA for grasps directed at the viewed cylinders converged towards the felt diameter of the middle-sized cylinder. Specifically, the mean PGA for grasps directed at the visually small cylinder increased [$t(23) = 2.00$, $p < 0.03$ (one-tailed)], whereas the mean PGA for grasps directed at the visually large cylinder decreased [$t(23) = -2.31$, $p < 0.02$ (one-tailed)]. Two further comparisons indicated that the reduction in DF's grip scaling was driven mostly by a decrease in PGA when she reached out to grasp the large cylinder [$t(16) = 2.00$, $p < 0.03$ (one-tailed)]. When DF directed her grasps towards the visually small cylinder, her PGA increased but not significantly so [$t(16) = 1.13$, $p = 0.27$ (one-tailed)]. Overall, both the controls and DF showed evidence for motor adaptation to the constant felt diameter of the grasped cylinder – a result that is consistent with Safstrom and Edin's (2004, 2008) findings in normally-sighted healthy adult populations.

3.3.4 Perceptual judgements of cylinder size

When manually estimating cylinder diameter, all of the controls showed reliable positive relationships between their MEAs and cylinder diameter [$p_{max} < 0.001$; $\bar{b} = 1.03$ mm/mm ($SD = 0.15$ mm/mm); $\bar{r'} = 1.78$ ($SD = 0.23$)]. DF also showed a reliable positive relationship between MEA and cylinder diameter, $b = 0.65$ mm/mm, $r' = 0.81$; $t(26) = 4.23$, $p < 9\times10^{-5}$. However, DF's slope was significantly shallower [$t(23) = 2.50$, $p < 0.01$] and her correlation significantly weaker [$t(23) = 4.09$, $p < 3\times10^{-4}$] than those of the control participants.

3.3.5 Perception-action dissociations when cylinders were used

There were three variants of the grasping task and one manual (perceptual) estimation task in which the cylinders were used. We therefore tested for dissociations of grip scaling to cylinder diameter between the manual estimation task and each of the three grasping tasks in DF. Because DF could reliably distinguish the cylinders using manual estimations (albeit not as well as the controls), it was not surprising that we failed to establish a clear dissociation between grasping and manual estimation for either of the tasks in which the mirror was used [VM task: $t(23) = 0.59$, $p = 0.56$; NVM task: $t(23) = 0.79$, $p = 0.44$]. Nevertheless, a dissociation was observed when DF grasped the cylinders in the NG task, in which the cylinders were viewed directly (i.e. without the mirror) [$t(23) = 1.79$, $p < 0.05$ (one tailed)].

In contrast to the results of the dissociation tests performed on the slopes, dissociations between each of the three grasping tasks and the manual estimation task were found when correlations were used as the measure of grip scaling. Thus, manual estimates were poorer than grip scaling in the VM task [$t(23) = 2.05$, $p = 0.05$], the NVM task, [$t(23) = 2.84$, $p < 0.01$], and the NG task, $t(23) = 2.35$, $p < 0.03$]. In summary, a dissociation between manual estimates and grip scaling, as measured by either slopes or correlations, was clearly observed for the NG task, whereas the same dissociation between manual estimates and grip scaling in the two mirror tasks was observed for the correlation analyses only.

3.3.6 Grip scaling to Efron block width during grasping

All of the control participants showed significant scaling to the width of the Efron blocks when reaching out to pick them up [$p_{max} < 2\times10^{-6}$; $\overline{b} = 0.65$ mm/mm ($SD = 0.16$ mm/mm); $\overline{r'} = 1.43$ ($SD = 0.18$)]. Not surprisingly, patient DF showed significant grip scaling to the width of the Efron blocks as measured by the slope and the correlation [$b = 0.38$, $r' = 0.93$, $p < 4\times10^{-5}$] (see Figs. 3-2 and 3-3). Her slope did not differ significantly from the controls, $t(23) = -1.64$, $p = 0.06$. Her grip scaling, as measured by correlation, however, was significantly weaker than that of the controls, $t(23) = 2.70$, $p < 7\times10^{-3}$.

3.3.7 Visual discrimination of Efron block width using manual estimations

Just as they had done with the cylinders, all control participants estimated the widths of the Efron blocks quite accurately [$p_{max} < 0.01$, $\overline{b} = 0.95$ mm/mm (SD = 0.13 mm/mm), $\overline{r'} = 1.86$, SD = 0.29)]. In stark contrast to her manual estimates of cylinder diameter, DF was clearly at chance when manually estimating the widths of the blocks, $b = 0.06$ mm/mm, $t(7) = 0.19$, $p = 0.85$. Not surprisingly, the slope relating her MEA to Efron width was significantly shallower than the control participants [$t(23) = -6.53$, $p < 6\times10^{-7}$] and the correlation was significantly weaker [$t(23) = -6.06$, $p < 2\times10^{-6}$] (see Fig. 3-2 and Fig. 3-3).

Using the same stimulus set, we also tested DF's ability to scale her grip aperture to width in a task in which these glow-in-the-dark Efron blocks were always presented at the same position. In this task, we presented each of these Efron blocks 4 times in a randomized order for a total of 12 trials. Not surprisingly, DF's estimates bore no significant relationship to target width [$b = 0.07$ mm/mm, $t(10) = 0.17$, $p = 0.87$]. Furthermore, a comparison of this condition with the variant in which the Efron was positioned at one of three different locations revealed no significant difference, $F(1,17) < 6\times10^{-4}$, $p = 0.98$.

In an additional estimation task, we permitted DF to reach out and pick up Efron blocks right after she provided a manual estimate of their width under normal viewing conditions and room illumination. All other aspects of the set-up and procedure were identical to the previous test of her Efron width perception, except that each Efron block was presented 10 times in a randomized order for a total of 30 trials. As Fig. 3-4C indicates, DF remained unable to reliably indicate the width, even with haptic feedback about the width of the object and environmental cues [$b = 0.08$ mm/mm, $r' = 0.25$, $t(28) = 1.33$, $p = 0.19$.]

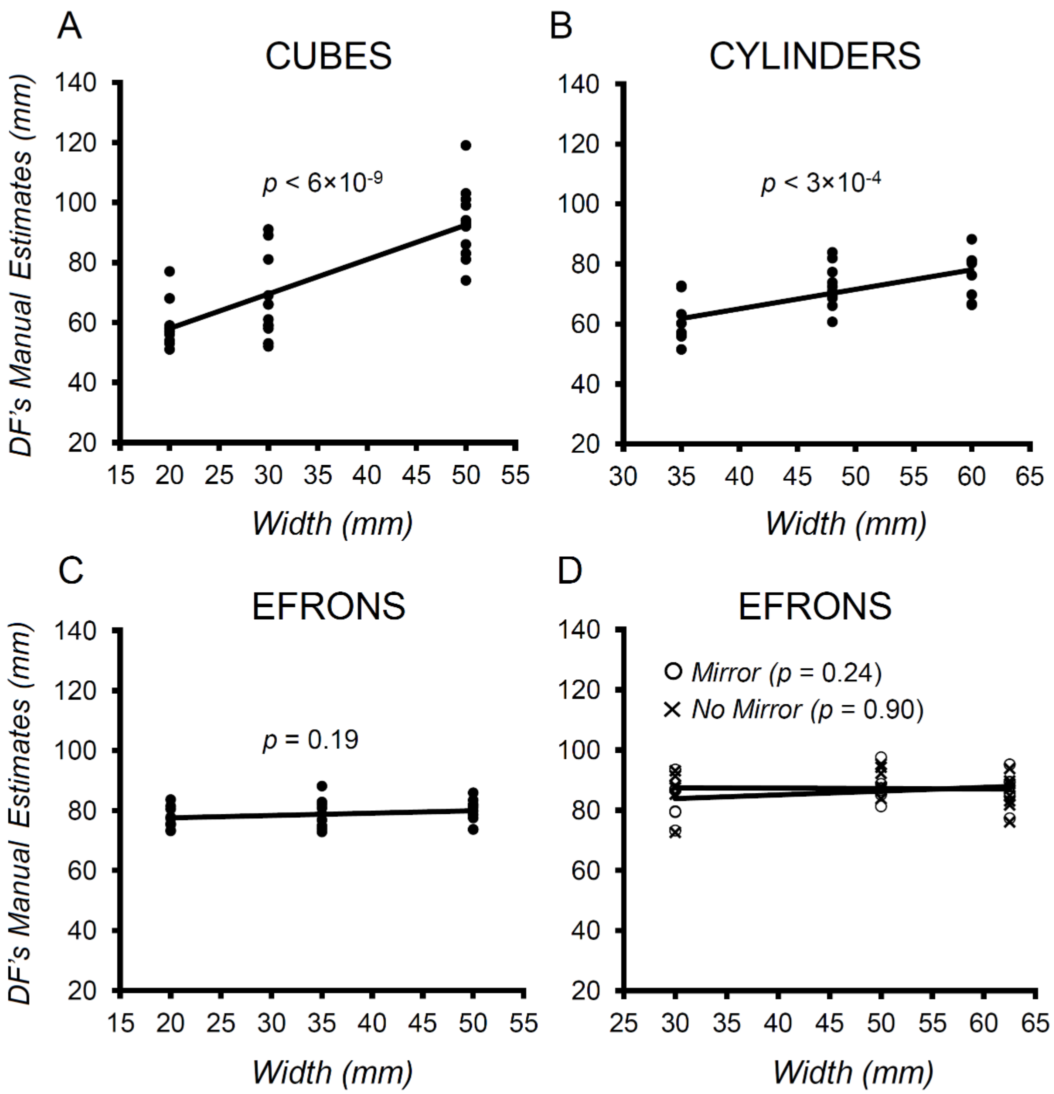

Figure 3-4. DF's manual estimations as a function of target type (cubes vs. cylinders vs. Efrons) and dimension (diameter vs. width). (A) DF's manual estimate aperture (MEA) as a function of the width of a set of three cubes of different sizes that were pseudorandomly presented at any one of three different distances (20, 30, or 40 cm away from her hand's starting position) when tested in 1991 (previously unpublished). Clearly, DF can use differences in the overall size (surface area) of the cubes to indicate differences in width [$b = 1.15$, $r' = 1.11$, $t(34) = 7.72$, $p < 6\times10^{-9}$]. (B) DF's MEAs as a function of the diameter of the set of three cylinders used in this study. DF is still capable of delineating the differences between the stimuli in this set, where again the stimuli differ in overall surface area. (C) DF's MEAs as a function of the width of the first set of Efron blocks used in this study. In this task, she was permitted to pick the Efrons up right after completing her estimate. As can be seen in this panel, DF's MEAs show no relationship to Efron width despite the opportunity to touch the blocks. (D) DF's MEAs as a function of the width of the second set of Efron blocks used in this study. DF viewed these Efrons in the mirror (open circles) or directly (crosses). Clearly, DF's estimates are

quite similar in both conditions and, in both cases, are not matched with the width of the Efron blocks. In short, the mirror does not significantly affect her poor judgments of Efron width.

Finally, we examined any influence of the mirror on DF's manual estimates. Viewing the Efrons directly [$b = -0.01$ mm/mm, $r' = 0.34$, $t(17) = -0.13$, $p = 0.90$] or as a reflection in the mirror [$b = 0.12$ mm/mm, $r' = 0.33$, $t(17) = 1.23$, $p = 0.24$] resulted in similarly poor grip scaling [$F(1,34) = 0.9$, $p = 0.35$] (see Fig. 4D). Overall, across a number of different variations of a manual estimation task, we found no evidence that DF could accurately or reliably match her grip aperture to the visually perceived width of Efron blocks.

3.3.8 Perception-action dissociations when Efron blocks were used

Given the difference in the accuracy of DF's estimates of the widths of the Efron blocks compared to her estimates of the diameters of the cylinders, it was not surprising that a strong dissociation between manual estimates and grip scaling for the Efron blocks was found for both slopes [$t(23) = 3.09$, $p < 0.006$] and correlations, $t(23) = 3.72$, $p < 6\times10^{-4}$. In short, when the overall surface area is controlled for, DF continues to scale her PGA to object width when reaching out to pick it up, despite failing completely to scale her perceptual estimates of width for the same stimuli.

3.4 Discussion

Despite a severe deficit in visual form perception, DF scaled her in-flight grip aperture to the task-relevant dimension of the goal objects in all five of the grasping tasks we used – and her grip-scaling slopes did not differ significantly from those of our age-appropriate and gender-matched control participants. These results reinforce a long history of work with DF in which a strong and compelling dissociation has been repeatedly demonstrated between her ability to use visual shape information to guide her grasping and her inability to perceive the shape of those same objects (for a recent review, see Goodale, 2011).

In two of the grasping tasks we used, the targets (cylinders) were hidden behind a mirror, using a set-up closely modeled on the one devised by Schenk (2012a). Even in this somewhat unnatural situation, DF's grip scaling did not differ from that of the normally sighted control participants. In one of our mirror tasks, the cylinder hidden behind the mirror remained unchanged from trial to trial, even though the cylinder viewed in the mirror continued to vary in diameter. Thus, on the majority of trials in this condition, haptic feedback from the grasped cylinder was completely uninformative. Under these circumstances, a reduction in grip scaling to the cylinder viewed in the mirror was to be expected, not because vision is unimportant, but because even in healthy individuals, grip aperture is adjusted over trials to reflect the real size of the grasped object by means of tactile feedback (Safstrom & Edin, 2004, 2008). Thus, the control participants in the present experiment showed a clear reduction in grip scaling in this version of the task – as their grip apertures converged on the diameter of the unchanging cylinder behind the mirror. Not surprisingly, DF showed a similar trend and her reduction in grip scaling was no different from that of the control participants. In short, it appears that DF's visuomotor system expresses the same capacity to adapt to visuo-haptic mismatch as the visuomotor system of the age-matched controls. The important point is that DF continued to scale her grasps to the viewed diameter of the cylinders as well as the controls – even when the haptic information was uninformative for grip scaling. This result contradicts a direct prediction from Schenk's (2012a,b) interpretation of DF's residual visuomotor capacities, according to which DF needs to have veridical haptic feedback in order to scale her grip aperture to the width of a goal object.

Schenk's (2012a,b) claim that haptic feedback is critical to DF's ability to scale her grasp is based on his finding that when there was no cylinder behind the mirror (and thus nothing to grasp), DF showed no evidence of grip scaling. Schenk argued that it was the absence of haptic feedback in this condition (his Task 4) that led to the deterioration in DF's performance. But as we mentioned in the Section 3.1 (Introduction), an alternative hypothesis for DF's grip-scaling failure in this task is not the absence of haptic information about the cylinder, but the absence of any feedback that she had reached the end of her grasp. Her hand would simply have closed on thin air. We suggest that without tactile feedback at the end of the grasp, the visuomotor system mediating grasping is not properly engaged, and that individuals are forced instead to carry out some sort of pantomimed grasp. To do this, DF (like anyone else) would have had to rely on what she perceived in the mirror to direct her pantomimed movement. But because of DF’s severe visual form agnosia, she would have had no perceptual foundation on which to base her pantomimed movement.

This interpretation of Schenk’s (2012a) results is supported by the fact that the control participants in his experiment also appeared to have behaved rather differently in this “air grasping” task than they did when there was an object present behind the mirror. Unlike the more shallow slopes that characterize grip scaling during real grasping, the slopes in the missing-cylinder task were much steeper, resembling the slopes observed during manual estimation. This suggests that the control participants in Schenk’s study were pantomiming their grasps on the basis of perceptual information, in much the same way as they estimated the diameter of the cylinder in the manual estimation task. In contrast, although our Non-veridical Mirror Task likewise provided no informative haptic feedback about size, it elicited much shallower grip scaling slopes in the controls than those seen in the missing-cylinder task. We suggest that the tactile input at the end of each grasp was sufficient to keep the visuomotor system engaged.

Our Non-veridical Mirror (NVM) task is similar in some respects to another of Schenk’s (2012a) grasping tasks in which the participants, including DF, were given intermittent haptic feedback (his Task 5). In this task, trials in which a matched cylinder was positioned behind the mirror were randomly interleaved with trials in which there was no cylinder behind the mirror. Under these conditions, DF’s grip scaling seems remarkably similar irrespective of whether haptic feedback was or was not present. Importantly, we do not know whether her grasp actually showed a significant relationship to cylinder diameter in this task, because DF's grip scaling was not explicitly tested. Furthermore, it is not clear whether DF's grip scaling actually improved following intermittent haptic feedback, because her grip scaling in this task and her scaling in the task in which haptic feedback was never available (Task 4) were never directly compared. Schenk's analysis did show that DF's grip scaling following the introduction of intermittent haptic feedback was significantly greater than the mean change in grip scaling for the controls. But as Whitwell and Buckingham (2013) pointed out, because the controls' grip scaling appears to be sharper in the 'no haptic feeedback' task than it is the 'intermittent haptic feedback' one, the test statistic would have been driven more by the large reduction in the controls' grip scaling than by the apparent increase in DF's grip scaling. In fact, recent findings from our laboratory indicate that grip scaling slopes of neurologically-intact individuals get significantly sharper when haptic feedback is unavailable throughout the task, than when it is always available (Byrne, Whitwell, Ganel, & Goodale, 2013). In short, it is not clear whether the intermittent haptic feedback, compared to the case in which haptic feedback is never available, significantly increases DF's grip scaling, or even whether it results in grip scaling that is comparable to that observed when haptic feedback is always permitted. As Schenk (2012a,b) pointed out, Bingham et al. (2007) has reported that the effects of 'no haptic feedback' on grasp kinematics (e.g., movement time, peak grip aperture, and peak hand velocity during the reach) can be mitigated by randomly interleaving such trials with trials in which feedback is available. Bingham et al., however, did not explicitly test whether grip scaling itself was significantly modulated by intermittent haptic feedback. As a consequence, we cannot be absolutely sure that intermittent haptic feedback results in grip scaling that is equivalent to that observed in real grasps and that the neural underpinnings of these two conditions are one and the same.

A final finding of Schenk's (2012a) that merits discussion is his observation that when DF was required to direct her grasp to a cylinder that was in a different location behind the mirror from its virtual image as viewed in the mirror (his Task 6), she no longer scaled her grasp. In this situation, she was certainly getting veridical haptic feedback about the width of the cylinder but this did not help her scale her grip aperture on subsequent trials. We believe that her failure in this task arose because her visuomotor system was forced to direct a grasp at a location that did not correspond to the location of the visible target. Under such conditions, there would be an inherent mismatch between the timing of the expected and experienced contact with the target resulting in a failure to reinforce the visually driven feedforward motor program. Moreover, the very act of directing one's hand to visually 'empty space' would not engage normal visuomotor control; instead, one would have to rely more on perceptual mechanisms that we know are unavailable in DF.

It is worth pointing out that the mirror set-up in all of these experiments is not without problems. In two critical ways, grasping an object in this situation differs from the typical laboratory grasping task. First, the mirror prevents participants from seeing their moving hand, despite being able to see the workspace where the hand should be. Second, when participants pick up the cylinder behind the mirror, the image of the cylinder in the mirror remains paradoxically stationary. These differences doubtless explain why we found that even veridical mirror grasping, in both DF and the control participants, was quite different from real grasping, in which the physical target and moving hand were clearly visible. It is not clear how these differences between the mirror task and the direct-view task come to affect grip scaling, but cognitive ‘supervisory’ factors as well as differences in visual feedforward and feedback processing may be involved. In short, the mirror task clearly has less ecological validity than the typical laboratory grasping task. This departure from real life was highlighted in our experiments by the fact that many of the control participants commented on the “strangeness” of reaching out behind a mirror to grasp the target: people found it “weird”. It is important to note that the mirror task is not the same as open-loop grasping. In the mirror task, there is a clear disconnection between what appears visually to be happening and what is actually happening, whereas in the open-loop task the fact that the lights have been extinguished (or goggles closed) is entirely consistent with the absence of visual feedback about the hand and target. Having said that, it is reasonable to suggest that practice and increased task familiarity could overcome the problems associated with grasping objects viewed in a mirror. One way to make the mirror-task less strange would be to run the experiment in open loop, as is typically done in with this kind of set-up (e.g. Hu & Goodale, 2000). But in any case, it is clear that the mirror grasping task is not an optimal way of testing visuomotor behaviour in either DF or in neurologically-intact individuals.

There is another problem with the cylinders that were used both in Schenk's original task and in our replication of his task. In our experiment, DF was able to indicate the diameter of the cylinders using her thumb and forefinger in the manual estimation task, just as she performed better than chance in one of Schenk's perceptual tasks. The reason she was able to do this is that the cylinders differed, not only in terms of the task-relevant feature (diameter) but also in overall surface area. Moreover, these two features were perfectly correlated. DF may have also used haptic and/or weight feedback from the many trials in which she grasped the cylinders to reinforce this visual difference in size. Since DF's perceptual judgements were thus almost certainly based on differences in the overall sizes of the cylinders, a sharp dissociation between sensitivity for grasping and manual estimates of width would necessarily be more difficult to establish using such stimuli. Nevertheless, even though she could perform manual estimations using differences in the overall size of the cylinders – without needing to use width *per se* – her grip scaling to the width of the cylinders in the present experiment was still significantly better than her manual estimates under the same viewing conditions (i.e. without the mirror).

DF's perceptual deficit is not one of detecting differences in overall size but rather one of detecting differences in shape or width. This was recognized early on in the investigations of DF's perceptual abilities, which is why, in the original study showing a dissociation between perception and action, Efron rectangles or blocks were used (Goodale et al., 1991). Efron blocks are matched for overall size but vary in width and length. In fact, unpublished data that was collected at that time clearly showed that DF could reliably and accurately indicate manually differences in the sizes of cubes (see Fig. 3-4) – even though in the same situation she could not indicate the width of Efron blocks. But despite this profound perceptual deficit, as was shown in the original report by Goodale et al. – and many times since – DF has no trouble scaling her grasp to the width of Efron blocks (for review, see Milner & Goodale, 2006).

DF was completely unable to indicate the width of any of the Efron blocks we used in the present study, even when she was allowed to pick the block up after each manual estimate. Nevertheless, she showed reliable grip scaling with these same blocks. Her preserved grip scaling in the task in which phosphorescent blocks were used is even more remarkable given that the conditions were far from optimal: she was wearing a glove and there were no cues to size and distance from the surrounding workspace. This again underscores the fact that despite her striking inability to discriminate between objects on the basis of their shape, DF's intact visuomotor networks are able to extract information about the relevant dimension for grasping from these same objects.

In conclusion, we have found in this study good evidence for a previously under-appreciated aspect of dorsal stream visuomotor function. Thanks to Schenk's (2012a)'s research, we have serendipitously stumbled on the fact that the visuomotor system is not engaged solely by being faced with a visual stimulus and with the task of reaching out to grasp it. Evolution has apparently placed another condition on the modus operandi of the dorsal stream – namely that the hand has to encounter a tangible endpoint of the action for the system to work.

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Chapter 4

4 DF's Visual Brain in Action: Visual feedforward control in a patient with visual form agnosia

Patient DF, who developed visual form agnosia following ventral-stream damage, is unable to discriminate the width of objects, performing at chance, for example, when asked to open her thumb and forefinger a matching amount. Remarkably, however, DF adjusts her hand aperture to accommodate the width of objects when reaching out to pick them up (grip scaling). While this spared ability to grasp objects is presumed to be mediated by visuomotor modules in her relatively intact dorsal stream, it is possible that it may rely abnormally on online visual or haptic feedback. We report here that DF's grip scaling remained intact when her vision was completely suppressed during grasp movements, and it still dissociated sharply from her poor perceptual estimates of target size. We then tested whether providing trial-by-trial haptic feedback after making such perceptual estimates might improve DF's performance, but found that they remained significantly impaired. In a final experiment, we re-examined whether DF's grip scaling depends on receiving veridical haptic feedback during grasping. In one condition, the haptic feedback was identical to the visual targets. In a second condition, the feedback was of a constant intermediate width while the visual target varied trial by trial. Despite this incongruent feedback, DF still scaled her grip aperture to the visual widths of the target blocks, showing only normal adaptation to the false haptically-experienced width. Taken together, these results strengthen the view that DF’s spared grasping relies on a normal mode of dorsal-stream functioning, based chiefly on visual feedforward processing.

4.1 Introduction

Humans and other primates are particularly adept at grasping and manipulating objects. Clearly, vision plays a crucial role in these abilities. Current views of target-directed actions, such as reaching out to pick up a goal object, propose that visual information about the target must be transformed from the spatial reference frame in which it is initially encoded into the spatial reference frame of the effector ultimately required for the movement about the target must be transformed from the spatial reference frame in which it is initially encoded into the spatial reference frame of the effector ultimately selected for the movement (for review see Cohen & Andersen, 2002; Crawford, Henriques & Medendorp, 2011). Target-directed actions are thought to be controlled by feedforward and feedback processes that exploit online sensory information about the target and the effector in order to formulate, maintain and update internal models of body position and body-target relationships (for review see Shadmehr, Smith, & Krakauer, 2010; Wolpert, Ghahramani, & Jordan, 1995; Wolpert, 2007).

Classically, the organization of visually-guided grasps is thought to comprise two coupled components: a transport component that directs the hand towards the target, and a grasp component in which the posture of the hand is adjusted to accommodate the target’s geometric properties (Jeannerod, 1988; Jeannerod 1999). Subsequent investigations have shown that the reach and grasp components are each mapped separately onto distinct fronto-parietal networks that operate in parallel in the primate brain (Cavina-Pratesi, Monaco, Fattori, Calletti, McAdam, Quinlan, Goodale, & Culham, 2010; Cavina-Pratesi, Ietswaart, Humphreys, Lestou, Milner, 2010; Jeannerod, 1994; Jeannerod, 1999; Jeannerod, Arbib, Rizzolatti & Sakata, 1995). Alternative models of the organization of grasping have proposed that the grasping digits are controlled independently (Smeets & Brenner, 1999; Smeets & Brenner 2001; Smeets, Brenner, & Biegstraaten, 2002; Smeets, Brenner, & Martin, 2009). According to this model, a precision grasp, for example, consists of reaching movements of the thumb and index-finger to two spatial positions that correspond to opposing edges of a goal object. Nevertheless, both models rely on the processing of a goal-object's geometric properties: under either scheme, the visuomotor system must process the geometry of the object in order to extract either the size of the grasped dimension (Jeannerod's account) or the spatial positions that correspond to opposing surfaces of the object (Smeets and Brenner's account).

Whatever the underlying organization of the elements that constitute a grasping movement might be, accumulating evidence from a broad range of studies from neurophysiology to neuropsychology suggests that the cortical visual pathways mediating the processing object geometric properties for the visual control of skilled actions, such as grasping, are distinct from those mediating the processing of object geometric properties for perceptual report (Jeannerod & Jacob, 2005; Milner & Goodale, 2006). Visual perception is served by the ventral visual pathways, which project to the lateral occipital and inferotemporal cortex.

In contrast, skilled and visually-guided target-directed actions are served by the dorsal visual pathways that project to posterior parietal cortex (Goodale & Milner, 1992; for recent and expanded functional-anatomical reviews of the dorsal and ventral pathways, see Kravitz, Saleem, Baker, Ungerleider, and Mishkin, 2013; Kravitz, Saleem, Baker, & Mishkin, 2011).

A key observation that led to the two-visual-systems proposal came from patient DF, who has a profound deficit in visual object-form perception (visual form agnosia) but retains the ability to use information about the form of objects to control her grasping (Milner, Perrett, Johnston, Benson, Jordan, Heeley, Bettucci, Mortara, Mutani, Terazzi, & Davidson, 1991; Goodale, Milner, Jakobson, & Carey, 1991). Despite a profound impairment in her ability to name or copy simple line drawings of objects, DF can draw familiar objects from memory that she would have routinely encountered before her accident, such as an apple or a book, and other objects that she may have handled after her accident (Milner et al., 1991; Servos, Goodale, & Humphrey, 1993). DF's deficit in object form perception is believed to result from the bilateral damage to her lateral occipital cortex (James, Culham, Humphrey, Milner, & Goodale, 2003). The lateral occipital cortex is an area in the ventral stream that has been implicated in the recognition of the geometric properties of objects (Grill-Spector, 2003; Kourtzi, Kanwisher, 2001; James et al. 2003; Malach, Reppas, Benson, Kwong, Jiang, Kennedy, Ledden, Brady, Rosen, & Tootell, 1995). In line with these observations, DF shows no differential activation for line drawings anywhere in her ventral stream; she does, however, show preferential activity for reach to grasp movements over reaching movements in the cortical areas surrounding the anterior extent of the intraparietal sulcus (James et al. 2003).

The more medial and anterior regions of her ventral stream appeared to be largely spared, however (Bridge, Thomas, Minini, Cavina-Pratesi, Milner, & Parker, 2013; James, Culham, Humphrey, Milner, & Goodale, 2003), and it seems likely that these regions mediate DF’s residual ability to perceive visual surface properties such as colour and texture (Cavina-Pratesi, Kentridge, Heywood, & Milner, 2010a,b; Humphrey, Goodale, Jakobson, & Servos, 1994; Servos, Goodale, & Humphrey, 1993). Furthermore, she shows differential activation for coloured photographs of objects and for coloured scenes in the spared antero-medial areas of her ventral stream (James et al., 2003l Steeves et al., 2004). In other words, DF’s residual ability to recognize some objects would appear to depend on visual information that is processed in spared areas of her visual cortex. Thus, when she is confronted with the task of using vision to differentiate objects that have the same colour and texture but vary in shape, she performs at chance levels (pebble-like shapes: Goodale, Meenan, Bulthoff, Nicolle, Murphy, & Racicot, 1994b; or rectangular blocks of differing lengths and widths but the same overall surface area (Efron, 1969; Goodale et al. 1991). In short, DF’s perceptual deficit is one of visual object form.

Given DF’s failure to perceive differences in the form and orientation of objects, it is remarkable that she is able to use these properties to control the posture of her hand and fingers when reaching out to pick up those same objects (e.g., Goodale, Jakobson & Keillor, 1994; Goodale et al. 1991, 1994; Whitwell et al. 2014). Despite recent evidence of bilateral damage in more posterior parieto-occipital regions of her dorsal stream (Bridge et al. 2013; James et al. 2003), the anterior areas of the intraparietal sulcus that have been associated with visually guided grasping (Binkofski, Dohl, Posse, Stephan, Hefter, Seitz, & Freund, 1998; Cavina-Pratesi, Goodale, & Culham, 2007; Frey, Vinton, Norland, & Grafton, 2005) are largely spared (James et al. 2003). In line with this observation, the anterior intraparietal area in DF's brain showed the grasp-specific activation that is typically observed in this region when neurologically intact participants grasp objects (James et al. 2003) but not when they discriminate amongst objects on the basis of their width (Cavina-Pratesi, Goodale, & Culham, 2007). In summary, the behavioural dissociation between action and perception, coupled with the neuroanatomical and functional neuroimaging findings suggest that the preserved visual control of grasping in DF is mediated by relatively intact visuomotor networks in her dorsal stream, whereas her failure to perceive the form of objects is a consequence of damage to her ventral stream.

Importantly, whether DF's ability to grasp goal objects relies principally on visual feedforward programming or on online visual feedback processes remains unknown. There are no published investigations comparing DF's grasps with and without online visual input throughout the movement. Nevertheless, there are some instances where DF has been tested in tasks in which neither the target nor the moving hand is visible during the execution of the grasping movement (i.e. visual open loop). Schenk and Milner (2006), for example, examined DF's ability to scale her grasp to objects of different width in open loop using either her left or right hand or using a bimanual grasp with the index fingers of both hands. Remarkably, only the bimanual grasp showed clear evidence for ‘grip scaling’; evidence for grip scaling in the right hand was less convincing. The authors offer no explanation for DF’s superior bimanual performance. In any event, there was no opportunity to make a direct comparison between open- and closed-loop grasping in this situation. Furthermore, DF’s open-loop grip scaling was not compared to that of control participants. Interestingly, when the target remains visible throughout the movement but the hand does not, DF’s grip scaling to target width remains intact (Schenk, 2012a; Whitwell et al. 2014). It is important to note, however, that when the target remains visible, any change in the target’s oculocentric position due to eye, head, or body movements could be used to update the limb and hand movements as they unfold. Presumably, all of these concerns led Schenk (2012a) to include online visual feedback, along with haptic feedback and visual information from the ventral stream, in a list of factors that might be required for DF’s accurate grasping. One of the main aims of the current experiment, therefore, was to test DF’s grasps with and without visual feedback throughout her movement and to compare her performance in these conditions to that of control participants.

The second aim of the current investigation was to test a prediction that logically follows from an account of DF’s dissociation between grasping and perceptual estimation that is grounded in multimodal integration (Schenk, 2010, 2012a, 2012b; Schenk, Franz, Bruno, 2011). In normally-sighted individuals, visual and haptic information can be integrated to improve judgments about the size or width of a target object (see e.g., Ernst & Banks, 2002). Perhaps DF integrates haptic information about the target with some kind of degraded visual information about the target, resulting in a bimodal estimate that is more accurate than either estimate alone. According to this account, DF's accurate grip scaling when she reaches out to pick up a goal object is the result of the addition of haptic feedback about the object to a multimodal estimate of the relevant target feature. This would allow DF to compensate for what is primarily a visual deficit. In fact, when haptic feedback is removed altogether, DF no longer scales her in-flight grip aperture to the width of virtual-target cylinders (Schenk, 2012a). If this view is correct, however, then it logically follows that (1) the accuracy of DF's perceptual estimates of target width should also benefit from the addition of haptic feedback, and (2) DF's perceptual estimates of target width should benefit more than those of the control participants whose vision is not impaired. Previously, Whitwell et al. (2014) showed that DF provides poor estimates of the widths of Efron blocks even when she is permitted haptic information about the targets immediately after every estimate. DF's performance in this condition, however, was not compared to that of control participants. Thus, in the current investigation, we tested her data against a new data set sampled from a control population.

Finally, we re-visited the role that haptic feedback plays in the programming of DF's in-flight grip aperture. Our previous work showed that width of the target that she grasped need not correspond to its visible width in order for DF's grip scaling to remain normal. We demonstrated this by using a mirror-based virtual environment that allows the experimenter to dissociate the viewed object from the one that is actually picked up (Bingham, Coats, & Mon-Williams, 2007; Schenk, 2012a; Whitwell et al., 2014). In this experiment, DF reached out and grasped virtual cylinders that varied in width from trial to trial. Critically, in one of the conditions, the width of the cylinder that she actually grasped was always the same intermediate size, irrespective of the virtual visual target presented on a given trial. In this condition, DF's in-flight adjustments in grip aperture continued to scale to the width of the visual cylinder even though its felt size remained constant from trial to trial. After a number of trials of course, DF's grip apertures (just like those of the controls) began to converge on the width of the intermediate-sized cylinder. These results suggest that (1) the programming of grip aperture principally relies on visual input and does not require congruent haptic feedback about the width or the finger contact positions, and (2) the visuomotor networks of DF's dorsal stream that program grip aperture retain the normal capacity to adapt to the haptic (i.e. real) size of goal objects (Whitwell et al. 2014). Nevertheless, this work revealed one important limitation in the interpretation of these experiments as well as Schenk's (2012a) original study. It turns out that the cylinders used in both studies are sub-optimal for testing dissociations between grasping and perceptual estimation because the critical target feature of the cylinders, their width, was correlated with other features that DF is known to be capable of perceiving (e.g., overall surface area or size). In fact, this is undoubtedly why DF's ability to indicate the widths of these cylinders was better than chance when manually estimating this feature and when asked to point to the larger of two simultaneously-presented cylinders (Schenk 2012a; Whitwell et al. 2014). Thus, the third aim of the current investigation was to replicate the findings of this ‘constant haptic-width’ experiment using target objects that vary in width but have the same overall surface area (“Efron blocks”, Efron, 1969). The use of such objects, which DF cannot tell apart perceptually, would provide even stronger evidence that DF’s intact grip scaling (and limited motor adaptation) depends on dorsal-stream mechanisms.

4.2 Methods

4.2.1 Participants

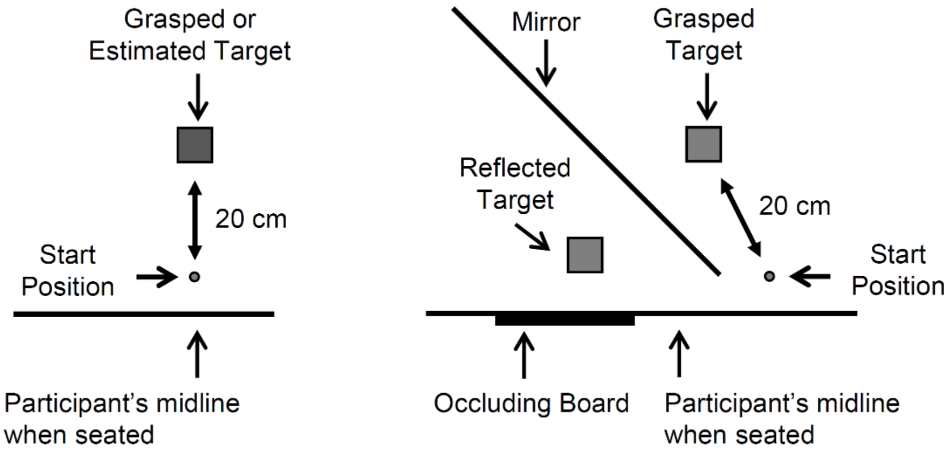
As a result of accidental carbon monoxide poisoning in 1988, patient DF (58 years of age at the time of testing), developed a severe and long-lasting visual form agnosia. Neurological scans soon after her accident revealed bilateral lesions to her lateral occipital cortex (Milner et al. 1991), and later scans revealed additional small bilateral lesions to her superior parietal occipital cortex (Bridge et al. 2013). Psychophysical testing revealed that her visual acuity, colour, intelligence, and haptic recognition were intact, although there was a log-unit reduction in her sensitivity to spatial frequencies under 5 cycles/deg. Her visual fields were also intact up to approximately 30° (Milner et al. 1991) and have remained so for some time (see Hesse, Ball, & Schenk, 2012). In addition to testing patient DF, we tested 20 normally-sighted gender-matched and age-appropriate controls (*M* = 59.6 years of age, *SD* = 9.6 years). The experimental procedures were approved by the local Ethics committee and were in accordance with The Code of Ethics of the World Medical Association (Declaration of Helsinki) for experiments involving humans. Informed consent was obtained from all of the participants before the experimental session began. The controls were compensated $20 for their time.

4.2.2 Experimental Apparatus, Protocol, and Design

All of the participants, including DF, were seated comfortably in front of a table for the duration of the experiment. DF was tested in Durham, UK, whereas the control participants were tested in London, Canada. An Optotrak 3020 optoelectronic recording system (Waterloo, ON, Canada) was used to capture the control participants' hand movements, whereas a trakSTAR (Ascension Technologies) motion capture system recorded DF's hand movements. Both motion-capture systems tracked the positions of their respective markers at 80 Hz. The Optotrak 3020 was configured to record for 3 s at the beginning of the trial, whereas the trakSTAR was configured to record for 4 s. For both the control participants and DF, one motion-tracking marker was attached to the distal interphalangeal joint of the thumb, a second marker was attached to the distal interphalangeal joint of the index-finger, and a third marker was attached to the metaphalangeal joint of the index-finger. For the practice and experimental trials, the participants wore PLATO LCD goggles (Translucent Technologies Inc., Toronto, ON, Canada) to prevent the participants from viewing the workspace between trials. The goggles are equipped with lenses that switch from a translucent default state that permits only diffuse vision to a transparent one in less than 6 ms.

We used two different sets of ‘Efron blocks’ as the target objects. As such, the members of both sets possessed identical weight surface area (25 cm^2 for each of the sets we used) but they possessed different heights and were painted differently (1 cm in height, matte grey vs. 1.5 cm in height, matte yellow phosphorescent paint). Each set varied in their lengths and widths (grey set, $w \times l$: 3 cm × 8.3 cm, 5 cm × 5 cm, and 4 cm × 6.3 cm, side ratios: 2.8, 1, and 1.6; yellow set, $w \times l$: 2 cm × 12.5 cm, 3.6 cm × 6.9 cm, and 5 cm × 5 cm, side ratios: 6.3, 1.9, and 1). Both sets were used to test DF in a previous experiment (see Whitwell et al., 2014). The yellow set was administered to test DF’s ability to use haptic information to improve the accuracy of her manual (perceptual) reports of Efron block width. In the initial tests of shape recognition following DF’s accident, Milner et al. (1991) showed that her ability to discriminate pairs of adjacent blocks depended to some extent on the differences in their aspect ratios. The grey set included additional members which allowed a subset of blocks from this set to be selected that possessed side ratios that varied less than those of the yellow set. Whitwell et al. opted to use this set to determine whether viewing the blocks directly or in a mirror had any influence on DF’s manual estimates. Here, we simply followed suit. This allowed us to (1) use the manual estimation task in which she viewed the targets directly to explore the effect of online visual feedback on the tests for dissociation and (2) use the manual estimation task in which she viewed the targets in a mirror to explore the effect of constant haptic feedback on the tests for dissociation. Both sets of blocks were presented against a white background under normal room illumination. The start button was located approximately 5 cm from the edge of the table facing the participant along the participant's sagittal plane, and the target was located approximately 20 cm from the starting position such that its target extent (width) was parallel to the participant's sagittal plane (see Fig 4-1A).

A. Schematic bird's eye view of the setups



B. Protocols for the experiments

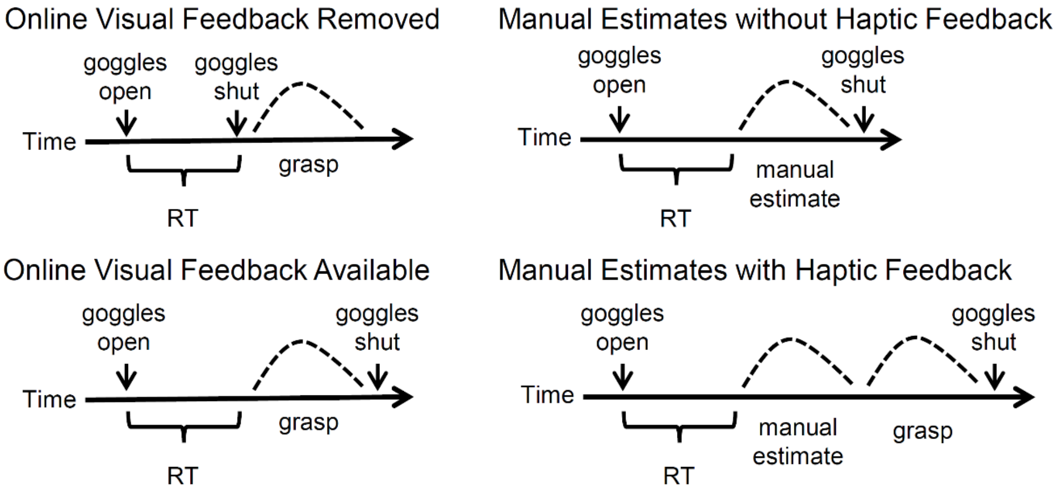


Figure 4-1. Schematic illustration of the setup and protocol. (A) A schematic above-view of the experimental setups for (Left) the tests of (1) online visual feedback on grasping and (2) haptic feedback on manual (perceptual) estimation and (Right) the tests of visual-haptic incongruence on DF's grasps. (B) The within-trial timing of the events for (Left) the grasping tasks with and without online visual feedback and (Right) the manual estimation tasks with and without haptic feedback immediately after each estimate. The mirror-based grasping tasks were performed with online visual feedback about the target, but because the mirror obstructed the participants' view of their hand and arm during their reaches, they received no re-afferent visual feedback. The start button was positioned so that the participants could see their hand at the start of the trial. This was to allow them the opportunity to compare their grip aperture with the target during the manual estimation task.

The width of the target was verbally explained and manually indicated to the participant as the front-to-back dimension of the target before each task was administered. Before the start of each trial, the participants assumed a default starting posture in which the tips of their thumb and index-finger were pinched together, depressing the start button, while their hand rested on the table. At the beginning of all trials, the lenses of the goggles cleared to allow the participants a full view of the workspace, including the target and the participant's hand. For all of the grasping and perceptual estimation tasks, the "go" signal was the opening of the goggles. In each experiment, the manual estimation trials were administered before the grasping trials, so as to minimize the putative contribution haptic feedback about the target might make to width estimation. To familiarize the participants with the tasks and the timing of the events in the trials, the participants were allowed three non-recorded practice trials before the start of the experimental trials.

4.2.3 Testing the role of online visual feedback on grasping

For this experiment, a manual estimation task was first administered so that the tests for dissociations with and without online visual feedback throughout the grasping movement involved the same set of Efron blocks. For the manual estimation task, the participants were instructed to keep the base of their hand positioned firmly on the table at all times. The participants were asked to fixate the target once the goggles cleared at the start of the trial and then indicate their estimate by lifting their fingers from the start button and separating their thumb and index finger an amount that matched the width of the target. Following the release of the start button, the control participants were provided with two additional seconds of full vision to complete their response. The participants were asked to be as accurate as possible when estimating the width of each block. To this end, the participants were informed of the time limit and that that they could look freely between the target and their hand. The participants were also asked to keep their fingers as still as possible once they were satisfied with their estimate, so that their manual estimate aperture (MEA) could be determined offline using grip stability (by measuring grip aperture velocity). Given the visual nature of her impairment, DF was provided with four additional seconds of full vision following her release of the start button. All participants were presented with each block six times in the pseudorandom order.

Next, we administered the grasping tasks: one with vision removed from the beginning of the movement onwards (visual open-loop) and one with vision available throughout the movement (visual closed-loop). For these grasping tasks, the participants were asked to reach out to pick up the target across its width using their thumb and index-finger as quickly and accurately as they could, place it back down on the table and then return to the start button as soon as the goggles cleared. Again, we used the grey set of Efron blocks for this task. As was done for the manual estimation task, the width of the target was explained to the participants (and indicated as such) as the near-far dimension of the target. In the visual open-loop condition, when the participants released the start button, the goggles switched from their clear state to their translucent one and remained so until the start of the next trial. Thus, in this condition, the participants could no longer view the workspace as their limb and hand moved to pick up the object, put it back down, and return to the start button. In the visually closed-loop condition, however, the goggles remained clear for 2 s following the release of the start button. This meant that the participants could see their hand and the target throughout the movement, which included the point at which the participants grasped the target. Thus, when the participant's hand closed down on the target, both visual and haptic feedback about the target were available (see Fig. 4-1B). For all participants, including DF, one series of open-loop grasping trials were administered before one series of closed-loop grasping trials. In a given series of trials, each Efron block was presented four times in a pseudorandom order such that each target block had an equivalent probability of being preceded by itself or any of the other blocks. One trial was added, of course, to account for the fact that the first trial possesses no immediate trial history. These orders have the advantage of minimizing any effects of autocorrelation on biasing measures for one target block over another, particularly for condition comparisons within an individual (see e.g. Whitwell et al. 2014).

4.2.4 Testing the role of haptic feedback on visual perceptual size-estimation

The experimental manual estimation task without haptic feedback was identical to the manual estimation task discussed in Section 2.2.1, except that we used the yellow set of Efron blocks rather than the grey ones. In fact, DF was tested in a variant of this task previously (see Whitwell et al. 2014). In that task, each of the Efron blocks was administered five times in a pseudorandom order, and so we simply administered the same protocol for the controls.

The manual estimation task in which haptic feedback was made available was identical to the manual estimation task in which haptic feedback was not available, except that after the participants were satisfied with their estimate, they were asked to reach out and pick up the target, place it back down on the table, and then return to the start button to await the next trial. Furthermore, the participants were provided an additional 4 s following the release of the start button so that they could see their hand reaching out and grasping the target just like they would do for the grasping trials in which visual feedback was permitted. This protocol also permitted the time from object contact on one trial to the start of the following trial to be consistent with that of the grasping tasks. Again, the participants were informed of how long the goggles would remain open once they released the start button. For this task, we used the yellow set of Efron blocks (as reported for DF in Whitwell et al. 2014), and each Efron block was administered 10 times in a pseudorandom order. Note that this variant of the manual estimation task was administered in a separate series of trials immediately after the estimation task without haptic feedback was completed.

To test for a dissociation between each of the two variants of the manual estimation task and grasping, a grasping task was administered using the same set of yellow Efrons. This grasping task was performed with 2 s of full vision throughout the response. Each Efron block was presented five times in a pseudorandom order. The participants were asked to reach out to pick up the target across its width using their thumb and index-finger as quickly and accurately as they could, place it back down on the table, and then return to the start button.

4.2.5 Testing the role of haptic feedback on grasping

A few months after the tests of online visual feedback and haptic feedback on grasping and manual estimation were administered, the 20 participants were invited back for one additional test session in which grasping and manual estimation tasks were performed using the mirror-based virtual environment (see Fig. 4-1A). The participants first performed a manual estimation task without haptic feedback as discussed in Section 4.2.4, except, of course, that the participants viewed the Efron blocks in the mirror rather than directly. Next, the participants were asked to reach out to pick up the Efron blocks that they viewed virtually via the mirror in two grasping tasks. In one version of the task, an identical block was positioned behind the mirror such that it was spatially coincident with the apparent spatial location of the visual one. In a second version, the block positioned behind the mirror was always of the same intermediate-width and was centered at the apparent position of the virtual block. The grey set of Efron blocks was used for these tasks, and each of the three Efron blocks from this set was presented six times in a pseudorandom order for each task with one additional trial in the veridical haptic feedback variant to balance the immediate trial history of the presentation order. Note that in this condition, re-afferent online visual feedback about the moving hand and limb was not available as soon as the hand moved behind the mirror (see also Schenk, 2012a; Whitwell et al. 2014).

4.2.6 Data preprocessing and analysis

The data were processed offline with custom software written in Matlab (Mathworks Inc., Natick, MA, USA). The positional data from the markers was low-pass filtered at 20 Hz using a 2nd order Butterworth digital filter. Grip aperture was computed as the Euclidean distance between the marker placed on the thumb and the marker placed on the index-finger, and the instantaneous velocities were computed for each of the three markers and for grip aperture.

The principal measures for the grasping tasks were peak grip aperture (PGA) and peak hand velocity (PHV). The PGA reflects the maximum extent that the thumb and index-finger opens as the hand approaches the target but before the hand contacts it. The PHV reflects the maximum velocity achieved by the hand during the movement. Thus, for each grasping trial, a search window was isolated and the PGA and PHV then extracted from it. The onset of the target-approach phase of the movement was defined as the first of 20 consecutive sample frames (250 ms) during which the instantaneous speed of the index finger marker exceeded 20 mm/s. The duration requirement was used to avoid incorporating incidental finger movements into the analysis. The end of the approach phase of the grasp was defined as the first sample frame in which the speed of the index finger marker fell below 100 mm/s.

The principal measure for the manual estimates was the manual estimate aperture (MEA). The MEA was operationally defined as the first of 10 consecutive frames (125 ms) during which the rate at which the aperture changed fell below 10 mm/s following the onset of the movement. The same threshold for the onset was used for the manual estimations as was used for the grasps, but because manual estimates are typically shorter in duration than grasping movements, the duration criterion for the onset was relaxed to 10 consecutive frames for this task. Because the participants were asked to keep their thumb and index-finger stable once they were satisfied that their aperture reflected the target's size, this definition was designed to capture their considered estimate. Each trial was visually inspected for gross errors in the automated selection of the dependent measures (PGA and MEA). Corrections for such errors were made by increasing or decreasing the duration criterion, and, on rare occasion [seven of the 20 control participants; of those seven, 1.9 trials (or 1.5 %) on average], raising or lowering the velocity threshold by relatively small increments.

4.2.7 Statistical analysis

Concerning the relationship between DF's PGA and the width of the target (i.e. 'grip scaling', or grasp 'target-size tuning'), previous examinations have reported one or more of *b*, *r*, or r^2 (Goodal, Jakobson, & Keillor, 1991; Goodale et al. 1991; Hesse, Ball, & Schenk, 2012; Himmelbach, Boehme & Karnath, 2012;

Marotta, Behrman & Goodale, 1997; Schenk 2012a; Whitwell et al. 2014). We examined the unstandardized bivariate regression coefficient (*b*), and the standardized one (i.e. Pearson's product-moment correlation, *r*). For each task, ordinary least-squares bivariate linear regression modelled the dependent measure on the independent measure in raw units (unstandardized coefficients) or in Z-transformed ones (standardized coefficients, or, more simply, the correlations). Thus, *b* reflects the predicted change in the dependent measure (in mm) following a 1 mm increase in target width. In contrast, *r* reflects the predicted change in the dependent measure, in units of SD, following a unit increase in target width SD. As such, *r* reflects how tightly the raw data points cluster around *any* non-zero slope: the greater the variability in the response measure around each target width, the smaller *r* will be (see e.g., Rodgers & Nicewater, 1988). In short, both the slopes and the correlations can be viewed in the present context as meaningful indicators of grip scaling that reflect related but different aspects of the relationship between grip aperture and target width. Following the recommendation of Cohen, Cohen, West, & Aiken (2003) and Crawford, Garthwaite, Howell, & Venneri (2003), the *r* values were Fisher-transformed, *r*′, before being aggregated and submitted for inferential analysis.

Paired-samples t-tests were employed for the targeted between-task comparisons of the dependent measures (*b*, *r*′, PGA, and PHV) for the controls. Independent samples t-tests were employed for the comparisons between the controls and DF (Crawford et al. 2003b; Crawford & Garthwaite, 2004; Crawford and Howell, 1998). The tests of normality/abnormality of DF's grip scaling when grasping objects were two-tailed because (1) our previous investigation showed that DF's grip scaling on grasping tasks is sometimes steeper than the mean grip scaling observed in the controls, and (2) the novel nature of the two experimental conditions does not warrant the use of a one-tailed test. For consistency, the tests for DF's manual (perceptual) estimates of the widths of the Efron blocks were also two-tailed. Note further that DF's estimates have been routinely shown to be severely impaired, and so the increase in statistical power that would follow a one-tailed test seemed unnecessary. When testing for a dissociation (i.e. comparing the differential performance of DF across pairs of tasks to that of the controls), we used the 'unstandardized difference test' for 'classical' or 'strong/differential' dissociations (Crawford & Garthwaite, 2005; Crawford, Garthwaite, & Gray, 2003). This test uses the sample variance of the controls' paired *task-difference scores* to evaluate the abnormality of the patient's task difference score (Crawford & Garthwaite, 2005; Crawford, Howell, & Garthwaite, 1998). Unlike the Crawford, Howel, & Garthwaite (1998) variant, the unstandardized difference test does not Z-transform the patient's scores on each task. Note that the unstandardized measure (i.e. the regression slope, *b*) is quite meaningful as it stands: it is in the same units across all tasks and taken from the same hand and fingers. The unstandardized difference tests were two-tailed. The alpha criterion was set to 0.05 for each of the tests we employed.

The comparisons of DF's grip scaling between the grasping tasks with and without visual input throughout the movements were implemented using a fixed-effects 'heterogeneous slopes' Analysis of Covariance (ANCOVA) in which DF's

PGA for each trial was treated as an independent observation. Note that (1) the lag-1 autocorrelation on her PGA yielded no significant trial-to-trial correlations for any of the grasping tasks, and (2) an inspection of the residuals plotted as a function of the independent variable showed no evidence for a non-linear relationship between PGA and target width. Thus, we compared the ‘full’ and ‘restricted’ model of DF’s PGAs regressed on the block width (the covariate), an effect-coded variable for the two tasks, and the interaction between the covariate (target width) and the task factor (i.e. the product of the covariate and task factor). The residual error for the full model was compared to the residual error for a restricted model that lacked the interaction term (see e.g., Rutherford, 2011).

4.3 Results

4.3.1 Tests of the effect of online visual feedback on grasping

4.3.1.1 Grip scaling

Without online visual feedback throughout their movements (open loop), all of the control participants showed a significant positive linear relationship between their PGA and target width as indicated by their slopes and correlations. The same was true when online visual feedback was available throughout their movements (closed loop). Patient DF also reliably scaled her PGA to target width when grasping in either open loop ($p < 5\times10^{-4}$) (see Fig. 4-2A) or closed loop, $p < 6\times10^{-6}$ (see Fig. 4-2B). Under open-loop conditions, her grip scaling did not differ

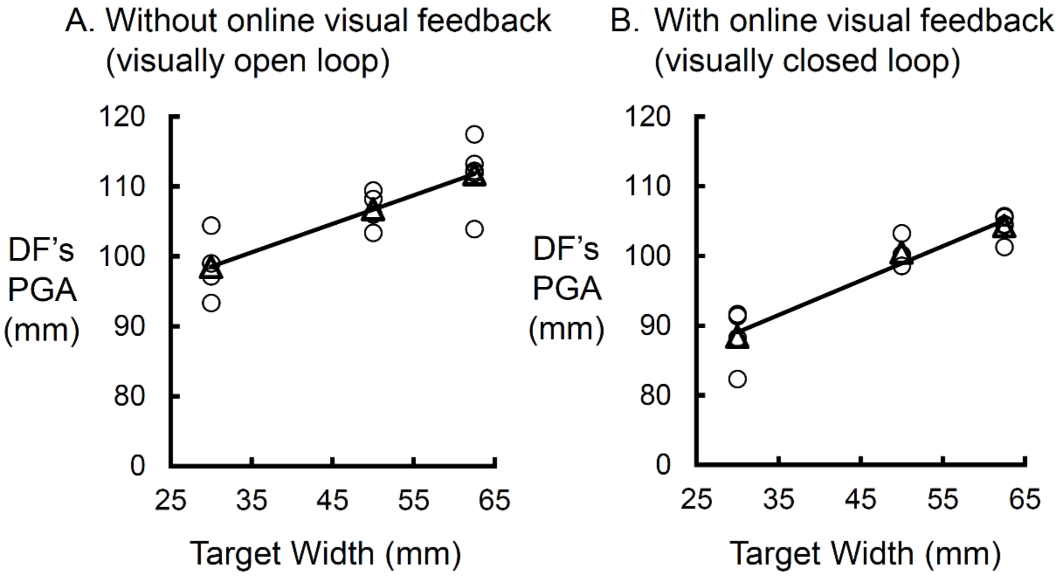


Figure 4-2. Patient DF's peak grip aperture as a function of target size (width of the Efron blocks). (A) Online visual feedback was not available throughout the movement. (B) Online visual feedback was available throughout the movement. In both conditions, DF's PGA adjusts in-flight to suit the width of the target block. Also evident is an overall increase in DF's PGA when online visual feedback is not available throughout the movement.

significantly from those of the controls as measured by slopes (p = 0.08) (see Fig.4-2A) or correlations, p = 0.24. Under closed-loop conditions, DF's grip scaling was significantly poorer than the controls' as measured by slopes ($p < 7\times10^{-3}$) (see Fig. 4-3A). When measured with correlations, however, DF's grip scaling in closed loop did not differ significantly from those of the controls, p = 0.12.

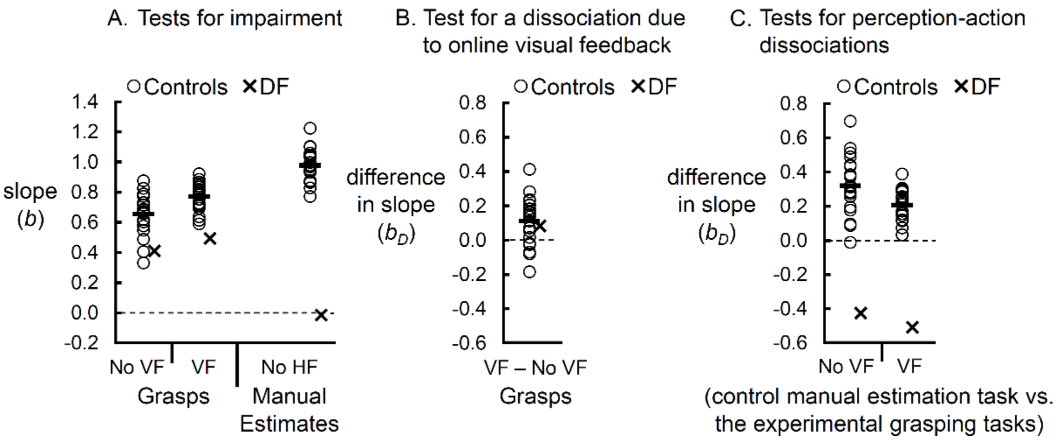


Figure 4-3. Tests of DF's slopes for impairment on the grasping and manual estimation tasks and for dissociations due to online visual feedback and due to task (perception-action dissociation). (A) The slopes *(b)* of the controls (circles) and of DF ('X's) relating either the PGAs (from the grasping tasks) or the MEAs (from the manual estimation task) to the widths of the grey Efron blocks. For the two experimental grasping tasks, online visual feedback was either absent (No VF) or present (VF) throughout the entire movement. In the manual estimation task, there was no haptic feedback about the target (No HF). In both grasping tasks, DF showed reliable positive slopes. However, her slopes fell outside the control range. DF's manual estimates bore no significant relationship to the target width, revealing a dramatic impairment in the processing of target width for perceptual report. (B) The effect of online visual feedback on the slopes (b_D). Visual feedback sharpened the relationship between the DF's PGAs and target width no more so than it did for the controls. (C) The tests for perception-action dissociations across the control manual estimation task and either the No VF or VF grasping task yielded strong/differential dissociation for both conditions.

Interestingly, compared to open loop, closed loop visual feedback increased the controls' grip scaling when either slopes ($p < 3\times10^{-3}$) or correlations ($p < 2\times10^{-3}$) were considered. DF's grip scaling showed a similar increase, but not a significant one, $p = 0.21$ (one-tailed). Nevertheless, the increase in DF's grip scaling under closed loop conditions did not differ significantly from the mean increase in the controls' grip scaling as measured by slopes [$p = 0.83$] (see Fig. 4-3B) or correlations, $p = 0.87$. Thus, in the control group, online visual feedback resulted in a mean increase in the steepness and strength of the relationship between the controls' PGA and target width. The increase in DF's grip scaling due to online visual feedback was not outside of what one can reasonably expect to be observe in the control population.

4.3.1.2 Performance on the manual (perceptual) estimation task

Not surprisingly, all of the controls in the manual estimation task showed a significant positive linear relationship between their MEAs and target width. DF's MEAs, however, bore no significant relationship to the widths of the targets, $p = 0.43$. Not surprisingly therefore, DF's slope relating her MEAs to target width was significantly shallower ($p < 2\times10^{-8}$) (see Fig. 4-3A), and the strength of the relationship between her MEAs and target width was significantly weaker ($p < 2\times10^{-6}$), than those of the controls. Thus, as expected, DF expressed a profound perceptual deficit in her ability to render explicit judgments of visual target width.

4.3.1.3 Tests for perception-action dissociations

In line with previous studies of DF's grasps with online visual feedback, DF's performance dissociated across the grasping task and the manual estimation task when either slopes ($p < 5\times10^{-7}$) (see Fig. 4-3C) or correlations ($p < 2\times10^{-3}$) were considered. Critically, we found a similar result for the open-loop variant of the grasping task. That is to say, the difference between DF's scaling when she manually estimated the widths of the targets in the control task and when she reached out to pick up the targets without online visual feedback was significantly greater than the controls' mean difference across these tasks, when either the slopes ($p < 3\times10^{-4}$) (see Fig. 4-3C) or correlations ($p < 5\times10^{-3}$) were considered. Thus, regardless of whether or not online visual feedback was available to her throughout her grasping movements, DF's performance dissociated from the controls' across the grasping and manual estimation tasks.

4.3.1.4 Peak grip aperture (PGA) and peak hand velocity (PHV)

The controls' mean PGA was significantly larger when their grasps were executed in open loop than when they were executed in closed loop, $p < 4\times10^{-4}$. DF's PGA was also significantly larger when her grasps were executed in open loop than in closed loop, $p < 6\times10^{-3}$. This increase in DF's PGA did not differ significantly from the mean increase observed in the controls' PGA, $p = 0.45$ (see Fig 4-4A). In short, DF's PGA increased just as much as the controls did in the absence of online visual feedback throughout her movements.

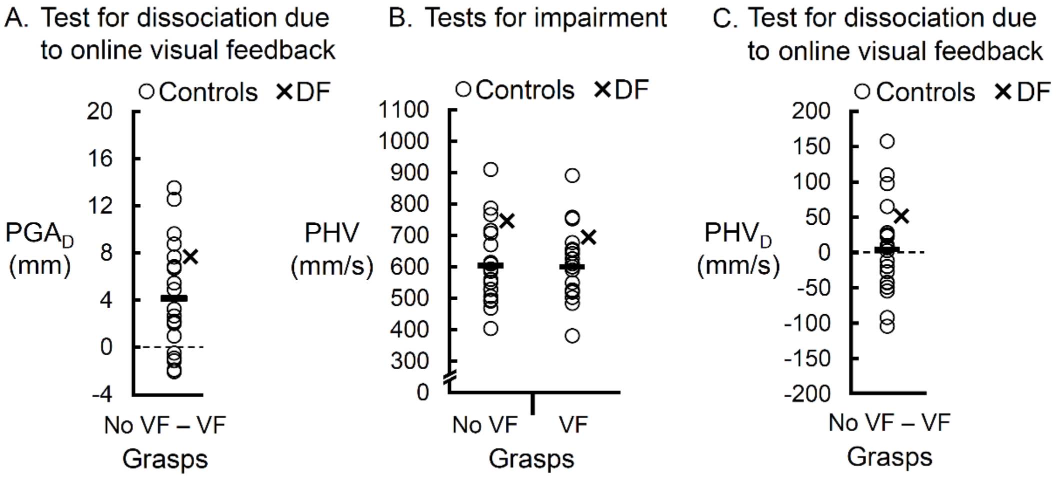


Figure 4-4. Tests for abnormality and for dissociations in DF's peak hand velocity and in the difference in DF's peak grip aperture between grasps with and without online visual feedback. (A) The difference in the controls (circles) and DF's ('X') peak grip aperture (PGA) (PGA_D) when visual feedback was suppressed throughout the grasping movement. Removing online visual feedback (No VF) significantly

increased the PGAs in the controls and in DF. The extent of this effect on DF's PGA did not fall outside of the range of those observed in the controls, suggesting that DF exhibits a normal response to the loss of online visual control throughout the movement. (B) Same as Panel A, except that peak hand velocity (PHV) is depicted for grasps executed with and without online visual feedback. The controls showed no net effect of removing online visual feedback on their PHVs. DF's PHV, however, was significantly faster without online visual feedback than with online visual feedback. Importantly, DF's PHV fell within the range of PHVs observed in the controls in each of the two grasping tasks. (C) The test for a dissociation due to online visual feedback yielded no evidence to support the notion that DF's PHV changed any differently than the controls did when online visual feedback was available.

The peak hand velocity (PHV) of DF's reaches did not differ from the controls' PHV when the grasps were executed in closed loop ($p = 0.41$) or in open loop, $p = 0.22$ (see Fig. 4-4B). DF's peak hand velocity increased significantly when her grasps were executed in open loop, $p < 0.02$. However, as Figure 4B indicates, first, the differences in the controls' PHVs were, in some cases, larger than DF's. Second, there does not appear to be any systematic effect of online visual feedback on the controls' PHV. Not surprisingly, therefore, a formal comparison of the controls' PHVs between the two tasks failed to yield any evidence for a significant effect, $p = 0.47$. Critically, the difference in DF's PHV between the two visual feedback conditions was not outside of the range of changes reasonably expected to be found in the control population, $p = 0.75$, indicating that online visual feedback fails to influence the PHV of DF's grasps any differently than it does those of the controls (see Fig 4-4C).

4.3.2 Tests of the effect of haptic feedback on manual (perceptual) estimates of target width

4.3.2.1 Performance on the manual estimation tasks

All of the controls showed reliable positive relationships between their MEAs and target width both with and without haptic feedback about the target. In fact, the addition of haptic feedback did not reliably influence the steepness ($p = 0.52$) or the strength ($p = 0.3$) of the relationship between the controls' MEAs and target width. In contrast to the controls' performance, DF's MEAs bore no significant relationship to the width of the targets regardless of whether she did ($p = 0.19$) or did not receive haptic feedback about the target immediately after she provided each of her estimates ($p = 0.23$). Not surprisingly, therefore, the test of the relationship between DF's MEAs and target width indicated a significant impairment when haptic feedback was available [slopes: $p < 4\times10^{-9}$ (see Fig. 4-5A); correlations: $p < 7\times10^{-8}$] and when it was not [slopes: $p < 2\times10^{-9}$ (see Fig. 4-5A); correlations: $p < 6\times10^{-5}$]. Finally, the effect of haptic feedback, if any, on the relationship between DF's MEAs and target width did not differ from that on the controls when either the slopes ($p = 0.79$) (see Fig. 4-5B) or correlations ($p = 0.85$) were considered.

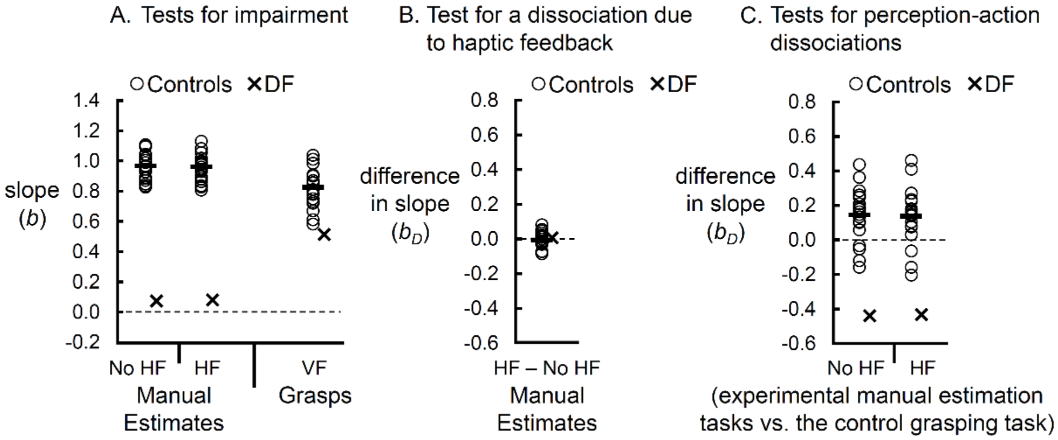


Figure 4-5. Tests of DF's slopes for impairment on the manual estimation and grasping tasks, for dissociation due to haptic feedback, and for the perception-action dissociation. (A). The slopes (*b*) of the controls (circles) and of DF ('X's) relating either the MEAs (from the manual estimation tasks) or the PGAs (from the grasping task) to the widths of the yellow Efron blocks. For the two experimental manual estimation tasks, haptic feedback was either unavailable (No HF) or available (HF), but visual feedback was available in both. In the latter variant, the participants reached out to pick up the target with visual feedback immediately after each estimation. In the grasping task that was administered as a control for the two estimation tasks, online visual feedback was available throughout the movement (VF). In each of the manual estimation tasks, DF's MEAs bore no significant relationship to target width, revealing a dramatic impairment in perceptual width processing, regardless of the availability of haptic feedback after each of her estimates. Although DF's PGAs were significantly related to target width, her slope fell outside of the range of slopes observed in the controls in this task (B) The effect of haptic feedback on the manual estimation slopes (b_D). The addition of haptic feedback did not change the slope relating either DF's MEAs to target width or mean slope relating the controls' MEAs to target width. The test for dissociation due to haptic feedback in the manual estimation tasks yielded no evidence to support the notion that the addition of haptic feedback altered DF's manual estimation slopes any differently than it did for the controls (C) The tests for perception-action dissociations indicated a strong/differential dissociation when the manual estimation included haptic feedback about the target and again when the manual estimation task did not include haptic feedback.

4.3.2.2 Grip scaling in the grasping task

All of the control participants scaled their PGA to target width in the grasping task that was administered to permit tests for dissociations across the grasping and manual estimation tasks with and without haptic feedback. DF also scaled her

PGA to target width in this control grasping task, $p < 4\times10^{-5}$. Her grip scaling, as measured by slopes, indicated an impairment ($p < 0.02$) (see Fig. 4-5A). When correlations were considered, however, DF's grip scaling fell within the control range, albeit towards the lower end, $p = 0.14$.

4.3.2.3 Tests for perception-action dissociations

A test of the difference in DF's performance between the grasping task and the manual estimation tasks with and without haptic feedback against the respective differences in the controls' performance indicated a dissociation regardless of whether the manual estimation task included haptic feedback about the target block [slopes: $p < 3\times10^{-3}$(see Fig. 4-5C); correlations: $p < 8\times10^{-3}$] or not [slopes: $p < 8\times10^{-4}$ (see Fig. 4-5C); correlations: $p < 0.02$].

4.3.3 Tests of the effect of varying visual width while keeping haptic width the same

4.3.3.1 Grip scaling in the grasping tasks

Patient DF ($p < 3\times10^{-7}$) and all of the control participants showed significant grip scaling when visual and haptic widths of the Efron blocks were congruent (veridical haptics) and when the visual and haptic widths were incongruent due to the fact that the haptic width remained the same intermediate size from trial to trial (constant haptics) (DF: $p < 5\times10^{-4}$). Importantly, DF's grip scaling did not differ significantly from the controls' grip scaling for either the two mirror-based grasping tasks when either slopes (veridical haptics: $p = 0.36$; constant haptics: p

= 0.25) (see Fig. 4-6A) or correlations (veridical haptics: $p = 0.63$; constant haptics: $p = 0.48$) were considered.

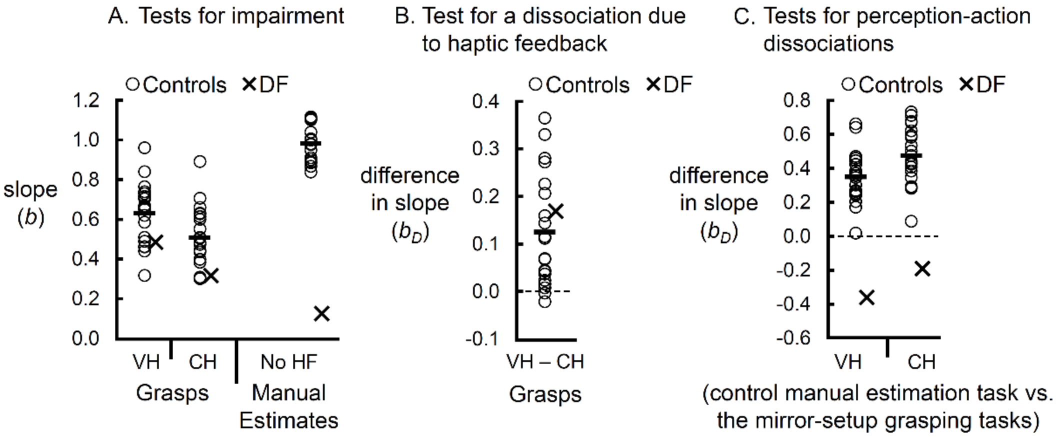


Figure 4-6. Tests of DF's slopes for impairment on the grasping tasks with and without congruent haptic feedback and grasping tasks, for dissociation due to incongruent haptic feedback, and for the perception-action dissociation. The slopes (b) of the controls (circles) and of DF ('X's) relating either the PGAs (from the grasping tasks in which the mirror was used) or the MEAs (from the manual estimation task) to the widths of the grey Efron blocks. In the grasping tasks, the visual and haptic width of the target were congruent (veridical haptics: VH), or the haptic width, but not the visual one, remained the same (constant haptics: CH). In the control manual estimation task, there was no haptic feedback about the target (No HF). In both grasping tasks, DF showed reliable positive slopes that fell within the control range. DF's manual estimates bore no significant relationship to the target width. (B) Grasping a target of varying visual width and a constant intermediate-sized haptic width blunted the slope relating DF's PGA and target width (b_D) no more than it did for the controls. (C) The tests for perception–action dissociations across the control manual estimation task and the two mirror-based grasping tasks (VH and CH) yielded a classical dissociation for both.

The controls' grip scaling was significantly reduced when the haptic widths of the Efron blocks were constant than when they were veridical (slopes: $p < 2\times10^{-4}$; correlations: $p < 7\times10^{-5}$). DF showed a similar effect ($p < 0.04$, one-tailed). Notably, the differences in DF's grip scaling across the two conditions fell well within the range of differences observed in the controls [slopes: $p = 0.72$ (see Fig. 4-6B); correlations: $p = 0.88$].

4.3.3.2 Performance on the manual (perceptual) estimation task

Not surprisingly, all of the controls in the manual estimation task showed a significant linear relationship between their MEAs and width of the blocks viewed in the mirror. DF's MEAs, however, bore no significant relationship to the widths of the targets, $p = 0.24$. Not surprisingly, DF's slope relating MEA and target width was significantly shallower ($p < 2\times10^{-8}$) (see Fig. 4-6A) and the strength of the relationship significantly weaker ($p < 3\times10^{-6}$) than those of the controls. Thus, as expected, DF expressed a profound perceptual deficit in her ability to render explicit judgments of visual target width.

4.3.3.3 Tests for perception-action dissociations

The difference in DF's performance across the manual estimation task and the mirror-grasping task in which the visual and haptic width of the target were congruent (veridical haptics) fell well outside the range of differences scores observed in the controls when either slopes ($p < 2\times10^{-4}$) (see Fig. 4-6C), or correlations ($p < 6\times10^{-4}$) were considered.

Critically, we found a similar result when the test involved the mirror-grasping task in which the haptic width of the target remained the same intermediate size (constant haptics) –

DF's difference score fell well outside of the normal range of difference scores when either slopes ($p < 4\times10^{-4}$) (see Fig. 6C) or correlations ($p < 3\times10^{-3}$) were considered. Thus, DF's grip scaling during grasping showed a clear dissociation from her manual estimation performance, regardless of whether or not haptic feedback about the object was veridical or constant.

4.3.3.4 Adaptation in the peak grip aperture (PGA)

The controls' PGA was significantly larger when the target's haptic width remained the same intermediate size (constant haptics) than when the visual and haptic widths were congruent (veridical haptics), $p < 2\times10^{-3}$. DF's PGA showed a similar, though not significant increase ($p = 0.23$). Nevertheless, the increase in DF's PGA did not fall outside of what we observed in the controls' PGA, $p = 0.52$.

As compared with the congruent haptics task, adaptation of grip aperture to the target's constant intermediate haptic-size predicts an increase in the PGA when the participants reach out for the block with a smaller visual width and a decrease in the PGA when the participants reach for the block with a larger visual width. Note, however, that the overall difference in PGAs between the two tasks renders this intuitive and direct test of the PGAs problematic. Fortunately, the prediction can be reformulated in a way that avoids this confound. Relative to when the visual and haptic widths of the target blocks are congruent, adaptation to the target's constant intermediate-sized haptic width predicts an overall smaller deviation from the task mean PGA when the participants reach out for the block with the small or large visual width.

In line with this prediction, when the control participants viewed the block with the small width, the mean deviation in PGA was significantly smaller when the haptic width remained the same intermediate size than when the haptic and visual width were congruent, $p < 7\times10^{-4}$. A similar effect was observed for the complementary comparisons for the block with the large visual width, $p < 2\times10^{-3}$. Interestingly, DF showed similar effects, although the deviation in her PGA was significant only for the block with the large visual width ($p < 0.03$, one-tailed). Critically, this adaptation in DF's PGA did not differ significantly from the mean adaptation in the controls' PGA for either the block with the small ($p = 0.36$) visual width or the one with the large visual width, $p = 0.69$ (see Fig. 4-7).

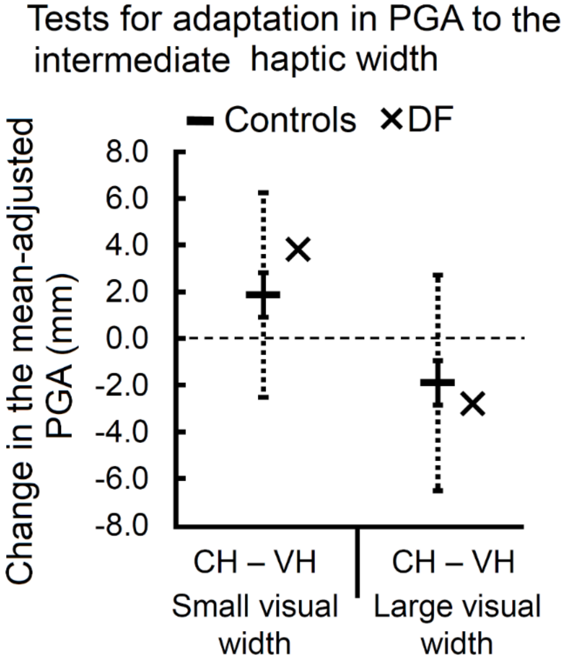


Figure 4-7. Partial adaptation in patient DF's peak grip aperture to the haptic width of the target. Adaptation was assessed by a comparison of the grasping task in which the visual and haptic width of the target were congruent (veridical haptics: VH) and the grasping task in which the haptic width (but not the visual one) remained the same (constant haptics: CH). Adaptation is evidenced by changes in the task-mean adjusted PGA towards the haptic width of the target. Specifically, for grasps directed at the target block with the small visual width, the task-mean adjusted PGA is larger in the CH task than it is in the VH task. For grasps directed at the target block with the large visual width, the task-mean adjusted PGA is smaller in the CH task than it is in the VH task. Solid error bars reflect 95% confidence interval for a comparison of the controls' mean adaptation against zero.

The dashed error bars reflect the 95% confidence interval for comparisons of DF’s adaptation against the controls’.

4.3.3.5 Peak hand velocity (PHV)

DF’s PHV when the visual and haptic widths of the targets were congruent (veridical haptics) and when the haptic width of the target remained the same intermediate size (constant haptics) did not deviate significantly from those of the controls for either of the two tasks (veridical haptics: $p = 0.95$; constant haptics: $p = 0.81$). DF’s reaches achieved significantly faster PHVs when the haptics were veridical then when they were constant, $p < 2\times10^{-3}$. Many of the controls, however, showed larger deviations, but since there was no systematic direction of the difference scores, the PHV of the controls remained unchanged across the two mirror-grasping tasks, $p = 0.78$. Critically, the difference between tasks in DF’s PHV was similar to the mean difference in the controls ($p = 0.53$). In short, DF’s PHV did not differ in any respect from what we can reasonably expect to observe in the control population.

4.4 Discussion

Goodale and Milner (1992) have argued that DF’s spared ability to scale her grasp when reaching out to pick up objects relies on relatively intact processing by visuomotor modules in the dorsal stream. Recently, however, it has been suggested that “visual information in the dorsal stream about the target object” by itself is not enough to mediate accurate grasping and that “either haptic information, visual information from the ventral stream, or online visual feedback is also required” (page 2017: Schenk, 2012a). The results of the current experiments do not support this claim that online visual feedback or visual processing in the ventral stream are required for accurate grasping, at least for simple objects like rectangular blocks. Moreover, simple tactile feedback signaling the end of the movement would appear to be all that is required to maintain normal target-directed grasping behaviour. Milner, Ganel, & Goodale (2012) have argued that, without tactile feedback, the grasping movements become pantomimed, and recent evidence suggests that this is true (Byrne, Whitwell, Ganel, & Goodale, 2013). In short, our findings support the original proposal by Goodale and Milner that visual processing in the dorsal stream is sufficient to mediate accurate grasping in DF, and presumably in healthy individuals as well.

In the first of three experiments, we demonstrated that when DF was denied visual information about the target or her moving hand during the execution of the grasp, her in-flight grip aperture continued to reflect the width of the target, just as it did in the control participants. Nevertheless, suppressing vision throughout the movement was not without consequences for DF or for the control participants. Compared to grasps executed with visual feedback, grasps that were executed without online visual feedback showed a significantly shallower and weaker relationship between grip aperture and target width and a significantly larger overall grip aperture. These findings are largely in agreement with those of previous investigations of the influence of online visual feedback on grip scaling and the overall peak grip aperture (PGA) in normally-sighted individuals in our laboratory and others, and reflect the normal influence of online visual feedback in the programming and updating of grip aperture (Hesse & Franz, 2009; Hesse & Franz, 2010; Jakobson & Goodale, 1991; Tang, Whitwell, & Goodale, 2014; Whitwell & Goodale, 2009; Whitwell, Lambert, & Goodale, 2008). Importantly, neither the reduction in the sharpness or strength of grip scaling nor the increase in overall PGA that was observed in DF was different from that observed in the neurologically healthy participants. This finding converges on other work showing that DF is able to orient her wrist correctly in a posting task in the absence of any online visual feedback from either the target slot or her moving hand (Hesse & Schenk, 2014). In our grasping tasks, the peak speed of DF's hand on its approach to the targets did not differ significantly from that of the control participants no matter whether online visual feedback was available or not. Nor did the effect of online visual feedback on this aspect of DF's grasping differ significantly from the overall null effect observed in the controls. In other words, online visual feedback did not systematically influence DF's peak hand velocity any differently than it did the controls', making it unlikely that her successful grip scaling without online visual feedback was the result of some sort of speed-accuracy trade-off. In short, the processing of online visual feedback during prehension appears to operate normally in DF. Overall, these results lend additional support to the idea that, in programming DF's grasp, the visuomotor machinery in her dorsal stream operates chiefly in a feedforward manner, making use of visual information about the target that is processed before movement onset.

As discussed earlier in Section 4.1 (Introduction), it has been suggested that the reason DF does better on grasping than on manual estimation tasks is that she typically gets haptic feedback at the end of each target-directed grasp but never after providing a perceptual estimate of target width (Schenk, 2012a). In other words, in the manual estimation task, unlike grasping, DF never has an opportunity to compare her manual estimation with feedback from actually touching the object at the end of the trial. Perhaps DF integrates haptic information about the target with degraded visual information about the target, resulting in a combined estimate that is superior to either estimate alone. The combined estimate would, it is argued, allow her to compensate for her impoverished form vision in the grasping task but not in the manual estimation task. As it turns out, this explanation is not correct. In an earlier study (Whitwell et al., 2014), we demonstrated that when DF is provided with such feedback by allowing her to pick up the object after she has made her estimate of its width, her performance does not improve. In that study, however, we did not compare her relative performance in the two conditions (manual estimations with and without haptic feedback) with that of healthy control participants. In the second experiment of the present study, we have shown that DF’s performance on manual estimation is significantly worse than that of 20 control participants – irrespective of whether or not she is allowed an opportunity to pick up the target objects. Her performance is essentially at chance in both conditions. In contrast, the controls performed equally well in both conditions. In short, there is no evidence that the absence of haptic feedback about object width is responsible for

DF's inability to report the width of objects. She has a fundamental deficit in visual form perception, which no amount of haptic feedback can ameliorate.

In a final experiment, we tested the dependence of DF's accurate grasping on veridical haptic feedback, using targets which she could not discriminate amongst. In fact, we had examined this same question in an earlier experiment which used the same mirror apparatus (Whitwell et al. 2014). We found that DF continued to scale her grasp to the width of a virtual cylinder that varied in size from trial to trial, despite the fact that the width of the actual target behind the mirror retained the same intermediate size throughout. However, the cylinders used in Schenk's (2012a) and therefore in our own earlier study varied in both width *and* overall size, and DF can visually discriminate objects on the basis of differences in their overall size (Whitwell et al. 2014). Thus, it is possible that she could use this information to scale her grip aperture to target width. To rule out this possibility, we repeated the experiment here using Efron blocks in which the width but not the overall size varied. Again we found that DF was able to scale her grasp successfully despite an absence of veridical haptic feedback, suggesting that the dorsal stream, rather than the ventral stream, mediates her spared grip scaling, even when the haptic width of the target remains the same size.

One additional observation from the current study warrants some discussion. In our final experiment, we replicated a finding from Whitwell et al.'s (2014) experiment in which DF and the controls reached out to grasp virtual cylinders that varied in their visual width but had, in fact, a constant intermediate haptic width. In that study, DF's peak grip aperture, and indeed those of the controls, began to converge towards the width of the grasped cylinder behind the mirror. In the current study, we observed the same tendency in both DF and the controls but with Efron blocks, which DF has been shown to be particularly bad at discriminating. In other words, in the absence of any explicit access to the form of these objects, DF's peak grip aperture began to adapt over the course of the experiment to the width of the intermediate-sized block behind the mirror, and the adaptation we observed in DF did not differ from that observed in the controls. The observation that grip aperture in normally-sighted individuals is updated to reflect the haptic width of the grasped object is not novel and is in agreement with the results of previous investigations that have used a similar manipulation (Gentilucci, Deprati, Toni, Chieffi, & Saetti, 1995; Pettypiece, Goodale, & Culham, 2010; Saftstrom & Edin, 2004, 2008). Nevertheless, the fact that DF shows a similar capacity in the absence of any perceptual information about target width is an important and new contribution – one which suggests that the ventrolateral structures in the ventral stream that are critical for form perception are not necessary for updating the programming of grip aperture and that such updating is carried out instead by visuomotor networks in the dorsal stream.

In any event, the present findings, coupled with Schenk's (2012a) original observation that DF failed to scale her grasp to target width in the absence of any haptic feedback from the target, suggests that simple terminal information from contact with the object, rather than veridical haptic information about the object, is enough to keep the visuomotor networks in DF's dorsal stream operating effectively – and that DF's grip scaling, like that of healthy participants, chiefly relies on visual feedforward information. These findings are in agreement with the observation that intermittent haptic feedback from the goal object is sufficient to keep DF's grip aperture tuned to the target's visual width (Schenk, 2012a). Importantly, the present findings show that *veridical* haptic feedback about the target is not necessary to maintain grip scaling provided that the haptic and visual targets are coarsely co-localized (e.g. co-centered) and are highly similar in shape (e.g., cylinders that vary in diameter only, or simple rectangular and square blocks).

Interestingly, if we accept that contact with the surface of the workspace constitutes terminal tactile feedback for target-directed grasps, then terminal tactile feedback can explain why DF continues to show significant grip scaling when reaching out to pick up 2D Efron shapes (Westwood et al. 2002). Terminal tactile feedback might influence two aspects of a target-directed grasp. First, it might operate on top-down processes, minimizing cognitive supervision and preventing the participants from changing the way they approach the task. Second, terminal tactile feedback might operate on the bottom-up aspects of the programming of grasps. Presumably, contact with the visual target at the end of the grasping movement contributes spatial information about the width of the target and/or information about the timing of the finger contact with the target that the visuomotor system uses to update the programming of grip aperture for subsequent grasping movements.

In summary, the results of these experiments and our earlier work (e.g., Goodale et al. 1991; Whitwell et al. 2014) converge on the idea that DF's spared visual control of grasping makes use of feedforward visual information in a manner similar to that in neurologically intact individuals. The results also suggest that the dorsal stream alone, without the help of form-processing areas in the ventral stream, is able to use tactile feedback about the width of the target to update the programming of grip aperture. Moreover, the clear dissociation between DF's perceptual and visuomotor abilities in these experiments, coupled with evidence from other neuropsychological, neuroimaging, and neurophysiological studies (for review, see Goodale, 2011; Milner & Goodale, 2006, 2008; Westwood & Goodale, 2011), continues to provide strong support for the Two Visual Systems hypothesis. In short, the visual perception of objects relies on neural mechanisms that are to a large degree separate from those mediating the visual control of object-directed actions (Goodale & Milner, 1992).

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Chapter 5

5 Real-time vision, tactile cues, and visual form agnosia: Removing haptic feedback from a ‘natural’ grasping task induces pantomime-like grasps

Investigators study the kinematics of grasping movements (prehension) under a variety of conditions to probe visuomotor function in normal and brain-damaged individuals. ‘Natural’ prehensile acts are directed at the goal object and are executed using real-time vision. Typically, they also entail the use of tactile, proprioceptive, and kinaesthetic sources of haptic feedback about the object (‘haptics-based object information’) once contact with the object has been made. Natural and simulated (pantomimed) forms of prehension are thought to recruit different cortical structures: patient DF, who has visual form agnosia following bilateral damage to her temporal-occipital cortex, loses her ability to scale her grasp aperture to the size of targets (‘grip scaling’) when her prehensile movements are based on a memory of a target previewed 2s before the cue to respond or when her grasps are directed towards a visible virtual target but she is denied haptics-based information about the target. In the first of two experiments, we show that when DF performs real-time pantomimed grasps towards a 7.5 cm displaced imagined copy of a visible object such that her fingers make contact with the surface of the table, her grip scaling is in fact quite normal. This finding suggests that real-time vision and terminal tactile feedback are sufficient to preserve DF’s grip scaling slopes. In the second experiment, we examined an ‘unnatural’ grasping task variant in which a tangible target (along with any proxy such as the surface of the table) is denied (i.e. no terminal haptic feedback). To do this, we used a mirror-apparatus to present virtual targets with and without a spatially coincident copy for the participants to grasp. We compared the grasp kinematics from trials with and without terminal tactile feedback to a real-time pantomimed grasping task (one without tactile feedback) in which participants visualized a copy of the visible target as instructed in our laboratory in the past. Compared to natural grasps, removing tactile feedback increased RT, slowed the velocity of the reach, reduced in-flight grip aperture, sharpened the slopes relating grip aperture to target width, and reduced the final grip aperture. All of these effects were also observed in the real-time pantomime grasping task. These effects seem to be independent of those that arise from using the mirror in general as we also compared grasps directed towards virtual targets to those directed at real ones viewed directly through a pane of glass. These comparisons showed that the grasps directed at virtual targets increased grip aperture, slowed the velocity of the reach, and reduced the slopes relating grip aperture to the widths of the target. Thus, using the mirror has real consequences on grasp kinematics, reflecting the importance of task-relevant sources of online visual information for the programming and updating of natural prehensile movements. These results provide compelling support for the view that removing haptic feedback, even when the grasps are target-directed, induces a switch from real-time visual control towards one that depends more on visual perception and cognitive supervision.

Providing terminal tactile feedback and real-time visual information can evidently keep the dorsal visuomotor system operating normally for prehensile acts.

5.1 Introduction

Being able to reach out and grasp objects with considerable skill is one of the defining features of primates. The act itself typically involves the use of real-time visual information and is directed at a visible object. It also results in contact with the object, manipulation, and haptic feedback. Detailed analysis of movements of the fingers, hand, and wrist show that the posture and orientation of the moving hand reflect the geometric properties of the goal object (e.g., Gentilucci et al. 1996; Jakobson & Goodale, 1991; Jeannerod 1988; Paulignan et al. 1991a,b). The visually-mediated control of grasping is thought to involve the dorsal stream of visuomotor pathways in the posterior parietal cortex (PPC) and their interconnections with premotor areas of the frontal lobe (for review see: Culham & Valyear, 2006; Davare et al. 2011; Grafton, 2010). In line with this view, disrupting the activity of the anterior areas of the intraparietal sulcus of the PPC with transcranial magnetic stimulation (TMS) affects the grasp kinematics in neurologically healthy individuals (e.g., Glover et al. 2005; Rice et al. 2006; Rice et al. 2007; Tunik et al. 2005). Furthermore, damage to dorsal-stream structures in the PPC can result in selective visuomotor deficits involving misreaching and/or poor grasp formation (Binkofski et al. 1998; Cavina-Pratesi et al. 2011; Goodale et al. 1994a; Jakobson et al. 1991; Jeannerod, 1986; Jeannerod et al. 1994; Milner et al. 2001; Perenin & Vighetto, 1988; Karnath & Perenin, 2005). Despite their deficits in real-time visuomotor control, however, some patients with dorsal-stream lesions show relatively preserved visual perceptual abilities on comparable tasks that require object form processing (Goodale et al. 1994a; Jakobson et al. 1991; Jeannerod et al. 1994; Milner et al. 2001).

In contrast to the effects of lesions to the dorsal stream, lesions that are largely restricted to the ventral stream often produce gross deficits in the ability to report the features of visual stimuli, such as colour, visual texture, and form. A deficit in form vision is typically referred to as 'visual form agnosia' (for review, see Goodale & Milner, 2013). One of the best known examples of such a patient is DF (Milner et al. 1991; for review see Whitwell, Milner, and Goodale, 2014; but see also patients JS and MC; Karnath et al., 2009; Wolf et al. 2008, respectively). DF and other similar patients had sustained bilateral lesions of varying extent to occipito-temporal cortex and, as a result, were left with a persistent deficit in visual form perception. Nevertheless, when these patients reached out and grasped objects, the online configuration of their grasping hand reflected the spatial and geometric properties of those objects (Goodale et al. 1991; Goodale et al. 1994a; Goodale et al. 1994b; Karnath et al., 2009; Marotta, Behrmann, & Goodale, 1997; Westwood, Danckert, Servos, & Goodale, 2002; Whitwell et al 2014a; Whitwell et al. 2014 (in press); Wolf et al. 2008). Their relatively normal performance is made all the more remarkable by the fact that these patients were all demonstrably at chance when asked to manually indicate the widths of exemplars from a set of so-called 'Efron blocks' (Efron, 1969) placed directly in front of them. The Efron blocks vary in length and width but, critically, are matched for cues that these patients, including DF, can perceive such as weight, texture, colour, and overall surface area. In other words, despite gross deficits in visual object perception, these patients were capable of making relatively normal-looking visually guided target-directed actions, such as reaching and grasping, presumably by virtue of having spared visuomotor networks in the dorsal stream. These studies, together with the complementary neuropsychological studies of patients with dorsal-stream lesions described above, as well as demonstrations of dissociations between perceptual report and visually guided actions in normally-sighted individuals, (e.g., Ganel, Tanzer, & Goodale, 2008; Stottinger et al. 2010; Stottinger et al. 2012) have provided compelling support for the Two Visual Systems Hypothesis (TVSH) (Goodale & Milner, 1992; Milner & Goodale, 2006), which in turn has influenced subsequent and expanded proposals on the functional organization of the primate visual system (Kravitz et al. 2011; Kravitz et al. 2013; Rizzolatti & Matelli, 2003).

In a seminal investigation, Goodale et al. (1994b) explored the dependence of the dorsal stream on real-time visual control by examining how normal DF's grasps looked when she was forced to rely on a memory of a recently previewed target. To do this, the authors compared natural grasps to a variant Milner et al. (2001) later-called 'delayed-pantomimed grasping' (DPG) in which the participants, including DF, executed grasps to the remembered location of targets viewed as recently as 2 s before the cue to respond occurred. In this task, the participants' view of the workspace was restored following the delay period. Critically, however, the experimenter removed the object during the delay period and so it was no longer present when the participants were cued to reach out and pretend to pick up the remembered object “as if it was still physically present” (p. 1165). The DPG task therefore differed from the natural grasping task in two respects: (1) online visual input about the target was not available when the response was cued and (2) no haptics-based object information was available at the end of the movement. The results showed that all of the participants, including DF, moved their hand towards the previewed location of the target. Nevertheless, there were some clear differences in the hand kinematics of the two grasping tasks. Compared to natural grasps, the DPGs of the participants, including DF, took longer to complete, exhibited slower peak hand velocities, and showed smaller anticipatory grip aperture. The measure on which DF’s performance differed most-drastically from that of the controls was the in-flight, anticipatory adjustments in grip aperture to the widths of the remembered targets (grip scaling). Whereas the controls showed no change in their grip scaling slope (relating grip aperture to target width) moving from natural grasps to DPGs, DF’s slope bore no relationship whatsoever to target width. Goodale et al. argued that DF’s failure in the DPG task was due to her inability to form a visual percept of the target from which to extract width. Their reasoning was based on two assumptions: (1) that the DPG task required participants to use a remembered percept of the target’s width, and (2) that the creation of this percept required an intact object processor housed in the occipital-temporal cortex. Thus, their argument runs, DF’s failure in grip scaling was a direct result of the damage to these structures in her ventral stream, preventing her from forming a visual percept in the first place to store in memory.

Importantly, Goodale et al. (1994b) also tested DF and the controls in an additional variant of the ‘natural’ grasping task. In this new task, the participants, including DF, were presented with a visible Efron block and were asked to imagine an identical version of that object displaced to the right of it (7.5 cm), and then to reach out to grasp this imagined object “as if it were physically present” (Goodale et al. p. 1171–1172). Unlike the delayed-pantomime grasping task, this ‘real-time displaced-pantomime grasping’ (RPG) task allowed the participants a full view of the workspace throughout the trial which included the Efron block and the hand and limb. Thus, the availability of real-time visual input about the object was equivalent across the natural and the RPG tasks, even though the target-directedness of the two tasks along with the availability of haptics-based object information clearly differed. Nevertheless, the results showed that, compared to natural grasps, the RPGs took longer to complete, exhibited slower peak hand velocities, and showed smaller anticipatory grip apertures. Thus, regardless of whether the pantomime grasps of neurologically-intact individuals are planned using online or remembered visual information about the object, removing haptics-based object information slows the hand movement, increases the movement time, and reduces the overall grip aperture. Noting an increase in the variability in DF’s anticipatory grip aperture for the RPG task, Goodale et al. ultimately concluded that both the RPG and the DPG tasks produced catastrophic results for her grip scaling. Interestingly, however, in stark contrast to an absence of grip scaling in DF’s DPGs, DF’s grip aperture in the RPG task actually appears to be linearly related to the width of the target.

Common to both of Goodale et al.’s (1994b) pantomime tasks is an obvious requirement to pretend to pick up either the remembered or imagined target as if it were actually there and an absence of haptics-based object information. As we have already pointed out, the availability of real-time visual input following the cue to perform the grasp differed between the two tasks. Thus, this factor alone can reasonably account for any differences in DF’s performance across the two pantomime grasping task variants. As such, DF’s poor performance on the DPG serves as a striking example of the dependence of some visuomotor tasks (pantomime grasps) on ventral stream processing, not only in DF but, presumably, in neurologically-intact individuals as well. One perhaps less obvious requirement of Goodale et al.’s tasks is the fact that the dimensions of the Efron blocks (only 1 cm in height) that were used in these experiments allowed the participants to receive tactile feedback from the surface of the table at the end of their reach. This was because the participants could not reasonably be expected to refrain from touching the surface of the table with their fingertips when simulating reaching out to pick up short rectangular blocks. Thus, the table may well act as a proxy when the grasps are directed next to the visible object. Importantly, haptics-based object information need not correlate with the visual size of targets for DF’s grip scaling to be normal. Indeed, when the grasped object remains an intermediate size despite changes in the visual size from trial to trial, DF’s grip aperture scales to the visual size (Whitwell et al. 2014a; Whitwell et al.

in press). According to this view (see also Milner, Ganel, & Goodale, 2012), both terminal tactile feedback *and* real-time visual input are critical for normal, dorsally-mediated prehension. Unfortunately, Goodale et al., did not compare DF's performance in the RPG task directly against the performance of the controls, presumably because there were differences between DF and the controls in terms of the stimulus set (six Efron blocks vs. three) and the presentation protocol (one target position vs. three). Determining whether DF's grip scaling in this task is in fact normal or abnormal would help rule out (or rule in) the importance of terminal tactile feedback for normal, real-time prehension. Therefore, in the first of our two experiments, we aimed to fill in this gap by revisiting DF's grip scaling in Goodale et al.'s RPG task. We tested a new group of control participants using the same stimulus set and protocol that was used by Goodale et al. to determine whether DF's real-time pantomime grasps were indeed as good as the controls and, more importantly, whether or not her grip scaling in this task would actually dissociate from that of her 'natural' grasps as is commonly assumed.

5.2 Experiment 1

5.2.1 Methods

5.2.1.1 Participants

Eight self-reported right-hand dominant age-appropriate and gender-matched control participants ranging from 31 to 46 years of age (*M* = 39.1, *SD* = 5.7), volunteered to take part in the experiment to compare DF's grip scaling in the natural grasping and RPG tasks. The controls provided written informed consent and were compensated $20 for their time. All experiments were approved by the local ethics committee and were in accordance with the Declaration of Helsinki.

5.2.1.2 Apparatus and Stimuli

Details of the apparatus and stimuli used to test the controls for patient DF's data set can be found in Goodale et al. (1994b). Briefly, the stimuli consisted of a set of Efron blocks that were 1 cm in height but varied in their lengths and widths as follows: *l×w (in cm)*, 10×2.5, 8.3×3, 7.1×3.5, 6.3×4, 5.6×4.5, 5×5. The kinematic data was collected at 200 Hz using an optoelectronic recording system (OPTO*TRAK* 3020, Northern Digital, Waterloo, On, Canada) that recorded the 3D spatial locations of three infrared emitting diodes (IREDs). The IREDs were attached with adhesive tape at three positions on the right (grasping) hand: the distal left corner of the nail of the index-finger, the distal right corner of the nail on the thumb, and the skin blanketing the metacarpophalangeal joint (MCP) of the index-finger. The experimenter ensured that the pads of skin on the tip of the thumb and index-finger were uncovered to ensure normal tactile feedback from the goal objects when grasped. The leads from the IREDs were taped to the right forearm to ensure complete freedom of movement. There was only one target position, 30 cm along a sagittal plane from the start position. The start position was a raised button located 5 cm from the edge of the table facing the participant (see Fig. 5-1). Before the experiment began, the experimenter ensured that all of

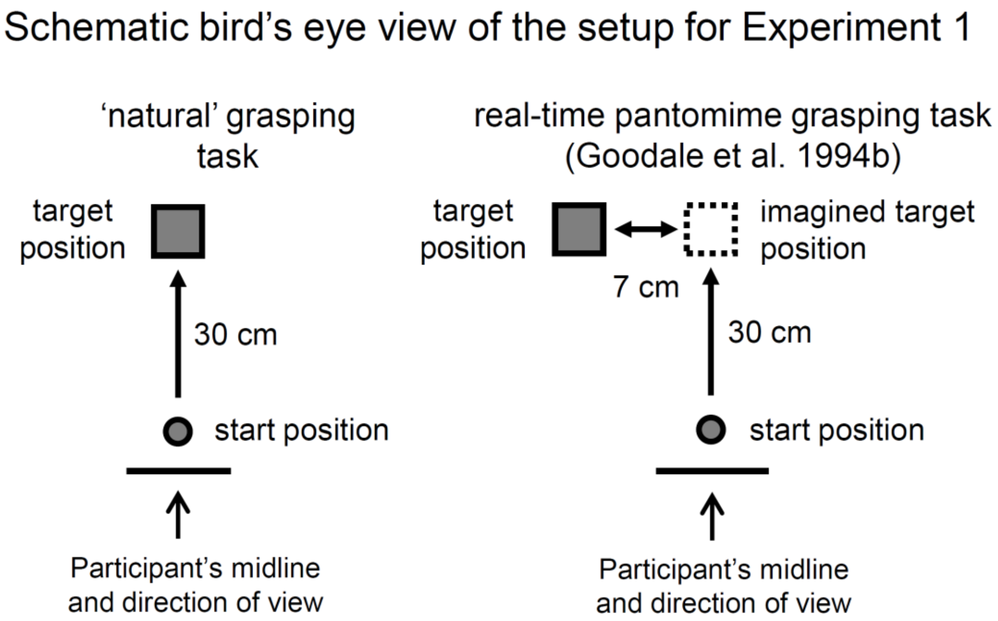


Figure 5-1. A bird's eye view of the setup for Experiment 1 As outlined in Goodale et al. (1994b), the targets were six Efron blocks (varied widths and lengths but a constant surface area, weight, height, colour and texture) positioned 30 cm from the start button along the participant's midline in the 'natural' grasping task. In the 'displaced'-pantomimed grasping task, the target was positioned 7 cm to the right of the position used for the natural grasping task. DF (in Goodale et al.'s study) and the control participants (in the current study) were asked to imagine the target was out in front of them, immediately to the right of its visible position and to reach out to grasp that imaginary target as if it were actually there.

the participants were seated comfortably and positioned close enough to the table so that they could grasp the objects at the farthest distance comfortably and without leaning forward.

5.2.1.3 Procedure and Design

Details of the procedure and design used to test the controls can be found in Goodale et al. (1994b). Briefly, before each trial was initiated, the participants closed their eyes and held the tips of their right index-finger and thumb together while depressing the start button. The experimenter then gave a verbal prompt to the participant to open her eyes. The experimenter then waited approximately 2s before giving a ‘go’ signal for the participant to execute their response. For the natural grasping task, participants were instructed to reach out, grasp across the width (near-far axis) of the Efron block, lift up, and put back down the Efron block using a precision grip (index-finger and thumb) as soon as they heard the go signal. At the beginning of the experiment, participants were asked to grasp the objects naturally: neither laboured nor speeded. For the real-time pantomime grasping (RPG) task, the participants were instructed to imagine that the visible target to their left was positioned at the same distance along their midline (see Fig. 5-1). They were further instructed to reach out to pick up the imaginary target as if it were physically there. The experimenter explained the procedure for the upcoming task before each block of trials. The experiment was comprised of 2 blocks of 36 trials each for a total of 72 trials. Each block of trials was dedicated to a different task. The block of natural grasps were performed before the block of RPGs. As Goodale et al. (1994b) cautioned, this order was chosen to give DF the maximum likelihood of being able to use the experience of actually grasping the objects when performing the displaced-pantomime grasps. The order of the blocks were the same across all of the participants, including DF. For each block of trials (i.e. for each task), each one of the six Efron blocks was presented 6 times each in a pseudorandom order.

5.2.1.4 Data Processing and Statistical Analysis

The data from the control participants were processed offline with custom software written in Matlab (Mathworks Inc., Natick, MA, USA). The positional information from the IREDs was low-pass filtered at 20Hz using a 2nd order Butterworth digital filter. Grip aperture was computed as the Euclidean distance between the IRED placed on the thumb and the IRED placed on the index-finger, and the instantaneous velocities were computed for each of the three IREDs and for grip aperture. We analyzed three principal measures: peak grip aperture (PGA), the slope relating PGA to the target size, and the peak hand velocity (PHV). The PGA was defined as the largest grip aperture within a search window that was designed to capture the forward-reach component of the movement. The beginning of this window (the 'movement onset') was operationally defined as the first of 30 consecutive sample frames (150 ms) in which the velocity of the MCP IRED exceeded a threshold of 50 mm/s. Normally, one could use the movement onset as a measure of reaction time. In this case, however, because the timing between the initiation of the data collection and the subsequent experimenter's verbal 'go' command was free to vary (as was the case in Goodale et al. 1994b), reaction time (RT) could not be referenced to a fixed point in time. Thus, RT could not be computed reliably. Nevertheless, the end of the search window was defined as the first sample frame in which the velocity of the IRED fell below 75 mm/s. Linear regression of PGA on the widths of the Efron blocks was performed separately for each task and the resultant regression coefficient (i.e. the slope, b) relating the average increase in PGA (in mm) per incremental increase in Efron block width (also in mm) was computed for DF and for the controls. The PHV was defined as the peak speed at which the MCP IRED travelled towards the target within the search window outlined above.

Notably, only DF's PGA was available from the data set reported by Goodale et al. (1994b). Thus, only PGA and the slopes relating PGA to target size could be compared against the control data set. The PHV of the control participants was analyzed to test Goodale et al.'s finding that RPGs are executed more slowly than natural ones in this slightly modified version of that task (one target position and six target sizes). The comparisons of interest in the control data were the differences in the PHV, overall PGA, and grip scaling slopes between the natural grasps and the RPGs. The comparisons of interest that involved DF included those measures that were common to both DF and the controls: the difference in overall PGA between the natural grasps and RPGs and the grip scaling slopes. A comparison of the PGAs between DF and the controls for each of the natural grasping and RPG tasks was not carried out given that inter-individual differences in IRED positioning and hand anatomy could have yielded spurious results. Comparisons of intra-individual differences involving PGA should be far less susceptible to this influence (if at all). Accordingly, we used independent-samples t-tests to assess the normality/abnormality of 1) DF's slope on each of the two grasping tasks and 2) DF's difference scores for both the slope and the PGA between the two grasping tasks. Together, these contrasts constitute tests for "strong/differential" or "classical" dissociations (Crawford & Garthwaite, 2005; Crawford, Garthwaite, & Gray, 2003). For all statistical tests, the alpha criterion for statistical significance was set to 0.05.

5.2.2 Results

5.2.2.1 Peak grip aperture (PGA), slopes, and the peak hand velocity (PHV)

The controls' overall PGA was significantly larger when they executed natural grasps than when they executed RPG, $t(7) = 8.23$, $p < 8 \times 10^{-5}$ (see Fig. 5-2A). A

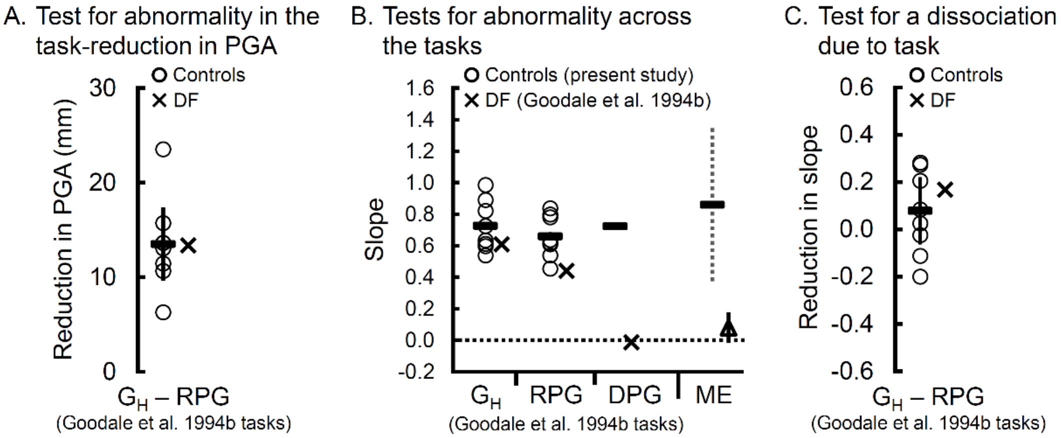


Figure 5-2. Tests for abnormality in and a dissociation of DF's peak grip aperture and slopes across the natural and real-time pantomime grasping tasks. Peak grip aperture (PGA) and slopes for the controls ('O's) and for DF ('X's). (A) Reduction in PGA between the G_H and RPG tasks. The solid error bar reflects the 95% confidence interval and indicates a significant reduction in PGA moving from G_H to RPG for the controls. As can be seen, DF showed a similar reduction in her overall PGA. (B) Slopes relating PGA to target size for the controls ('O's) and for DF ('X's) for the G_H and RPG tasks. Dashes indicate the mean slope for the controls. DF's slopes differ significantly from zero and are within the normal range in both tasks. For illustration, we included (1) the mean slope for the controls (solid dash) along with DF's slope ('X') computed from data reported by Goodale et al. (1994b) for the delayed-pantomimed grasping task (DPG) and (2) the mean slope relating grip aperture to Efron block width for DF (open triangle) and for the controls (solid dash) across 4 studies (Goodale et al. 1991; Westwood et al. 2002; Whitwell et al. 2014a; Whitwell et al. *in press*) of DF's manual (perceptual) estimations (ME). Evidently, the DPG task has a far more detrimental impact on DF's slope than does the RPG task. In fact, DF's slope in the DPG task failed to differ from zero ($p = 0.9$). Interestingly, DF's particularly poor slope for the DPG task resembles those that are typically observed when she performs the ME task. A 95% confidence interval around the controls' mean ME slopes can be used to compare DF's mean ME slope across those same four studies. Clearly, DF's mean ME slope falls well outside the normal range. The 95% confidence interval around DF's mean ME slope includes zero ($p = 0.09$), indicating that her slope does not differ significantly from zero (C) The controls slopes for the G_H and RPG tasks do not differ significantly and, critically, the difference in DF's slope between the two

tasks falls within the range of differences observed in the controls. Thus, when compared to the G_H task, the RPG task affected DF's slopes no differently than it did the controls.

comparison of the difference in the overall PGA across the two tasks yielded no significant difference, $t(7) = -0.02$, $p = 0.98$. In other words, the switch from natural grasps to RPGs affected DF's overall PGA no differently than it did the controls' overall PGA.

The controls' slopes relating PGA to target size did not depend on whether they executed natural grasps or RPGs, $t(7) = 1.29$, $p = 0.24$ (see Fig. 5-2B). DF's PGA was positively related to the size of the target in the natural grasping task [$t(28) = 6.01$, $p < 2\times10^{-6}$] and in the RPG task, $t(28) = 2.98$, $p < 6\times10^{-3}$. Importantly, DF's slopes did not differ significantly from those of the controls when she performed natural grasps [$t(7) = -0.69$, $p = 0.61$] or when she performed RPGs, $t(7) = -1.53$, $p = 0.17$. Moreover, the test for dissociation yielded a null result, $t(7) = 0.5$, $p = 0.62$ (see Fig. 5-2C). In other words, DF's slopes fell within the normal range regardless of whether she performed natural grasps or RPGs. Notably, DF's slopes on the natural grasping and the RPG tasks contrasts sharply with an absence of grip scaling on the DPG task in which her pantomimes were based on a memory of the previewed target (slope based on data reported in Goodale et al. 1994b) ($p = 0.9$; see Fig. 5-2B).

The controls' PHV was significantly slower when performing the RPGs than it was when they performed natural grasps, $t(7) = 2.79$, $p < 0.05$.

Finally, the time-normalized grip aperture (Fig. 5-3A) and velocity (Fig. 5-3B) profiles for the controls reveals a noticeable distinction between the natural

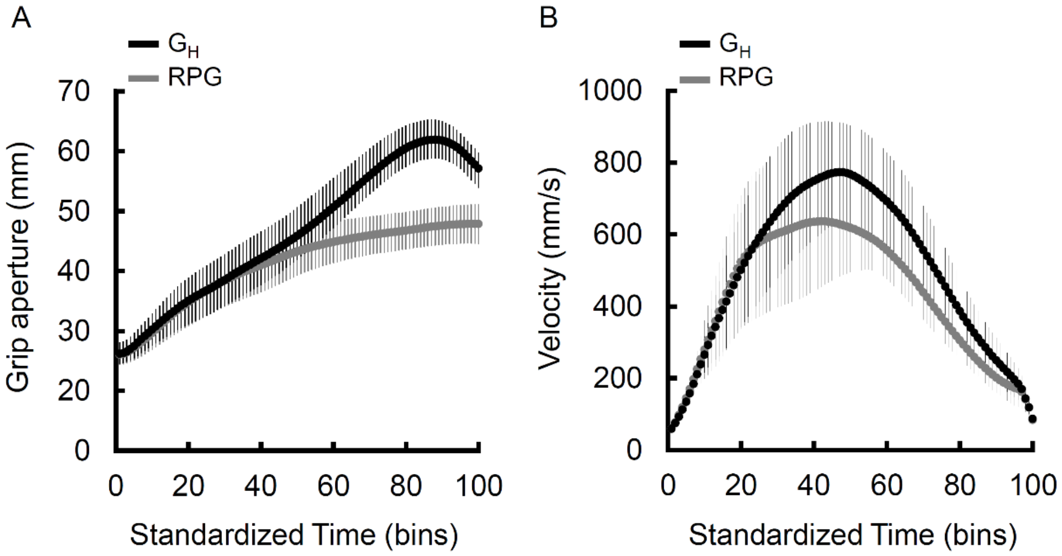


Figure 5-3. Normalized grand mean grip aperture and velocity profiles for the natural grasps and real-time pantomime grasps. Natural grasps (black trace), real-time pantomime grasps (grey trace). (A) Grip aperture normalized to 100 time bins for qualitative comparisons. Note that, overall, the real-time pantomime grasps lack a distinct peak and achieve lower grip aperture values than the natural grasps. The error bars reflect average within-participant standard deviations (B) Velocity of the wrist normalized to 100 time bins for qualitative comparisons. Note that, overall, the displaced-pantomime grasps appear to be executed more slowly than the natural grasps. The error bars reflect the between-participant standard deviations.

grasps and RPG that converges with the findings of Goodale et al. (1994b).

5.2.3 Discussion

In this experiment we re-examined DF's natural grasps and RPGs from an earlier study by Goodale et al. (1994b) by contrasting her performance on these two tasks with the performance of a new sample of normally-sighted control participants. When compared to natural grasps, the controls' RPGs yielded smaller overall PGAs and slower PHVs. Thus, we replicated Goodale et al.'s findings but in a version of the task that the authors had modified before testing DF by reducing the number of possible target positions from three to one and increasing the number of targets from three to six. Although we were unable to examine DF's

PHV, we found that the RPG task reduced DF’s overall PGA just as much as it did for the controls. We also examined DF’s grip scaling in terms of the slope relating PGA to target size and for the controls. Somewhat surprisingly, we found that DF’s slopes fell within the control range in both tasks. Her intact performance on this task contrasts sharply with her performance on the DPG task in which (quite unlike controls) she shows no evidence of scaling at all. As we pointed out in the Introduction, one evident difference between the two tasks is the availability of real-time visual input about the target in the RPG task. In other words, in the RPG task, information about the target can be used in real time to program the movement parameters, including grip aperture. This is obviously not the case in the DPG task. Indeed, because the movement is being programmed in real time in the RPG task, the relatively intact visuomotor networks in DF’s dorsal stream could presumably mediate this programming. Although this line of argument is appealing, recent experiments suggest that real-time visual input is not sufficient for ‘normal’ prehension (e.g., Bingham et al. 2007; Schenk, 2012a; Whitwell et al. 2014a; Whitwell et al. 2014b).

Several years after Goodale et al.’s (1994b) investigation, Bingham et al. (2007) introduced a novel variant of a grasping task which was later adapted by Schenk (2012a) to re-test DF’s grasps. Noting that movements that lack feedback are often more variable, Bingham et al. (2007) hypothesized that goal-directed movements, such as grasping, are precise because they can make use of haptic feedback (what we are referring to here as haptics-based object information) for calibrating each movement. Thus, Bingham et al. reasoned, the slower pantomime grasping movements that Goodale et al. (1994b) observed could be due to a decrease in precision and the lack of haptics-based object information in the DPG and RPG tasks. Bingham et al. set out to test how the provision of periodic haptic feedback about the target object would affect the grasps of normally-sighted individuals. To do this, Bingham et al. used an ingenious mirror apparatus that allowed the participants to view a virtual target in the mirror. This way, the participants could be instructed to reach out behind the mirror towards the apparent position of the virtual target to grasp it. An identical copy of the virtual target could be positioned behind the mirror so that it was spatially coincident with the visible one. Critically, the arrangement allowed the experimenter the choice to deny the participants an opportunity to grasp a real cylinder by refraining from positioning one behind the mirror. In short, this setup allowed Bingham et al. to preserve both the real-time visual information about the targets and the target-directedness of natural grasps in these new grasping task variants. Similar to Goodale et al.'s findings, Bingham et al. found that when participants were consistently denied an object to grasp, they showed slower hand velocities, longer movement times, and lower overall peak grip aperture.

Schenk (2012a) used a similar mirror-apparatus to re-examine patient DF's grasps. He was motivated by the observation that the dissociation in grip scaling between DF's grasping and her explicit perceptual estimates of target size might be due to the difference in the availability of haptic feedback about the target between grasping and perceptual estimation tasks. As Bingham et al. has suggested, haptic feedback might normally be used to calibrate actions. Perhaps

DF has developed some abnormal reliance on this source of information that allows her to calibrate the programming of her grasps (see also Schenk, 2012b). Rather than providing DF haptic feedback for her perceptual estimations of target size, however, Schenk opted to remove it from the grasping task as Bingham et al. (2007) had done. Critically, he found that DF's grip scaling was abolished when haptic feedback was consistently denied and concluded that haptic feedback was required to calibrate DF's grasping movements. Curiously, however, he did not appeal to the same pantomime-based explanation as Bingham et al. and Goodale et al. (1994b) had done in the past. Instead, he argued that DF uses haptic feedback to "compensate" for her visual perceptual deficit when reaching out to grasp objects (Schenk 2012a). According to this line of reasoning, no distinction between visual processes for perception and those for skilled goal-directed action is required, because DF's vision is merely degraded – haptics can help bootstrap her performance. As things turn out, this interpretation is untenable, because DF's inaccurate perceptual estimates of Efron width show no improvement when haptic feedback is available to putatively calibrate her estimates: she was permitted to reach out to pick up the Efron blocks immediately after each of her explicit estimates (Whitwell et al. 2014a; Whitwell et al. 2014 *in press*). Thus, DF's dissociated performance on perceptual estimation and grasping tasks continues to support a fundamental distinction between dorsal and ventral stream object processing.

Nevertheless, one important factor was overlooked in both Schenk's and Bingham et al.'s experiments: the participants in the 'no haptic feedback' tasks of both studies were unlikely to have encountered anything other than ‘thin air’ at the end of their reaching movements. For example, in Schenk’s study, the visual targets were vertically-standing cylinders 7 cm tall, requiring a horizontal grasping motion across the diameter of the visible target. In Bingham et al.’s investigation, the objects were shorter (though >3 cm in height) and the participants were explicitly instructed not to touch the surface of the table at the end of their reach and encouraged to adopt a particular approach that would minimize this possibility. At any rate, denying participants objects to grasp not only removed haptics-based object information in these studies but also any terminal tactile feedback about the end of the movement (Milner, Ganel, and Goodale, 2012). This was not the case in Goodale et al.’s (1994b) study (and therefore in Experiment 1 of the present study) in which the participants, including DF, clearly made contact with the surface of the table next to the visible target. In fact, given DF’s normal grip scaling, the results from Experiment 1 support an important distinction between haptic-based object information and the information derived from terminal tactile input. Adapting the term as it was used by Bingham et al. and Schenk, we hereafter use ‘haptic feedback’ in an overarching sense to refer to the denial of an object or even a proxy at the end of the movement (i.e. terminal tactile/haptic feedback).

Notably, a critical role for terminal tactile feedback in maintaining DF’s grip scaling is supported by the fact that DF scales her grip aperture to target size when she reaches out to ‘grasp’ 2-D images of Efron blocks presented on a table top (Westwood et al. 2002). Furthermore, DF’s normal grip scaling in this 2D-grasping task cannot reasonably be attributed to the availability of online visual feedback to update her movements as they unfold or to update the programming of subsequent movements or even some sort of ‘visuo-manual matching’ strategy, because she continues to show grip scaling to Efron width in the absence of any online visual feedback whatsoever (Whitwell et al. 2014 *in press*). Additional support for the role of terminal tactile feedback in maintaining DF’s grip scaling comes from the fact that her grip scaling is normal when she reaches out to grasp objects that vary in their visible (virtual) size but are always a constant, intermediate haptic size (Whitwell et al., 2014a, in press). In other words, haptics-based object information need not provide veridical information about the width of the visible target to maintain normal dorsal-stream mediated grasping. Indeed, the results of Experiment 1 indicate that DF shows normal grip scaling when terminal tactile feedback from the table surface is available to her, even when she performs RPGs. Interestingly, the results of Experiment 1 promote the real-time nature of a natural grasping task over the target-directedness of it *per se*. Thus, the two critical factors underlying DF’s grip scaling slope appear to be terminal tactile feedback and real-time visual input.

In the second experiment reported here, we addressed whether or not the task requiring DF and the control participants to reach out to a visible target that is not physically present results in grip scaling that resembles that of a more explicit pantomimed grasping task as Milner et al. (2012) suggest. After all, as Whitwell and Buckingham (2013) point out, a desirable and novel feature of the grasping task used by Bingham et al. (2007) and Schenk (2012a) is that the resultant movements are programmed and executed in real-time and directed at the target – conditions under which the dorsal visuomotor system typically operates. Despite these similarities, there is some indication that the neurologically intact controls in Schenk's (2012a) experiment showed an increase in grip-scaling and inter-subject variability. DF's grip scaling to object size, as we pointed out earlier, was abolished in this task. Thus, the removal of haptic feedback appears to have changed DF's grip scaling *and* that of the controls, but in different ways. Unfortunately, however, the controls' grip-scaling with and without haptic feedback was never formally compared in that study. Thus, one aim of the second experiment reported here was to directly test whether removing haptic feedback from a target-directed grasping task influences grip scaling in neurologically-intact individuals. An additional aim (related to the first) was to directly contrast grasping in the target-directed task in which haptic feedback is removed against a variant of the RPG task in which the participants must imagine the visible target at a different location. This way, the responses when haptic feedback is denied in a target-directed grasping task could be compared to the responses in a task that quite obviously requires a pantomimed grasp. In order to implement these tasks, we adopted a mirror apparatus not unlike the one discussed above.

Finally, we took the opportunity that the mirror setup presented us to explore more systematically how the mirror itself might influence natural grasps. Although the mirror apparatus allows for the haptic and visual information about the target to differ, it has at least three possible drawbacks. (1) the mirror apparatus does not allow the participants to view their hand and limb throughout their grasping movement. The unavailability of any visual input about the hand and limb throughout the movement is of course quite different from what occurs with natural grasps. After all, normally when we reach out to pick things up, the hand and limb do not suddenly disappear from sight. A number of studies have shown that when vision is suppressed during the execution of a grasping movement in neurologically-intact individuals, grip aperture increases and, in many cases, the grip scaling slopes decrease (Fukui & Inui, 2006; Fukui et al. 2006; Hesse & Franz, 2009, 2010; Tang et al. 2013; Whitwell et al., 2008; Whitwell & Goodale, 2009; Whitwell et al. 2014 *in press*). In fact, DF shows similar changes in her grip aperture and grip scaling when vision is suppressed during the movement (Whitwell et al. 2014b). Presumably, these effects reflect an effort to ensure a sufficient margin of error in the absence of visual information that is normally used for online control. (2) When the participants make contact with the hidden object and pick it up, the virtual object remains stationary in the mirror. In short, there is a clear disconnect between what the participant sees in the mirror and what actually happens. (3) The mirror might be treated as an obstacle which has to be avoided. Any one or a combination of these three factors could have been responsible for reducing grip scaling in both normally-sighted individuals and in DF, because natural grasps that were directed at virtual targets in a mirror were contrasted against natural grasps that were directed at targets in plain view (Whitwell et al. 2014a). Thus, in an additional manipulation, we substituted a pane of glass in for the mirror to assess two effects of using a mirror:

the removal of online visual input about the moving hand and limb, and the obvious disconnect between the behaviour of viewed and hidden targets after contact. In total, therefore, we set out to test four tasks: grasping real targets (cylinders) viewed through a pane of glass ($G_{G\text{-}H}$); grasping virtual targets viewed in a mirror with haptic feedback ($G_{M\text{-}H}$); grasping virtual targets viewed in a mirror without any haptic feedback (i.e., no cylinder was present behind the mirror, $G_{M\text{-}NH}$); and real-time pantomime grasps that were based on virtual targets viewed in a mirror but displaced to the side without any haptic feedback (RPG_{NH}).

Moving forward, we grouped the task comparisons according to our apriori predictions: (1) that natural grasps directed at virtual targets ($G_{M\text{-}H}$) would result in larger grip apertures than those directed at real targets viewed directly through glass ($G_{G\text{-}H}$), and (2) in the absence of haptic feedback, target-directed grasping movements would resemble RPG_{NH} grasps that are directed towards an imagined copy of the virtual target.

5.3 Experiment 2

5.3.1 Methods

5.3.1.1 Participants

Twenty-five self-reported right-hand dominant individuals (9 males) ranging from 17 to 33 years of age (*M* = 21.3, *SD* = 3.7), volunteered to take part in the second study. In a follow-up pair of control experiments that was prompted by some of our results, we tested an additional group of 18 self-reported right-hand dominant individuals (6 males) ranging from 18 to 32 years of age (*M* = 21.4, *SD* = 3.5).

The participants in both groups provided written informed consent and were compensated $10 for their time. All experiments were approved by the local ethics committee and were in accordance with the Declaration of Helsinki.

5.3.1.2 Apparatus and Stimuli

The apparatus and stimuli did not differ from that described in Experiment 1 except as noted below. The stimuli consisted of three pairs of black cylinders with diameters of 3.5 cm, 4.8 cm, and 6 cm and a height of 7 cm. Depending on the task, the workspace comprised either a mirror or a pane of glass positioned 45° from the edge of the table facing the participant. For all of the tasks that involved the mirror setup, the target cylinder was always positioned in front of the mirror. A vertically-standing occluding board was attached to the edge of the table that faced the participant. The occluding board was positioned to the left of the participants' midline so as to block them from viewing the target cylinder directly. This way, the participant could only see the reflection of the cylinder (i.e. its virtual image) placed in front of the mirror. The occluding board was left in place throughout the experiment. The cylinders could be placed at two different positions in front of and (at corresponding positions) behind the mirror. The 'near' target position was located 14 cm away from the mirror along the participant's sagittal plane. The 'far' position was located 10 cm farther away from the mirror along the same plane. The hand's resting start position was a small black button located 22 cm to the right and 7 cm in front of the nearest target position (see Fig. 5-4). Before the experiment began, the experimenter

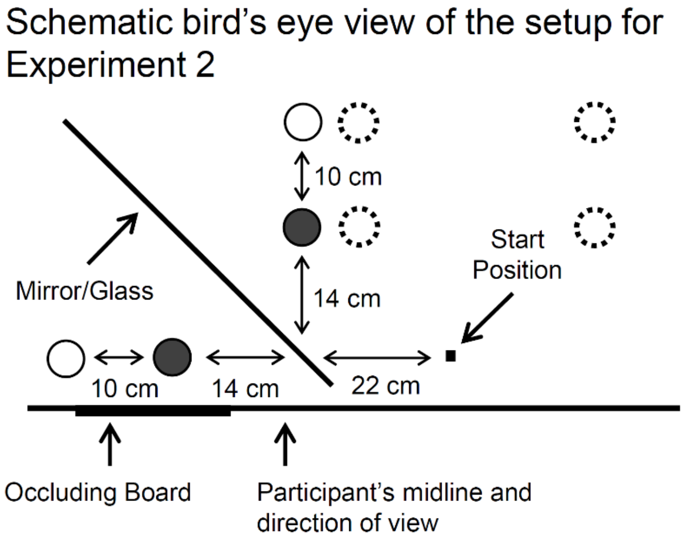


Figure 5-4. A bird's eye view of the mirror setup used for Experiment 2. The cylinders (indicated by circles with a solid-line border) were placed in front of the mirror at one of two possible positions from trial to trial (the near position is indicated with a filled-in circle). The cylinder was hidden from direct view by an occluding board, and so the participants viewed a virtual cylinder in the mirror. An identical cylinder could be positioned behind the mirror (again indicated by circles with a solid-line border) such that it was spatially coincident with the apparent position of the virtual one. This way, haptic feedback about the object could be permitted ($G_{M\text{-}H}$) or denied ($G_{M\text{-}NH}$) by removing the cylinder from behind the mirror. In one of the tasks, the mirror was replaced with a pane of glass so that participants viewed the cylinder directly ($G_{G\text{-}H}$). For the 'real-time' pantomime grasping task (RPG_{NH}), the participants imagined the virtual cylinder at the mirror-symmetrical position (dashed open circles) opposite a sagittal plane that was aligned with the start button. In a brief follow-up investigation, the RPG_{NH} task was modified such that the target was imagined immediately next to the visible one (also indicated with dashed open circles).

ensured that all of the participants were positioned close enough to the table so that they could grasp the objects at the farthest distance comfortably and without leaning forward. The experimenter also ensured that the participants could see each of the target cylinders binocularly in the mirror.

5.3.1.3 General Procedure and Design

Before each trial was initiated, the participants held the tips of their right index-finger and thumb together while depressing the start button. The participants were instructed to reach out, grasp, and lift up the cylinder using a precision grip (index-finger and thumb) as soon as the lenses of the goggles cleared. Participants were asked once they grasped and lifted the objects to simply move the objects to the center of the table. In all conditions, the lenses of the goggles remained transparent for 2.5 s following the participants' release of the start button before returning to their translucent state (i.e. visual closed-loop feedback). Participants were asked to grasp the objects naturally, neither laboured nor speeded. The experimenter explained the procedure for the upcoming task before each block of trials. The experiment was comprised of 4 blocks of 24 trials each for a total of 96 trials. Each block was dedicated to a different task. For each block of trials (i.e. for each task), the six combinations of target-cylinder size and location were presented 4 times each. The block order (i.e. task order) was counterbalanced across participants.

5.3.1.4 Grasping real targets viewed through a pane of glass

The participants viewed the cylinders through the pane of glass and were asked to reach out to pick them up as described in Section 5.3.1.3.

5.3.1.5 Grasping virtual targets viewed in a mirror with haptic feedback

The participants viewed the cylinders in the mirror. The experimenter ensured that the cylinder behind the mirror matched the one that the participants viewed. The participants were asked to reach out behind the mirror to pick up the cylinder as described in Section 5.3.1.3. Note that the mirror blocked the participants' view of their hand during the movement. Thus, a comparison of this task with the one in which the participants grasped real targets viewed through a pane of glass tests the effect of online visual feedback of the hand and limb during the movement.

5.3.1.6 Grasping virtual targets viewed in a mirror without haptic feedback

This task was identical to the previous task (see Section 5.3.1.5) in all respects, except that, after the matched cylinder was placed behind the mirror, it was immediately removed and the trial then initiated. Positioning a target behind the mirror was done simply to preserve the overall 'feel' and timing of the events between trials. Neither haptics-based object information nor any terminal tactile feedback was available in this task. In accordance with the instruction to simulate a real grasp, the participants were asked to refrain from sending their fingers or hand through the imagined cylinder.

5.3.1.7 Pantomime grasping visualized copies of virtual targets viewed in a mirror

The participants viewed the cylinders in a mirror, but were asked to execute their grasps as if the cylinder was located to the right of where it appeared to be. From the participant’s perspective, this location was to the right of the start button at a distance that equaled the distance from the visible cylinder to a sagittal plane aligned with the start button (see Fig. 5-4). The experimenter explained this contingency to the participant and reinforced it by indicating the target locations for each of the two possible positions for the viewed cylinder. In accordance with the instruction to simulate a real grasp, the participants were asked to refrain from sending their fingers or hand through the imagined cylinder.

5.3.1.8 Data Processing and Statistical Analysis

The data were processed offline with custom software written in Matlab (Mathworks Inc., Natick, MA, USA). The positional data from the IREDs was low-pass filtered at 20Hz using a 2nd order Butterworth digital filter. Grip aperture was computed as the Euclidean distance between the IRED attached to the thumb and the IRED attached to the index-finger, and the instantaneous velocities were computed for each of the three IREDs and for grip aperture.

The peak grip aperture (PGA) was defined as the largest grip aperture within a search window that was designed to capture the forward-reach component of the movement. The beginning of this window, the movement onset, was operationally defined as the first of 20 consecutive sample frames (100 ms) in which the velocity of the IRED attached to the index-finger exceeded a threshold of 50 mm/s. The movement onset was also used to calculate the reaction time (RT). The end of the search window was defined as the first sample frame in which the velocity of the IRED fell below 150 mm/s. Linear regression of PGA on the widths of the cylinders was performed separately for each task and the resultant regression coefficient (slope, b_{PGA}) relating the average increase in PGA (in mm) per incremental increase in cylinder width (also in mm) was computed. The peak hand velocity (PHV) was defined as the maximum velocity achieved by the knuckle IRED within the search window. One additional measure was operationally defined: the final grip aperture (FGA). The FGA was determined on the basis of grip stability (grip aperture velocity). Grip stability was used to identify the plateau phase of the grip aperture profile during which the participant holds the target ($G_{\mathrm{G\text{-}H}}$ and $G_{\mathrm{M\text{-}H}}$ tasks), pretending to hold a visible target ($G_{\mathrm{M\text{-}H}}$ task), or pretending to hold an imagined copy of a visible target (in the case of the RPG_{NH}). Linear regression of FGA on the widths of the cylinders was performed separately for each task and the resultant regression coefficient (slope, b_{FGA}) relating the average increase in FGA (in mm) per incremental increase in cylinder width (also in mm) was computed. Note that the b_{FGA} should be at or close to 1 for the natural grasps, and so the tests of this measure indicate how faithfully the participants reflected changes in target size from trial to trial in their FGA in the absence of haptic feedback.

To test for differences amongst the tasks, a one-way repeated measures Analysis of Variance (rmANOVA) was conducted separately for each of the dependent measures (RT, PHV, PGA, b_{PGA}, FGA and b_{FGA}) with Task as the main factor. The significant rmANOVAs were followed up with planned paired t-tests designed to test the specific effect of removing online visual feedback on the natural grasps and that of removing haptic feedback. The test of the former effect involved a comparison of the grasps directed at ‘real’ cylinders viewed directly through a pane of glass ($G_{G\text{-}H}$) and the grasps directed at ‘virtual’ cylinders viewed in a mirror with haptic feedback ($G_{M\text{-}H}$). The tests of the latter effect involved comparisons amongst the three tasks in which virtual cylinders were visible in the mirror: The $G_{M\text{-}H}$ task, the variant without haptic feedback ($G_{M\text{-}NH}$), and the real-time pantomime grasps directed away from the virtual cylinders and towards imaged ones without haptic feedback ($RPG_{M\text{-}NH}$). With respect to this set of contrasts, it should be noted that the $RPG_{M\text{-}NH}$ entailed online visual feedback. Therefore, we included a comparison of this task with the natural grasping task in which online visual feedback was available (i.e. $RPG_{M\text{-}NH}$ vs. $G_{G\text{-}H}$). Greenhouse-Giesser epsilon multipliers were applied to the degrees of freedom to all ANOVAs to compensate for potential violations of sphericity of the variance-covariance matrices. The F-statistics which were adjusted in this way are reported in-text as F_{adj}. Violations of sphericity were assessed using Mauchley’s test and assessed at a liberal alpha criterion of 0.15 as Kirk (1995) recommends for tests of underlying assumptions. For all other statistical tests, the alpha criterion for statistical significance was set to 0.05.

5.3.2 Results

5.3.2.1 Reaction Time

The rmANOVA of the reaction times (RTs) yielded a significant main effect of Task, $F(3,72) = 26.7$, $p < 2\times10^{-11}$, $\eta^2_p = 0.53$ (see Fig 5-5A). There was

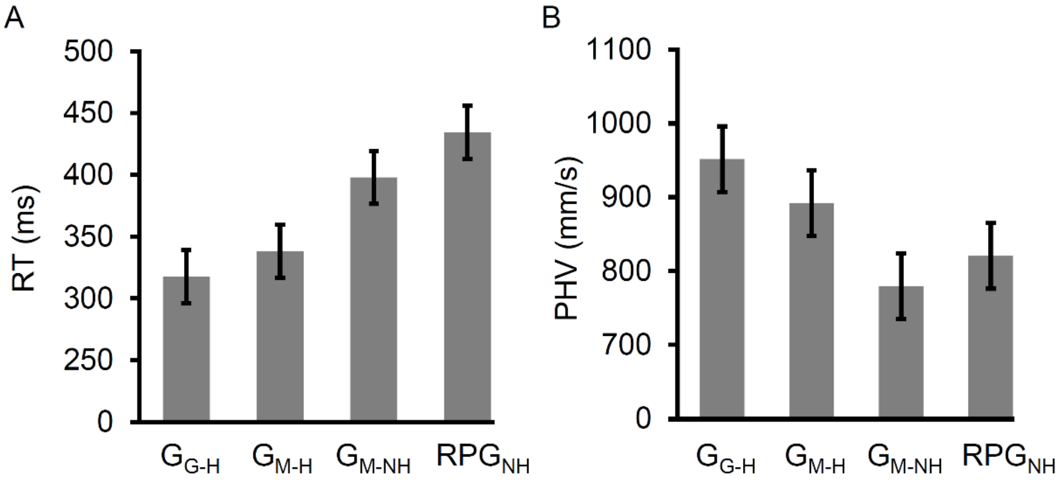


Figure 5-5. Reaction time and peak hand velocity across the four tasks. Within each panel, the tasks are arranged from left to right as follows: grasps directed at real (i.e. viewed through a pane of glass) targets ($G_{G\text{-}H}$) with haptic feedback, grasps directed at virtual targets (i.e. viewed in a mirror) with haptic feedback ($G_{M\text{-}H}$), grasps directed at virtual targets with no haptic feedback ($G_{M\text{-}NH}$), and the 'real-time' pantomime grasps directed at imagined copies of the virtual targets (RPG_{NH}). Note that the error bars reflect 95% confidence intervals extracted from the mean square error term from the rmANOVA (corrected for violations of sphericity where appropriate). (A) RT increased when a mirror was used rather than a pane of glass for target-directed grasps with haptic feedback. The RT increased further when haptic feedback was denied and increased further still when the participants performed displaced-pantomime grasps. (B) Peak hand velocity (PHV) slowed when a mirror was used rather than a pane of glass for target-directed grasps with haptic feedback. PHV slowed further when haptic feedback was denied and when the participants performed displaced-pantomime grasps.

no significant difference in the RTs between $G_{G\text{-}H}$ and $G_{M\text{-}H}$ [$t(24) = 1.75$, $p = 0.09$], indicating no effect of online visual feedback on the velocity of the reach.

The RTs were slower for $G_{M\text{-}NH}$ than the RTs for $G_{M\text{-}H}$, $t(24) = 2.81$, $p < 0.01$. In turn, the RTs for RPG_{NH} were significantly slower than those for $G_{M\text{-}H}$, $t(24) = 6.52$, $p < 1\times10^{-6}$. However, the RTs for RPG_{NH} were significantly faster than the RTs for $G_{M\text{-}NH}$, $t(24) = 3.11$, $p < 5\times10^{-3}$. Thus, the removal of haptic feedback induced a partial shift in the RTs towards pantomimed grasps. In other words, removing haptic feedback slowed the RTs and displacing the grasps slowed the RTs further still. Finally, the RTs for $G_{G\text{-}H}$ were significantly faster than the RTs for RPG_{NH}, $t(24) = 8.57$, $p < 1\times10^{-8}$, suggesting that the slowing of RT that occurs when haptic feedback is denied occurs regardless of whether online visual feedback of the hand and limb is available or not.

5.3.2.2 Peak Hand Velocity (PHV)

The rmANOVA of peak hand velocity (PHV) yielded a significant main effect of task, $F_{adj}(2,43) = 21.2$, $p < 1\times10^{-6}$, $\eta^2_p = 0.47$ (see Fig. 5B). The PHV was significantly slower for $G_{M\text{-}H}$ than for $G_{G\text{-}H}$ [$t(24) = 5.34$, $p < 2\times10^{-5}$], indicating a role for online visual feedback of the hand and limb in the velocity of the reach.

The PHV was significantly slower for $G_{M\text{-}NH}$ than for $G_{M\text{-}H}$, $t(24) = 5.87$, $p < 5\times10^{-6}$. Furthermore, the PHV was significantly slower for RPG_{NH} than the PHV for $G_{M\text{-}H}$, $t(24) = 2.29$, $p < 0.04$. Finally, the PHV did not differ significantly between $G_{M\text{-}NH}$ and RPG_{NH}, $t(24) = 1.75$, $p = 0.09$. Thus, the removal of haptic feedback resulted in a complete shift in the PHV towards pantomime grasps. In other words, regardless of whether the grasps were target-directed or not, the velocity of the reach was slower when haptic feedback was denied.

The PHV was significantly faster for $G_{G\text{-}H}$ than it was for RPG_{NH} [$t(24) = 4.54$, $p < 2\times10^{-4}$], suggesting that the slowing of PHV when haptic feedback is denied occurs regardless of whether online visual feedback of the hand and limb is available or not.

5.3.2.3 Peak Grip Aperture (PGA)

The rmANOVA of the mean PGA revealed a significant main effect of Task, $F_{adj}(2,47) = 18.5$, $p < 2\times10^{-6}$, $\eta^2_p = 0.44$ (see Fig. 5-6A). The PGA for $G_{M\text{-}H}$ was

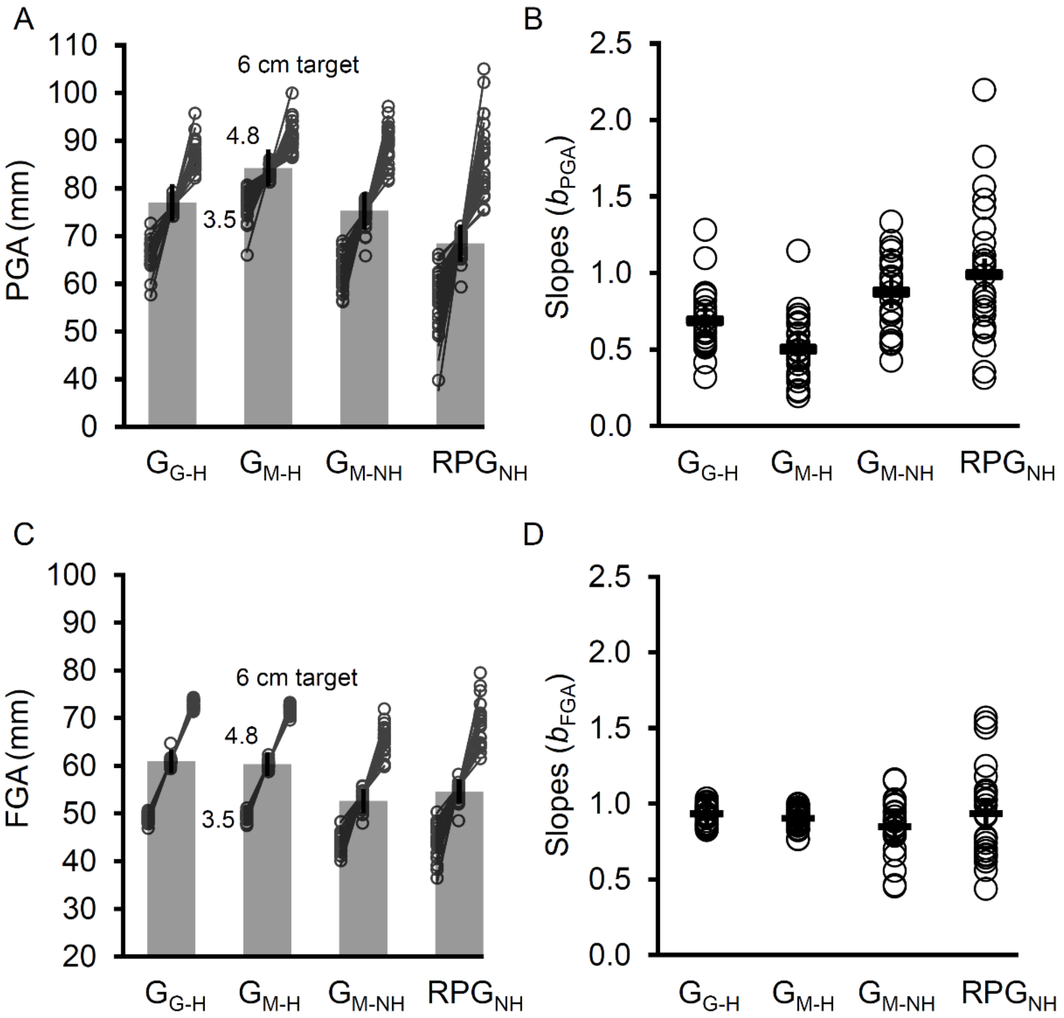


Figure 5-6. Peak grip aperture, the slopes relating peak grip aperture to target size, the final grip aperture, and the slopes relating final grip aperture to target size across the four tasks of Experiment 2. (A) The overall peak grip aperture (PGA) increased when a mirror was used ($G_{M\text{-}H}$) rather than a pane of glass ($G_{G\text{-}H}$) for target-directed grasps with haptic feedback. For grasps directed a virtual targets,

removing haptic feedback ($G_{M\text{-}NH}$) reduced the PGA. The PGA was reduced further for the real-time pantomimed grasps (RPG_{NH}). For each task the mean PGA for each target size plotted for each participant. Evidently, denying haptic feedback increased b_{PGA}. (B) The participants' b_{PGA}s (open circles) and the mean b_{PGA} (dashes) for each task. The b_{PGA}s for $G_{M\text{-}H}$ were smaller than those for $G_{G\text{-}H}$, indicating a significant role for online visual feedback of the hand and limb. The b_{PGA}s was greater, however, whenever haptic feedback was denied, regardless of whether the grasps were target-directed ($G_{M\text{-}NH}$) or not (RPG_{NH}). (C) The overall final grip aperture (FGA) was reduced when haptic feedback was not available. Plotted for each task is the mean FGA for each target size for each participant. Even in the absence of haptic feedback, the FGAs were well-related to target size. (D) The b_{FGA} (open circles) did not differ amongst the four tasks. Note that the error bars reflect 95% confidence intervals extracted from the mean square error term from the rmANOVA (corrected for violations of sphericity where appropriate).

significantly larger than the PGA for $G_{G\text{-}H}$ [$t(24) = 5.16$, $p < 3\times10^{-5}$], indicating a significant effect of online visual feedback of the hand and limb in the programming and/or execution of natural grasps.

The PGA was significantly smaller for $G_{M\text{-}NH}$ than the PGA for $G_{M\text{-}H}$, $t(24) = 3.4$, $p < 3\times10^{-3}$. In turn, the PGA for RPG_{NH} was significantly smaller than the PGA for $G_{M\text{-}H}$, $t(24) = 6.43$, $p < 2\times10^{-6}$. However, the PGA for RPG_{NH} was significantly smaller than the PGA for $G_{M\text{-}NH}$, $t(24) = 4.01$, $p < 6\times10^{-4}$. Thus, removing haptic feedback induced a partial shift in the PGA towards pantomimed grasps. In other words, removing haptic feedback reduced the PGA, but displacing the grasp reduced the PGA further still.

The PGA for the $G_{G\text{-}H}$ task was significantly larger than the PGA for the RPG_{NH} task [$t(24) = 4.36$, $p < 3\times10^{-4}$], suggesting that the reduction in PGA when haptic feedback is denied also occurs regardless of whether online visual feedback of the hand and limb is available or not.

5.3.2.4 Regression coefficients (slopes) relating PGA to target width

The rmANOVA performed on the slopes (b_{PGA}) revealed a significant main effect of Task, $F_{adj}(2,52) = 24.4$, $p < 2\times10^{-8}$, $\eta^2_p = 0.5$ (see Fig. 5-6B). The b_{PGA} for $G_{\text{M-H}}$ was significantly smaller than b_{PGA} for $G_{\text{G-H}}$, $t(24) = 4.46$, $p < 2\times10^{-4}$.

The b_{PGA} for $G_{\text{M-NH}}$ was significantly greater than the b_{PGA} for $G_{\text{M-H}}$, $t(24) = 7.31$, $p < 2\times10^{-7}$. In turn, the b_{PGA} for RPG_{NH} was significantly greater than the b_{PGA} for $G_{\text{M-H}}$, $t(24) = 6.33$ $p < 2\times10^{-6}$. Finally, the b_{PGA} did not differ significantly between $G_{\text{M-NH}}$ and RPG_{NH}, $t(24) = 1.79$, $p = 0.09$. Thus, the removal of haptic feedback resulted in a complete shift in the grip scaling slopes toward pantomime grasps. In other words, regardless of whether the grasps were target-directed or not, the slopes were steeper when haptic feedback was denied.

The b_{PGA} for $G_{\text{G-H}}$ was significantly smaller than the b_{PGA} for RPG_{NH} [$t(24) = 4.06$, $p < 5\times10^{-4}$], suggesting that the increase in b_{PGA} when haptic feedback is denied also occurs when online visual feedback of the hand and limb is available.

Finally, we opted to test for a difference in the b_{PGA} between the controls of Experiment 1 and the participants in the $G_{\text{G-H}}$ task of Experiment 2 using an independent samples *t*-tests with appropriate adjustments for violations of homogeneity where necessary. We found no significant difference in the b_{PGA} across the two groups ($p = 0.64$), suggesting that the pane of glass did not affect the b_{PGA} in Experiment 2. Interestingly, pooling the no haptic feedback conditions in Experiment 2 (i.e. $G_{M\text{-}NH}$ and RPG_{NH}) to test for an effect of the absence of haptic feedback compared to terminal tactile feedback (i.e. the RPG task of Experiment 1) revealed an increase in the b_{PGA} (steeper grip scaling slopes) for the former, $t(28) = 3.36$, $p < 3\times10^{-3}$. Thus, the results of these additional tests support the findings of Experiment 1 that terminal tactile feedback helps 'normalize' grip scaling slopes.

5.3.2.5 Final Grip Aperture (FGA) – grip stability at the end of the reach

The rmANOVA of FGA revealed a significant main effect of Task, $F_{adj}(2,43) = 20.1$, $p < 2\times10^{-6}$, $\eta^2_p = 0.46$ (see Fig. 5-6C). Not surprisingly, the FGA for $G_{M\text{-}H}$ and $G_{G\text{-}H}$ did not differ significantly [$t(24) = 1.41$, $p = 0.17$.], presumably because this measure was constrained by the widths of the cylinders in these tasks. Thus, the removal of haptic feedback resulted in a complete shift in the FGA toward pantomime grasps. In other words, regardless of whether the grasps were target-directed or not, the FGA was smaller when haptic feedback was denied.

The FGA for $G_{M\text{-}NH}$ was smaller than the FGA for $G_{M\text{-}H}$, $t(24) = 5.3$, $p < 2\times10^{-5}$. In turn, the FGA for RPG_{NH} was significantly smaller than the FGA for $G_{M\text{-}H}$, $t(24) = 3.72$, $p < 2\times10^{-3}$. However, the FGA for $G_{M\text{-}NH}$ did not differ significantly from the FGA RPG_{NH}, $t(24) = 1.69$, $p = 0.1$. Thus, the removal of haptic feedback resulted in a complete shift in the FGA toward pantomime grasps. In other words, regardless of whether the grasps were target-directed or not, the FGA was smaller when haptic feedback was denied.

The FGA for G_{G-H} was significantly larger than the FGA for RPG_{NH} [$t(24) = 4.19$, $p < 4\times10^{-4}$], suggesting that the reduction in FGA when haptic feedback is denied also occurs when online visual feedback of the hand and limb is available.

5.3.2.6 Regression coefficients (slopes) relating FGA to target width

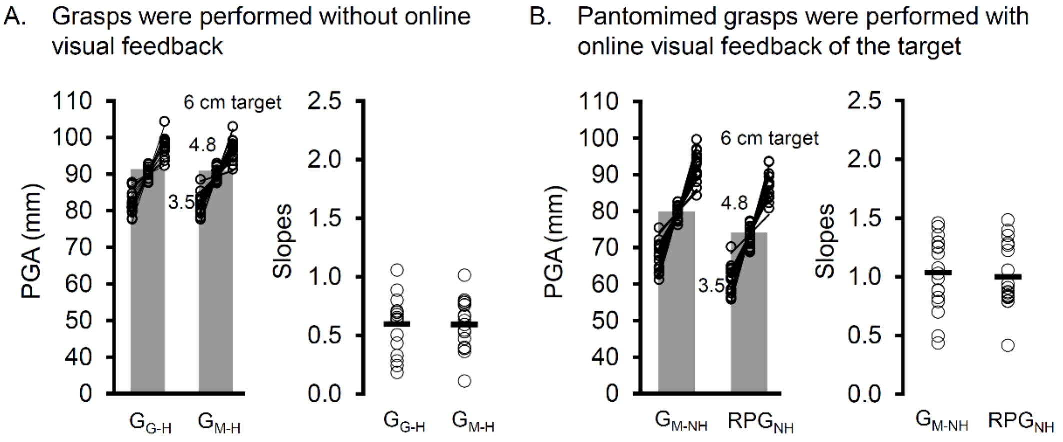
The rmANOVA performed on the slopes relating FGA to target size (b_{FGA}) indicated no significant main effect of Task, $F_{adj}(2,38) = 1.6$, $p = 0.22$ (see Fig. 5-6D), suggesting that, even in the absence of haptic feedback, participants on the whole took into account differences in the widths of the virtual cylinders when simulating their grip around them (in the case of G_{M-NH}) or around imagined copies of the virtual cylinders (in the case of the RPG_{NH}).

Finally, we examined the change in the slopes relating PGA to target size (b_{PGA}) and those relating FGA to target size (b_{FGA}) for each task (i.e. $\Delta b = b_{FGA} - b_{PGA}$). This analysis provides an indication of how consistent the slope was from the point in the response at which PGA was achieved (i.e. while the hand was in-flight) to the point at which the FGA occurred (i.e. while the fingers held the object for simulated holding one). A significant Δb was observed for G_{G-H} [$M = 0.25$, $SD = 0.18$, $t(24) = 6.88$, $p < 5\times10^{-7}$] and G_{M-H}, $M = 0.4$, $SD = 0.21$, $t(24) = 9.7$, $p < 9\times10^{-10}$. In contrast, the Δb for G_{M-NH} [$M = -0.03$, $SD = 0.18$, $t(24) = 0.76$, $p = 0.47$] and RPG_{NH} [$M = -0.06$, $SD = 0.28$, $t(24) = 1.13$, $p = 0.27$] failed to differ significantly from zero. Thus, the Δb appeared to be largely driven by the availability of haptic feedback. To confirm this, a rmANOVA performed on the Δb indicated a main effect of Task, $F(3,72) = 39.9$, $p < 3\times10^{-15}$. Given the null findings amongst the tasks with respect to the b_{FGA}, the differences in Δb amongst the tasks are quite likely to have been driven by the differences in the b_{PGA} we reported above. Indeed, follow up tests (not reported) showed that this was true. Thus, the analysis of the Δb indicates that in the absence of haptic feedback, the participants grip aperture faithfully reflected differences in the widths of the targets while their hand was in-flight and when it was simulating holding a visible or imagined cylinder.

5.3.2.7 Testing for possible methodological issues with respect to use of the mirror

Given the significant differences between $G_{\text{G-H}}$ (natural grasps directed at real targets viewed through a pane of glass) and $G_{\text{M-H}}$ (natural grasps directed at virtual targets viewed in a mirror) tasks across a number of measures, we tested an additional group of participants (see Section 5.3.1.1) to test for factors other than the online visual feedback of the hand and limb that could be driving this effect. In this follow-up experiment, we employed the $G_{\text{G-H}}$ and $G_{\text{M-H}}$ tasks (see Sections 5.3.1.1–5.3.1.5) however, the grasps in this additional experiment were performed entirely in open loop. In other words, the lenses of the goggles switched from a transparent state to a translucent one as soon as the participants' fingers left the start button. Thus, the only difference between the tasks was that nature of the target image (one being virtual and the other real). If other methodological factors (e.g. subtle mismatch in the placement of the copy of the virtual target or differences in lighting) were responsible for the differences in grasping in the two tasks (rather than the differences in online sources of visual input) then we should replicate the pattern of results that we observed, because these differences would still be present despite the loss of online visual feedback throughout the movements.

The results were clear: in the absence of any visual input throughout the grasping movements, viewing virtual or real targets did not significantly affect the RTs [$t(17) = 1.22$, $p = 0.24$], PHVs [$t(17) = 1.16$, $p = 0.26$], PGAs [$t(17) = 0.26$, $p = 0.8$], or the b_{PGA}, $t(17) = 0.14$, $p = 0.89$ (see Fig. 5-7A). Thus, the differences in


A. Grasps were performed without online visual feedback

B. Pantomimed grasps were performed with online visual feedback of the target

*Figure 5-7. The peak grip aperture and slopes relating peak grip aperture to target size across the natural and pantomimed grasping tasks without online visual feedback.*The peak grip aperture (PGA) and slopes (open circles, mean slope indicated by a dash) relating PGA to target width for the two variants of target-directed grasping tasks in which the participants executed their grasps in the absence of any online visual feedback (visual open loop). Grasps were directed at 'real' (i.e. viewed through a pane of glass) targets ($G_{G\text{-}H}$) and virtual (i.e. viewed in a mirror) targets ($G_{M\text{-}H}$) in visual open loop (vision was occluded at the start of the movement). In the case of $G_{M\text{-}H}$, haptic feedback was available when participants made contact with a spatially coincident duplicate that was positioned behind the mirror. Whether the grasps were directed at virtual targets or real ones made no difference across any of the dependent measures, including PGA and the slopes.

(B) The PGA and slopes for the GDVT task in which haptic feedback was denied and the displaced-pantomime grasping (RPG_{NH}) task in which the grasps were directed immediately to the right of the visible location of the target towards an imagined copy. Whether the grasps were directed towards or beside the virtual target did not affect the slopes, which appear to be quite steep in both tasks. Sending the hand to a location right beside the object did, however, reduce the overall PGA, just as it did for displaced-pantomime grasps to locations more distant from the location of the virtual target.

the PHVs, PGAs, and slopes between grasps directed behind the mirror and grasps directed behind the pane of glass in Experiment 1 are unlikely to have been driven by methodological factors putatively introduced by using a mirror.

5.3.2.8 Removing online visual feedback from the 'real-time' pantomime grasping task

As we have seen, the PGA for $G_{M\text{-}NH}$ was smaller than the PGA for $G_{M\text{-}H}$ yet larger than the PGA for the $RPG_{NH.}$ A similar result was observed for the RTs. Specifically, the RTs for $G_{M\text{-}NH}$ were slower than those for $G_{M\text{-}H}$ yet faster than those for RPG_{NH}. The partial shifts in these measures for $G_{M\text{-}NH}$ towards those observed in the pantomime grasping task (i.e. RPG_{NH}) suggest that the target-directed nature of the $G_{M\text{-}NH}$ task might have partially compensated for the effect of removing haptic feedback. It also possible, however, that the availability of online visual feedback of the hand and limb or the added shift in gaze or attention that the RPG_{NH} task demanded (as participants looked to towards the empty workspace to imagine a copy of the target) increased the RT. To test these possibilities, we carried out an additional experiment. We reasoned that altering RPG_{NH} so that the grasps were directed to a location immediately next to the virtual target should minimize differences between the two tasks in terms of the availability of visual feedback, shifts in attention, and other factors such as a difference in biomechanical constraint. A difference in PGA or RT following a comparison of the $G_{M\text{-}NH}$ and modified RPG_{NH} (i.e. the grasps were directed to the side of the virtual target) would support the suggestion that the target-directed nature of the $G_{M\text{-}NH}$ can at least partially compensate for an absence of haptic feedback.

Compared to $G_{M\text{-}NH}$, the modified RPG_{NH} showed slower PHVs [$t(17) = 3.73$, $p < 2\times10^{-3}$] (attributable to the modest overall reduction in distance the hand travelled in this task) and, importantly, a smaller PGA, $t(17) = 2.75$, $p < 0.02$. Thus, directing the hand away from the target and towards an imagined copy appears to reduce the PGA no matter how far away from the visible object the hand is directed. The results also indicated no significant differences in the RT [$t(17) = 0.23$, $p = 0.82$] or in the b_{PGA}, $t(17) = 0.14$, $p = 0.89$ (see Fig. 6-7B) between $G_{M\text{-}NH}$ and modified RPG_{NH}.

5.3.2.9 Between-groups tests of the regression coefficients (slopes) relating PGA to target width

Testing the additional group of participants also afforded us an opportunity to test for a replication of one of the critical finding of Experiment 2 concerning the grip scaling slopes (b_{PGA}). In a series of independent–samples *t*-tests involved the b_{PGA} of the $G_{M\text{-}NH}$ and RPG_{NH} tasks from the first and second group of participants, and the $G_{M\text{-}H}$ task from the first group, and in the series of independent–samples *t*-tests for the tasks in which the targets were virtual (i.e. viewed in a mirror) and the goggles remained clear for the duration of the movement (i.e. closed-loop with respect to the target). We adjusted the multiple post-hoc independent–samples t-tests using Holm's step-down Bonferroni procedure (Holm, 1979). The results, again, showed that the critical factor for this measure was the absence of haptic feedback. The b_{PGA} for $\mathrm{G}_{\mathrm{M\text{-}NH}}$ ($p < 7\times10^{-7}$) and $\mathrm{RPG}_{\mathrm{NH}}$ ($p < 5\times10^{-8}$) from the second group of participants were significantly steeper than the b_{PGA} for the $\mathrm{G}_{\mathrm{M\text{-}H}}$ from the first group of participants. Furthermore, none of the tasks in which haptic feedback was denied differed between the two groups of participants ($p_{max} = 0.14$, uncorrected).

5.4 Discussion and Conclusions

One of the principal aims of Experiment 2 was to determine whether or not removing both haptics-based object information and terminal tactile feedback (together referred to here as 'haptic feedback') from a target-directed grasping task shifts the response mode away from a natural one and towards a more pantomimed (i.e. simulated) kind as has been suggested by Milner et al. (2012). To do this, we compared target-directed grasps with ($\mathrm{G}_{\mathrm{M\text{-}H}}$) and without haptic feedback ($\mathrm{G}_{\mathrm{M\text{-}NH}}$) to pantomime grasps ($\mathrm{RPG}_{\mathrm{NH}}$) in which the participants were asked to imagine a copy of the target in another location in the workspace and to grasp that imaginary object as if it were actually there (e.g., Goodale et al. 1994b; Holmes et al. 2013a). We found that when participants reached out to grasp virtual targets, removing haptic feedback slowed the reaction times (RT) and peak hand velocity (PHV), reduced peak grip aperture (PGA), increased the slopes relating PGA to the width of the target, and reduced the final grip aperture (FGA). Just as important was the fact that the grasps directed at virtual targets (viewed in a mirror) without haptic feedback were statistically indistinguishable from the pantomime grasps in terms of the PHV, the slopes relating PGA to target size, the slopes relating FGA to target size, and the FGA, suggesting a complete shift across these measures towards pantomimed grasping following the removal of haptic feedback. The only measures that differed between the two no haptic feedback tasks were the RT and the magnitude of the PGA. It is important to acknowledge, however, that removing haptic feedback from grasps directed at virtual targets *slowed* the RTs and *reduced* the PGAs. In other words, both of these measures registered a shift in the direction *away* from natural grasps and *towards* the pantomimed ones.

An additional aim of Experiment 2 was to determine whether or not the mirror itself has an effect on the kinematics of target-directed grasps. After all, the mirror introduces three key differences when compared to natural grasps: First, the mirror blocks the participant's view of their hand and limb as soon as the participant reaches behind it (removing re-afferent online visual feedback). Second once the participants make contact with the hidden object and the virtual target, the mirror imposes a disconnect between the felt movements of the hidden object and the apparently stationary target visible in the mirror. Although this effect might startle the participants at first, it is reasonable to suggest that the participants acclimate to this situation, growing more comfortable on subsequent trials. This says nothing, however, about any possible effects all of this might have on the unconscious 'automatic' online control mechanisms that normally mediate grasping. Third, the mirror might act as an obstacle that the participants attempt to avoid. Given these considerations, we implemented an additional task in which the participants reached out to grasp the target they viewed through a pane of glass. The pane of glass was the same size as the mirror and was positioned in the same way with respect to the participant. Compared to natural grasps directed behind the pane of glass, the ones directed behind the mirror resulted in slower PHVs, larger PGAs, and shallower slopes. Nevertheless, it was possible that some other aspects of the mirror task may have played a role. We ruled these factors out in a control experiment in which we removed online visual feedback altogether for both tasks. In this control experiment, all the differences between the grasps directed behind the mirror and the grasps directed behind the pane of glass completely disappeared, strongly implicating a role for one or more of the sources of online visual feedback outlined above in the programming and updating of target-directed grasps. Given Connolly & Goodale's (1999) null findings concerning the magnitude of the PGA and the fact that the participants in that study were permitted a view of the target and the hand making contact with the target, then the results of the current investigation suggest a significant role for vision during the contact and manipulation phase of the grasping movement in the programming of grip aperture on subsequent grasps.

Many of the additional findings in the present investigation can be explained through the changes in task demands and differences in the availability of visual and haptic input. For example, the overall reduction in PGA and FGA in the absence of haptic feedback (see also Bingham et al. 2007; Fukui & Inui, 2013) is likely due to the removal of the physical constraints that the object imposes on the fingers and, therefore, the minimum magnitude that the grip aperture would normally be required to achieve a suitable grasp. Without the physical constraints imposed on the fingers and hand by an actual object, there would be (1) no consequences for consistently under-sizing grip aperture, such as knocking the object away and (2) less effort (and perhaps even more comfort) in opening the hand a smaller amount. The FGA, being a measure of grip stability when the target is being held, would necessarily be restricted by the sizes of the cylinders. We speculate that the selective removal of haptics-based object information might also lift this restriction and result in a similar reduction in FGA. Nevertheless, unlike the FGA, the PGA was affected by both haptic feedback and online visual feedback of the hand and limb. Specifically, providing online visual feedback and removing haptic feedback each effected reductions in the PGA. The effect of online visual feedback of the hand and limb on PGA observed in the present study is in line with previous findings following a comparable manipulation (Whitwell et al. 2014a; Whitwell et al. 2014b) and is also in line with the broader literature on the effects of removing online visual feedback entirely (e.g., Hesse & Franz, 2010; Jakobson & Goodale, 1991; Whitwell et al. 2008; Whitwell & Goodale, 2009). The effect of removing haptic feedback on PGA observed in the present study is also in line with previous reports using comparably tall (> 7 cm in height) cylinders (Bingham et al. 2007; Fukui & Inui, 2013). Interestingly, (although not always explicitly tested), a similar effect on PGA appears to occur in the absence of haptics-based object information when shorter (e.g., ~1 cm in height) block-like stimuli (or even 2D images) are used in which the fingers are highly unlikely to avoid touching the surface of the table at the end of the reach (e.g., Cavina-Pratesi et al. 2011; Holmes et al. 2013a; Holmes et al. 2013b; Westwood et al. 2002). If we assume an additive model of the effects of online visual feedback and haptic feedback, then consideration of the details of the tasks of the present study readily explain the findings involving FGA and PGA.

In keeping with an appeal to differences in task demands, we should point out that we required the participants to refrain from sending their hand and fingers through the visible or imagined target for the tasks in which haptic feedback was removed. We would argue that most (if not all) tasks in which the participants *simulate* grasps carry with them analogous instructions, regardless of whether such instructions are stated explicitly by the experimenter or are tacitly understood by the participant. Critical to this is (1) any consideration the participants might give to the sizes and positions of the target in a situation in which the target is not actually there, and (2) how well the participants understand what their hand does when they reach out to pick up a goal object. It seems likely that these factors account for the increase in RT when haptic feedback was denied. A similar appeal to differences in task demands can explain the additional increase in RT that occurred when the grasps were directed at an imagined copy of the visible object. Unlike the other grasping tasks, the instructions for the pantomime grasps required the participants to imagine a copy of the visible target at a different location. Presumably, participants would first look at the visible target and then look towards the location where they were to imagine a copy of that object before or shortly after they initiated their response. In contrast, in the target-directed grasping tasks (with and without haptic feedback), the target's viewed position and the location to which the participants sent their hand are one and the same. We suspect that the addition of a preparatory shift in gaze in the pantomime grasping task likely increased the RT relative to the target-directed grasping task in which haptic feedback was denied. It is possible that the biomechanical difference in the direction that the participants sent their hand and limb in pantomime grasping task or the availability of online visual feedback might also play a role in the increase in RT. We should point out, however, that in the control experiment in which haptic feedback was denied, RT did not depend on whether the participants directed their hand towards the virtual target or beside it. In other words, the difference in RT between pantomimed and target-directed grasps without haptic feedback was abolished when the pantomime task was modified to minimize differences in shifts in gaze or attention, biomechanical constraints, and online visual feedback. Furthermore, we note that online visual feedback did not influence the RT of natural grasps in the current study – a finding consistent with previous investigations of natural grasps with and without online vision (e.g., Hesse & Franz, 2010; Whitwell et al., 2008). Thus, it seems unlikely that this factor can account for differences in RT in the absence of haptic feedback.

In contrast to the RTs and the PGA, the PHV, the slopes relating PGA to target size, the slopes relating FGA to target size, and the FGA were not affected by the added requirements of pantomime grasps when compared to the target-directed grasps without haptic feedback. In other words, for these measures of movement execution, the target-directedness of the response was not a critical factor. Instead, the removal of haptic feedback about the object appeared to dominate, independent of whether the grasp was directed to a visible or an imagined target. In line with Bingham et al.'s (2007) finding, without haptic feedback the PHVs were slower. The participants likely approached the targets more cautiously and deliberately, presumably because they were simulating what they would do if an object was actually there, making sure that their fingers did not go through the visible or imagined object. Importantly, the slopes increased relative to the slopes for grasps that received haptic feedback, approaching a 1:1 relationship between changes in the width of the target and changes in PGA. In fact, the slopes in these tasks resemble those observed during manual estimation tasks in which the participants indicate the width of a visible object by opening their thumb and index-finger a matching amount (e.g., Daprati & Gentilucci, 1997; Haffenden & Goodale, 1998; Pettypiece, Goodale, & Culham, 2010; Schenk, 2012a; Whitwell et al. 2014a; Whitwell el a. 2014 *in press*). Thus, the increase in the grip scaling slope when haptic feedback is not available would appear to reflect the deliberate consideration given to the sizes of the targets in these simulated grasps. As we have already noted, removing haptic feedback from a real-time grasping task appears to increase the slopes (Schenk, 2012a). In our experiment we explicitly tested this and found that, in the absence of haptic feedback, the slopes do, in fact, increase relative to natural grasping tasks. Interestingly, on a task that is not unlike the delayed-pantomimed grasping task devised by Goodale et al. (1994b), the slopes appear to increase relative to those observed on a natural grasping task regardless of whether vision of the workspace is available at the time of the movement or not (see Fukui & Inui, 2013). Overall, it seems reasonable to conclude that in the absence of haptic feedback, the geometric properties of the target are taken into explicit consideration when planning and programming the grasp. Thus, DF's poor grip scaling slope when haptic feedback is consistently denied (Schenk 2012a) can be attributed to a switch in the kind of response she provided towards a more pantomimed or simulated one as Milner et al. (2012) suggested. Interestingly, as we showed in Experiment 1, the provision of some proxy *next* to the visible target (in our case the surface of the table) has a normalizing influence on DF's and the controls' slopes. This finding adds to a growing body of work indicating that DF's slope remains normal provided that real-time visual input is available along with tactile feedback from a proxy of the target (Westwood et al. 2002; Whitwell et al. 2014a; Whitwell et al. 2014b).

Additional support for a distinction between haptics-based object information from a real (3D) object and that from the surface of a table comes from studies of the influence of a mismatch between the haptic and visual size of target objects. When normally-sighted participants reach out to grasp objects in which the apparent visual width of the objects differs from their felt width, they typically show some adaptation in their PGA to the actual (i.e., the felt) size of the target – even though they continue to scale their grip aperture to the visual width of the target (e.g. Gentilucci et al. 1995; Pettypiece et al. 2010; Safstrom & Edin, 2004, 2008). In fact, DF responds in an identical manner, suggesting that (1) the ventral stream is not required for the updating of grip aperture to reflect the real size of a target and that (2) veridical haptics-based object information is not required for DF to maintain normal grip scaling to trial-to-trial changes in the visual sizes of targets (Whitwell et al. 2014a,b). Rather, DF's dorsal stream can exploit terminal tactile feedback to update her grip aperture on subsequent grasping movements and to maintain normal visuomotor processing of target shape to program movements parameters like grip aperture. Thus, it seems reasonable to conclude that (1) provided real-time visual input is available, tactile feedback from the surface of the table is sufficient to keep the visuomotor networks in DF's dorsal stream engaged, and that (2) the damaged areas of DF's ventral stream are not necessary for grip scaling for grasps that are directed towards the table surface next to a visible object.

Since Goodale et al.'s (1994a) study, pantomime grasps have been used in many kinematic investigations and is considered a tool to test the role that perception plays in the visual control of skilled actions. For example, the PGAs of pantomime grasps have been shown to be more susceptible to the Muller-Lyer illusion than natural grasps (Westwood et al. 2000). In addition, the within-subject variability of the PGAs of pantomimed grasps, but not natural ones, obeys Weber's Law (i.e. the variability of the PGA increases linearly with target width; Holmes et al. 2013; although see Foster & Franz, 2013). In fact, even the movement preparatory time for pantomimed grasps, but not for natural grasps, is increased by the holistic object-perception that is thought to underlie Garner interference (Ganel & Goodale, 2003; 2014). Moreover, patient IG, who suffers from optic ataxia following damage to her posterior parietal cortex shows a paradoxical improvement in the correlation between her PGA and target width when she executes pantomime grasps following a delay period compared to natural grasps (Milner et al. 2001). Finally, provided the object is visible, the hand kinematics of magicians (who routinely pantomime actions to deceive their audiences) look far more like those of natural grasps than they do those of non-magicians (Cavina-Pratesi et al. 2011). In all of these studies, haptic feedback about the object was denied but not terminal tactile feedback about the end of the movement. Thus, tactile feedback from the tabletop is not enough to preserve all of the kinematics of a real grasping movement. Indeed, when neurologically-intact individuals pretend to pick up 2D images, the variability of their grip aperture scales with target size as Weber's law would predict (Holmes & Heath, 2013), just as it does for pantomimed grasps (Holmes et al.). Furthermore, grasps that are directed towards 2D objects invoke holistic processing (Freud & Ganel, 2015) in which the irrelevant and relevant target dimensions interact to influence processing times. This is not so for grasps that are directed at 3D objects (e.g., Freud & Ganel, 2015; Eloka, Feuerhake, Janczyk, & Franz 2014; Janczyk & Kunde, 2012).

Importantly, it remains to be seen whether the cognitive or perceptual effects associated with pantomimed grasps are indeed mediated by ventral stream processing as is commonly assumed. An interesting future direction might be to test DF's pantomime grasps for evidence of holistic processing (e.g., Garner interference) and relative sensitivity to stimulus magnitude (e.g. Weber's law).

Interestingly, pantomime grasps directed to the workspace next to a visible object fail to elicit preferential activity in the temporal-occipital areas in healthy participants, uniquely recruiting, instead, regions in the supramarginal gyrus, middle intraparietal sulcus, and supplementary motor area of the right hemisphere (Kroliczak et al. 2008) – areas that remain intact in DF. These findings, combined with those of Goodale et al. (1994b) and the present study, suggest that a delayed pantomime grasping task would invoke preferential activity in areas of the occipito-temporal cortex of healthy individuals that are damaged in DF. Interestingly, these areas are in fact recruited when reach-to-grasp movements are based on a memory of the target, albeit in the context of a delayed grasp (as opposed to a delayed pantomime grasp) which received haptic feedback about the remembered object at the end of the reach (Singhal, Monaco, Kaufman, & Culham, 2013). Thus, although pantomime grasps with tactile feedback invoke cognitive and perceptual influences that are absent in natural grasps, some of these influences (e.g., the effects of holistic processing on movement preparation time, or of stimulus magnitude) might well emerge from a combination of visual processes in the ventral stream and the inferior parietal cortex of the right hemisphere.

In summary, the current study shows clear evidence that the removal of haptic feedback induces a shift from natural towards pantomimed (simulated) grasps, as suggested by Milner et al. (2012). The pattern of changes in the grasps kinematics, longer initiation times, slower movements, and steeper slopes were indicative of a more deliberate process of responding in which the participants explicitly took into account the metrics of the object, the location to which they were directing their hand, and the path that their hand and fingers would take. Furthermore, as Fukui & Inui (2013) have pointed out, the reduction in grip aperture that followed the removal of haptic feedback presumably reflects a natural consequence of the removal of a physical object, which, normally, would impose a constraint on the grip aperture of a natural grasp. Thus, the removal of haptic feedback also changes the task incentives. Without haptic feedback, there is no obvious consequence for an inaccurate grasp. These results and those of other investigations highlight the importance of haptics-based object information, or, at the least, terminal tactile feedback, in maintaining normal grasps which, we have shown here with patient DF, depend on intact dorsal pathways.

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Chapter 6

6 General Discussion

Goodale and Milner's (1992) 'vision-for-action' and 'vision-for-perception' account of the division of labour between the dorsal and ventral 'streams' of cortico-cortical connections out of early visual areas has come to dominate contemporary views of the broad organization of the primate visual system. Nevertheless, some lines of evidence for the model remain controversial. Recently, Thomas Schenk (2012a) re-examined visual form agnosic patient DF's spared anticipatory grip scaling to object size - one of the principal empirical pillars of the model. Based on this new evidence, Schenk rejects the original interpretation of DF's spared ability that was grounded in segregated processing of object size and argues that DF's spared grip scaling relies on haptic feedback to calibrate visual egocentric cues that relate the posture of the hand to edges of the goal-object. Chapters 3–5, however, have shown that Schenk’s proposed mechanism is incorrect. This final chapter presents (among other things) a careful consideration of the tasks that Schenk employed, revealing some additional conceptual problems with his claim that should be taken into account in future work on the topic. Ultimately, the core issues of this controversy will require a closer examination of the role that cognition plays in the operation of the dorsal and ventral streams in healthy controls and in patient DF.

According to the TVSH (Goodale & Milner, 1992; Milner & Goodale, 2006), the ventral stream of cortico-cortical projections from the occipital to inferotemporal cortex mediates our conscious visual perception of the world, whereas the dorsal stream of cortico-cortical projections from the occipital to the posterior parietal cortex mediates the real-time visual control of skilled, goal-directed actions. No patient has contributed more to Goodale and Milner’s model than DF, who suffers from visual form agnosia. Remarkably, DF retains the ability to scale her grip aperture (the distance between the thumb and fingers) to the width of target objects when reaching out to pick them up (grip scaling), despite showing impairments when making explicit verbal or manual judgments about the same stimulus property (e.g., Goodale et al., 1991). Milner and Goodale (2006) have long argued that DF’s grip-scaling is possible because much of her PPC remains intact. Indeed, as detailed in Chapter 1, the published results of various scans of DF’s brain have revealed large bilateral lesions to the ventral pathways and much smaller lesions to the dorsal ones (e.g., James et al., 2003). Nevertheless, re-appraisals of evidence from a range of different lines of research mostly in humans have led some to question whether ‘vision-for-action’ and ‘vision-for-perception’ adequately captures the nature of visual processing in the dorsal and ventral pathways (see Schenk, 2010; Schenk & McIntosh, 2010).

Chapter 2 examines a hallmark measure of grip scaling, namely grip aperture, under conditions in which it should not relate to the size of the goal object. I found that PGA, unlike measures of grip aperture taken earlier or later on in the movement, was not predictive of the size of the unseen target. In Chapters 3–4, I examined (among other things) a proposal by Schenk (2012a) which dispenses with the notion that the size of a target serves as a common metric by which to contrast measures of grip aperture taken from grasping and perceptual estimation tasks. According to Schenk's proposal, prehensile acts do not entail processing the size of the goal object. Instead, reaching out to pick up a goal object entails processing information about the intended spatial positions on the edge of the object for the thumb and fingers to make contact with. This proposal, if correct, invalidates the use of size (and in effect the processing of size) as a variable to contrast grasping and estimation tasks and, therefore, invalidates Goodale et al.'s (1991) inference of dissociation of size processing for grasping and for perception in DF. If Schenk's proposal was limited to this alone, then there would be few (if any) ways to test it. After all, points in space that correspond to the boundary of the object determine size and theare inextricably linked: one cannot differentiate the distance between two visible points in space and those same two visible points all in the same prehensile act. Fortunately, Schenk's proposal also offered a testable mechanism: haptic feedback about spatial position of the fingers calibrates visual estimates of spatial position. In Chapter's 3 and 4, I showed that, contrary to Schenk's proposal and regardless of the nature of the visual input (be it spatial position or target size), DF does not rely on a spatial correspondence between visual- and haptic-based information about the target. I did this by asking DF and controls to reach out to pick up visible virtual targets that were co-centered with a real but unseen ‘haptic’ one. Critically, whereas the size of the virtual target changed from trial to trial, the size of the haptic one did not. In essence, this manipulation ensured that the edges of the unseen target did not co-vary with the edges of the visible one. As such, there was no systematically variable haptic signal that could be used to calibrate any visual ones. Despite this absence of visuohaptic correspondence, DF, just like the controls, continued to adjust her grip aperture to changes in the size of the visible target. In Chapter 5, I explored Schenk (2012a) denying neurologically-intact participants haptic feedback about a target affects their grasp kinematics. I did this by comparing their target-directed grasps with and without haptic feedback against a variant that was based on one of the seminal pantomimed grasping tasks implemented by Goodale et al. (1994). The variant I implemented, like Goodale et al.’s, required the participants to visualize a copy of a visible target at a pre-specified position away from the visible target and to reach out to that position and pretend to grasp the imagined target as if it were actually there. In short, I compared how the removal of haptic feedback from what is otherwise a ‘natural’ open-loop grasping task stacks up against a more formal pantomime grasping task. The results were clear: removing haptic feedback resulted in slower RTs, peak hand velocities, smaller PGA, smaller FGA, sharper grip-scaling slopes, independent of whether the hand was directed away from the visible target or directly at it.

6.1 The Visuohaptic Calibration Hypothesis of Prehension

In a recent investigation, Schenk (2012a) re-examined DF's intact grasping behaviour. On the basis of his findings, Schenk proposed that DF's dorsal-stream vision does not rely on visual size information [as Goodale et al., (1991) originally assumed it did] and instead relies on egocentric cues that specify the spatial relationship between the hand and the visible edges of a target object. According to Schenk, DF utilizes these egocentric cues not only when haptic information about the target is available but when this information is derived from an object that is spatially coincident with the visible one. Thus, the core difference between grasping and perceptual target-size estimation tasks is the multisensory nature of the former. In other words, vision alone is not enough for DF to produce reliable grip scaling, because she fails to show grip scaling 1) on a target-directed grasping task when haptic feedback about the target is removed entirely and 2) when her grasps are directed away from a visible object and towards a copy of that object that she cannot see and can, therefore, derive haptic information about the visible object. Schenk concludes that his results highlight the multimodal nature of the visual and association areas of the occipital and parietal cortex: All along, DF's unreliable and inaccurate estimates of target size are due to the unimodal nature of the classic visual perceptual tasks she has been asked to perform. In short, according to Schenk, DF's spared visuomotor abilities are the products of "multimodal integration".

As we have seen, however, DF's grip scaling does not in fact depend on congruent visual and haptic target information. Nevertheless, there are a number of assumptions that underlie Schenk's view which should be highlighted, particularly for future work on the topic of haptic contributions to patient DF's grasping ability and its extensions to neurologically intact adult populations. This chapter begins with a summary of Schenk's proposal, then moves on to a critical review of the tasks he employed. The chapter closes with some discussion about the role that visual feedback plays in grasping movements performed with no or only partial haptic sensation. This final consideration suggests a complex interplay between the dorsal, ventral, and haptic sources of input in the programming and guidance of prehension.

6.1.1 An Overview of the Tasks

In the first of Schenk's (2012a) tasks, DF viewed pairs of cylinders that were drawn from a set of three. The three cylinders varied in diameter only and, therefore, varied in overall size. Given DF's ability to perceive the surface properties of objects (such as their overall size), it seems possible that DF could discriminate amongst the cylinders on the basis of their overall surface area. Indeed, in the first of two of perceptual tasks that Schenk (2012a) administered, DF reliably pointed to the larger of two simultaneously presented cylinders when the largest cylinder was paired with the smallest one. In the second task, however, in which the cylinders were presented in isolation, DF showed no sensitivity to the size of the cylinders when she was required to estimate their size by opening her thumb and forefinger a matching amount (a perceptual 'manual estimate'). But as I subsequently showed in a later experiment, even in this task, DF can sometimes reliably discriminate one cylinder from another. Moreover, a data set collected in 1991 but remained unpublished until recently (Whitwell et al. 2014) clearly shows that DF could reliably estimate the width of cubes that varied in size. Thus, one of the principal issues with Schenk's data set concerns the generalizability of the tests for dissociation to the TVSH given that DF was not entirely 'blind' to the target dimension of the stimuli.

Nevertheless, to test the role that haptic feedback plays in determining the perception-action dissociation, Schenk used a mirror apparatus to present virtual cylinders as targets for DF to reach out and grasp. The mirror allowed a cylinder to be placed behind it, hidden from direct view. In the 'standard grasping' task, the position of the hidden cylinder matched the apparent position of the virtual one. Not surprisingly, DF performed well in this task. On other trials, however, no cylinder was presented behind the mirror and as a consequence participants would lack haptic feedback that one would normally experience once the fingers made contact with the target (the so-called 'no haptic feedback' grasping task). Without haptic feedback about the target from trial to trial, DF's grip scaling was unreliable, falling well-outside of the control range of slopes. In one final grasping-task variant, the position of the hidden cylinder and the apparent position of the viewed cylinder differed from one another. In this task, the unseen target's position remained constant from trial to trial and was cued with a red LED viewed in the mirror. Again, DF's grip scaling was unreliable, falling well-outside of the control range of slopes.

6.1.2 An Overview of the Schenk's Interpretation of the Results

To explain his findings, Schenk (2012a; 2012b) argued that DF's spared grip scaling relies on at least two critical factors: 1) egocentric visual cues relating the visible edges of the target to the (felt) position of her hand and 2) haptic feedback about the object. He suggested that the visual egocentric cues are reliable only when they arise from an object that is spatially coincident with the source of haptic information about the goal-object. Under these conditions, Schenk (2012a,b) argued, DF uses haptic feedback to calibrate the visual estimates of the target edges. According to this argument, requiring DF to grasp an unseen cylinder located away from the apparent position of its size-matched virtual counterpart disrupts her grip-scaling because the spatial dissociation deprives DF of the egocentric visual cues.

Ultimately, Schenk's interpretation of DF's preserved grip-scaling to object size relies on the 'offline' integration of multimodal cues, rather than the relationship between the task and the visual processes that mediate the required behavioral responses ("grasp the target" vs. "estimate the target's size") as Goodale and Milner (1992) originally suggested. Thus, in Schenk's view, his findings support the idea that the posterior parietal cortex is multisensory in nature, rather than the idea that there are distinct visual systems for conscious vision and unconscious visually-guided action. Importantly, however, Schenk's (2012a; 2012b) reasoning relies on some tacit assumptions that deserve closer scrutiny.

6.2 Critical Re-Appraisal of the Visuohaptic Calibration Hypothesis

6.2.1 The ‘Dissociated Positions’ Grasping Task

Consider first the task in which the visual and haptic spatial positions of the target were dissociated. Schenk (2012a,b) assumes that DF’s poor grip scaling in this task reflects a deficit in her ability to acquire a particular type of visual information about the object. He fails to acknowledge additional processes the task might recruit which could be responsible for her problems. To illustrate this, consider what DF must do (in the very least) to perform the dissociated positions grasping task successfully: she must 1) process the size of the visible cylinder and then apply this size information to the vacant (though cued) location, or 2) work out the egocentric relationships between her hand and the edges of the visible cylinder and then adjust these relationships to the vacant (though cued) location. In other words, successful performance on this task requires visual information about the object to be extracted, spatially manipulated, and then used to guide the grasp to a different and visually vacant location. Thus, we cannot be sure whether DF’s poor grip scaling was due to a deficit in manipulating task-relevant visual information or a deficit in extracting this information in the first place. Furthermore, Schenk also assumes that the instruction to send the hand to what appears to be an empty location rendered the egocentric cues about the visible object unavailable but preserved the cues to object size. However, Schenk does not offer an account of how (or why) the switch in task demands rendered one type of visual cue (egocentric visual cues vs. visual object size) unavailable while preserving the other.

Notably, the change in task instruction from something akin to “grasp the visible target” to something akin to “grasp visible empty space but base what you do on the visible target” is similar to the change in task instruction that Goodale et al. (1994) argues alters the neural underpinnings of the response. According to Goodale et al., a change in task instruction from ‘grasp the object you see’ to ‘grasp visually empty space but base the grasp on the object you see/saw’ switches the dependency of the task from dorsal to ventral visual processing: Simulated or pantomimed grasps (i.e. pretend grasps) rely on an explicit visual percept of the object which is processed in the ventral visual pathway (see also Milner et al. 2012). This argument was based on DF’s performance on the two pantomime grasping tasks employed by Goodale et al. (1994). In one of the experiments of that study, DF’s grip scaling was particularly poor when basing her pantomime grasps on a memory of an Efron block previewed 2s before her response was cued. Interestingly, as I showed in Chapter 5, when DF’s pantomimed grasps are directed to the surface of the table next to the visible Efron block (so-called ‘displaced pantomime grasps’), DF’s grip scaling remains intact. In fact, this task (rather than the delayed pantomimed grasping task in which DF’s grip scaling is at chance), most resembles Schenk’s dissociated positions task: the responses in both tasks are executed on the basis of real-time visual input about the target and are directed at vacant areas of the workspace. Nevertheless, there are some clear differences between the two tasks. In the displaced pantomime grasping task, DF's fingers contact the surface of the table but in Schenk's task DF's fingers contact an unseen identically-sized cylinder. Furthermore, in the displaced pantomime grasping task, DF is allowed full visual feedback throughout her movement, whereas in Schenk's task, visual feedback of her limb and hand were occluded by the mirror early on the movement. It seems unlikely, however, that visual feedback is the explanation for the stark difference in DF's grip scaling. As we saw in Chapter 4, DF's grip scaling when executing 'natural' grasps does not critically depend on online visual feedback. Furthermore, because DF is unable to report the visual size of Efron blocks, it seems unlikely that she could use re-afferent online visual feedback about her fingers to somehow critically augment some unconscious visual signal about size for pantomime grasps but not for natural ones. The difference in haptic feedback between the two tasks does not satisfactorily explain the difference in DF's grip scaling either: it is not clear how haptics-based object information from a copy of the visual one would result in catastrophically *poorer* grip scaling than would simple tactile feedback from the surface of the table (which, as Chapter 5 showed, results in normal grip scaling).

There is one other difference between the two tasks that warrants discussion. Goodale et al.'s (1994) displaced pantomime grasping task and Schenk's (2012a) dissociated positions task differ not only in terms of the distance between the visible target and the target position for the hand, but also in the direction of the difference. In Schenk's task, the distance between the object and the target position for the hand spanned a sagittal plane of DF. In Goodale et al.'s task, the distance between the object and the target position fell along a frontal plane. In other words, Schenk's task involved a difference in depth, whereas Goodale et al.'s task did not. Relevant to this point is the fact that there is evidence to suggest that DF might have problems considering spatial relationships between objects that differ in terms of depth. For example, she does not perform well when she must consider the spatial relationships between a set of 'standard' tokens placed along the sagittal plane and match the arrangement by adjusting a comparator set – even when the standard arrangement varies exclusively along a single sagittal plane: DF's arrangement of the 'comparator' set was clustered towards the central token of the 'standard' arrangement and veered left or right out into the periphery of the workspace for the standard tokens that were closer and farther away from her, respectively (Murphy, Carey, & Goodale, 1998). Thus, DF appears to possess a distorted perceptual representation of space which could play an important role when the task requires her to take into account more than one position of the workspace, particularly when depth is involved as it was in Schenk's (2012a) dissociated positions grasping task.

6.2.2 'No Haptic Feedback' Grasping Task

Notably, the conditions and instructions of this 'no haptic feedback' grasping task were quite different from those that Goodale et al. (1994) employed in their displaced pantomime task in which DF directed her hand *away* from a visible object and towards the table surface. If anything, the task instruction ('grasp the visible target') would seem to be optimal for the dorsal visual pathways to base their operation on, yet DF still failed to scale her grip aperture to object size in this task. Nevertheless, Schenk's (2012a) interpretation of this task suffers from the same assumption that underlined his interpretation of the dissociated positions grasping task. Specifically, he assumes that visual egocentric cues, rather than visual size, were deprived of haptic-based calibration and were, therefore, invalidated. Again, Schenk provides no reason why we should promote one visually-derived property of the object over the other. Milner et al. (2012)'s explanation for DF's poor performance on this task is that the absence of a tangible object (or proxy) converted the response to a pantomime grasp. Indeed, Chapter 5 highlights 1) the similarities in the grasp kinematics of healthy participants performing this 'no haptic feedback' grasping task and a displaced pantomimed version of this task and 2) the differences in these measures when participants perform the no haptic feedback grasping task and the 'standard' gasping task in which haptic feedback is consistently available. Thus, there is good empirical evidence to support Milner et al.'s interpretation of DF's poor performance in this task.

Importantly, however, a common pantomime mode of responding for the no haptic feedback and dissociated positions grasping does not explain why the grip scaling slopes of the control participants are so different in these tasks. For example, the mean grip scaling slopes for Schenk's (2012a) controls is ~50% steeper when haptic feedback about the object is removed than when haptic feedback is present in any of the other grasping tasks, suggesting that some other factor influenced their responses. Both Milner et al., (2012) and Schenk (2012a,b) have suggested that under normal circumstances, haptic feedback 'calibrates' the grasp. As Chapters 3 and 4 have nicely illustrated, Schenk's version of this calibration process is erroneous. Milner et al., maintain that haptic calibration is compatible with the two-visual systems model, because calibration and dorsal-stream vision reflect different but equally important aspects of the visuomotor system for accurate reaching and grasping. However, Milner et al., did not elaborate on how haptic calibration (or the lack thereof) came to affect DF's grip-scaling. In general, haptic feedback about object size might influence participants' grasps through mechanisms that use error signals that are computed as the difference between 'expected' and 'observed' sensory input and/or motor outflow to update (or calibrate) future actions (e.g., Johansson & Flanagan, 2009; Wolpert, 1996). We know, for example, from work by Safstrom and Edin (2004, 2008) that haptic feedback appears to automatically influence peak grip aperture in neurologically-intact individuals: perturbing the normal correspondence between the timing of the expected and/or observed moments of contact between the fingers and the target object alters the peak grip aperture of subsequent responses. Furthermore, the effects they observed appear to be independent of any awareness of a discrepancy between vision and haptics in terms of the goal-object's size. But Safstrom and Edin's work also indicates that grip-scaling to object size is not necessarily affected by visual-haptic mismatches in object size, and so it is difficult to conclusively attribute the controls' steep slopes in the absence of haptic feedback to this low-level mechanism. If a low-level mechanism seems an inadequate explanation for an increase in the grip scaling slopes following the denial of haptic feedback, then what remains? Perhaps the absence of haptic feedback triggers an increase in ‘cognitive supervision’. Specifically, control participants might explicitly categorize the stimuli on the basis of their size (“largest”, “smallest”, “somewhere in-between”) and produce stereotyped, categorized responses to suit. This might explain why the slopes observed in the absence of any haptic feedback resemble those derived from perceptual estimation tasks.

6.2.3 ‘Intermittent Haptic Feedback’ Grasping Task

The results of one final task of Schenk’s (2012a) remains to be discussed. In one version of the grasping task, Schenk randomly interleaved trials in which haptic feedback was available (standard grasping trials) with trials in which it was not (no haptic feedback trials). The presence/absence of a hidden cylinder (and therefore the presence or absence of haptic feedback), however, was signaled to the participants (including DF) by an LED light. Schenk introduced this task to test whether DF benefited from the addition of haptic feedback even if it occurred intermittently. However, it is not clear why he decided to inform the participants on each trial of the presence/absence of haptic feedback – a test of the effect of predictive knowledge (or explicit expectancy) of haptic feedback would require an additional condition in which the predictive knowledge was not available. To test whether DF benefited from the periodic introduction of haptic feedback, Schenk compared the grip-scaling slopes when haptic feedback was intermittent to those in the no haptic feedback grasping task. The test showed that the difference in DF’s slopes across the intermittent haptic feedback and no haptic feedback grasping tasks fell outside of the range of differences observed in the controls. On the basis of this significant test, Schenk argued that DF benefited from the addition of intermittent haptic feedback in Task 5 more so than did the controls. However, Schenk's comparison does not actually directly test whether intermittent haptic feedback affected DF's slope. Moreover, it is more likely that the difference in the controls slopes between the intermittent and no haptic feedback grasping tasks drove this test statistic at least as much as DF's. To understand these important points, consider first that when randomly interleaved, the standard and no haptic feedback grasping trials did not produce the dramatic difference in either DF's slope or those of the controls that it did when these two conditions were blocked separately in the standard grasping and no haptic feedback grasping tasks. Recall that when these two grasping tasks were blocked separately, DF's slope fell to null but that the controls' slopes *increased* by ~50%. Thus the comparison of the intermittent haptic feedback task and the no haptic feedback grasping task entails a comparison of two tasks with effects on the slopes of DF and the controls that were opposite in direction. In short, Schenk's putative test of the improvement of DF's grip scaling with intermittent haptic feedback hinges just as much on the direction and size of the difference in controls' slopes as it does on those of DF's slopes. As Chapter 5 revealed, removing the cylinder hidden behind the mirror altered the way in which healthy participants approach the task. Thus, it is not clear whether intermittent haptic feedback benefited DF or whether it benefited the controls by rendering the task less pantomime-like.

Surely more work is needed to determine the contributions that predictability (or expectancy) of the availability of haptic feedback make to the maintenance of ‘normal’ grasp kinematics. It should be pointed out that predictability is not the only factor that could be at work. Motor (or sensorimotor) memory could also be operating – traces of the motor program or the re-afferent sensory information from the previous trial might be incorporated into the programming of the subsequent trial. Finally, kinesthetic perception might also be utilized from one trial to the next. It seems likely that it would be easier to reproduce a movement from the recent past based on the perceptual sense of that movement than it would be to reproduce a movement from the more distant past. Thus, future investigators should be careful to tease apart these possible contributing factors.

6.3 A ‘Visuohaptic’ Association Account of DF’s Spared Grasping Ability

Finally, I briefly outline an associative learning account of Schenk’s (2012a) findings – one which is consistent with a “multi-modal integration” view. Milner et al. (2012) put forward a variant of this account as an explanation that they believed Schenk might argue for but that they themselves rejected. According to this association account, DF learned to scale her grip to the sizes of the cylinders through an association between degraded visual signals about the cylinders with more accurate size information obtained from haptics. However, Milner et al.

listed two reasons why this association account could not work. First, they argued that because DF did not have any way of perceptually distinguishing one object from another, an association between vision and the felt sizes of the cylinders would not be possible. Nevertheless, as I have pointed out, even Schenk's data set showed that DF was capable of extracting a visual signal about the target size. Moreover, as Chapter 3 revealed, DF may very well have learned to associate visual signals about the cylinders (however degraded) with the felt sizes of the cylinders when grasping them in order to perform as well as she did in the perceptual estimation task. Milner et al.'s second reason, however, highlights the fact that both visual and haptic information was presented to DF in Schenk's dissociated positions task and yet she still failed to scale her grip to object size. In short, this kind of learned association cannot explain DF's full pattern of results.

However, it is worthwhile to point out that there is no reason to assume that DF must rely on degraded visual information about the objects. It is possible that DF distinguishes the objects by virtue of any visual feature coded by the dorsal stream, independently of conscious awareness. In other words, the visual signal could be arbitrary as long as it can differentiate one cylinder from another and be associated with a haptic signal that can do the same. Importantly, this kind of learned visual-haptic association can explain 1) DF's poor grip-scaling when there is no haptic signal about object size and 2) her intermediate performance when the haptic signals are sporadic. According to this account, however, when the position of the visible object and unseen target are dissociated, directing one's hand towards what appears to be empty space fails to recruit the dorsal pathway the way it does when the grasp is target-directed. Interestingly, in neurologically-intact individuals similar pantomimed grasps invoke activity in quite different brain areas from those invoked during ‘real’ grasps (Kroliczak et al., 2007). Thus, it is possible that, despite receiving haptic feedback about the object, the unconscious visual signals DF uses to pantomime grasp are simply not available to her because they are processed in regions of her occipital and/or parietal cortices that are damaged. Importantly, however, the visuohaptic association account cannot explain why DF’s grip scaling remains intact in Chapters 3 and 4 where the felt (i.e. haptic) object remains the same size but the visual size varied from trial to trial. Recall that in this task, the participants (including DF) reached towards the visible target to pick it up. Thus, unlike when the positions of the felt (unseen) target object and the visible object are dissociated, there is no reason for why the visual signal would not be available to be exploited. In short, the association account would have predicted that DF would fail in this task.

6.4 The Role of Haptic Feedback in Visually-Guided Grasping

The discussion up until this point applies to neurologically intact participants and the patient population DF’s data would generalize to. Both populations retain intact haptic sensation. Thus, one aspect of the issue that has hitherto been ignored in the present discussion concerns the role that the loss of the capacity to conduct haptic signal to the cortex (i.e. de-afferentation). Although the limb movements of de-afferented patients have been studied in the context of manual aiming (e.g, Ghez, Gordon, & Ghilardi, 1995), Gentilucci, Toni, Chieffi, & Pavesi (1994) studied a patient, MB, who had developed large-fibre neuropathy following primary Sjogren's syndrome. The patient lost all tactile sensation in both hands and forearms and all proprioceptive sensation in the fingers and wrist. Even her ability to detect movement in her elbow and shoulder were restricted to the extremes of each range of motion. In normal, everyday life, MB experienced great difficulty performing tasks that involved dexterous movements of the hands, fingers and wrist, such as eating, drinking, and writing without visual feedback. She could no longer hold objects, such as a glass, for long periods of time without dropping them. Gentilucci et al. reported that stimulation of both median and ulnar nerves at the wrist and elbow failed to evoke cervical and cortical potentials as did stimulation of the median nerves of the first, second and third finger and stimulation of the ulnar nerve of the fifth finger.

Importantly, Gentilucci et al. (1994) asked MB (as well as controls) to reach out to pick up target objects with and without online visual feedback. As things turned out, although there was evidence for the overall lengthening of the various temporal components of the movement, MB was quite good at reaching out to pick up the targets in either condition. However, it should be noted that Gentilucci et al. operationalized the end of the movements to reflect grip stability. As such, we cannot know whether temporal differences between MB and the controls that during the later phases of the movement occurred pre or post-initial finger contact. Importantly, the measurements of grip aperture were unaffected by this issue. Interestingly, MB showed a preserved ability to scale her grip aperture to target size even in the absence of online visual feedback. In fact, in a follow-up study, Gentilucci, Toni, Daprati, & Gangitano (1997) anesthetized the fingertips of neurologically intact participants. The participants reached out to pick up targets with online visual feedback. Anesthesia affected a number of the measures, including the timing of different phases of the movement. Perhaps most important to the present discussion, these participants, like MB, continued to scale their grip aperture to target size. Thus, it would seem that even in cases of haptic deficit, the programming of prehensile movements is driven largely by visual input. How, then, can these facts be reconciled with the importance of haptic feedback to DF's prehensile ability? In the final analysis, the logical explanation is that either combination of real-time dorsal and ventral vision (in the case of deafferented patients) or real-time dorsal vision and haptic feedback is sufficient to produce normal grip scaling. The necessity of the dorsal pathway is evinced by the fact that damage to the PPC results in optic ataxia and deficits in prehension. Logically, therefore, a combination of real-time ventral vision and haptic feedback is insufficient.

6.5 Additional Examples of 'Perception-Action' Dissociations in Neuropsychology

As we pointed out earlier, the Two Visual Systems Hypothesis does not rest entirely on the evidence from DF. Support for the central ideas of the hypothesis comes from a broad range of studies, from monkey neurophysiology to human neuroimaging. Moreover, there is also converging evidence from other patients with visual form agnosia. Patient JS, for example, had bilateral lesions in ventral stream that were more medial than DF's, but showed a similar dissociation between visual form perception and the visual control of grasping (Karnath, Ruter, Mandler, & Himmelbach, 2009). In fact, there are a number of anecdotal reports in the long literature on visual form agnosia that such patients are able to reach out and grasp objects with surprising accuracy (e.g. Campion, 1987).

Patient DF's ability to use object form to guide the configuration of her grasping hand in the absence of conscious awareness of that form is reminiscent of what Weiskrantz and his colleagues called "blindsight" in an influential article published in *The Lancet* in 1974 (Sanders, Warrington, Marshall, & Weiskrantz, 1974). Patients with blindsight following damage to the early visual areas (e.g. primary visual cortex) are able to respond to visual stimuli presented in their blind field despite a complete absence of visual phenomenology in that field. In fact, subsequent investigations of patients with 'action' blind sight (for review, see Danckert & Rossetti, 2005) have revealed a dissociation between prehension and perceptual size-estimation (Brown, Kroliczak, Demonet, & Goodale 2008; Jackson, 1999; Marcel, 1998; Perenin & Rossetti, 1996; Whitwell, Striemer, Nicolle, & Goodale, 2011). These patients typically have lesions to 'early' visual cortical areas, typically including primary visual cortex or even the pathways from the lateral geniculate nucleus that innervate these areas. In a recent paper, Whitwell, Striemer, Nicolle, & Goodale (2011) found that a young woman with a unilateral lesion of V1 was nevertheless able to scale her hand to the width of objects that she could not perceive. This observation coupled with many others demonstrating spared visuomotor control in patients with V1 lesions suggest that the posterior parietal cortex enjoys privileged access to visual inputs that bypass the retino-geniculo-striate route. One possible route for such transmission is the well-known set of projections from the superior colliculus in the midbrain to the pulvinar – and from there to the middle temporal area and the posterior parietal cortex. There are other candidate pathways as well (for review see Goodale, 2011). It seems unlikely that these extra-geniculo-striate projections evolved to be a ‘back up’ should V1 happen to be damaged, but rather play a more integral role in the mediation of visually guided movements in neurologically intact individuals. It seems likely that these pathways normally supply the dorsal stream with essential information for the visual control of movements such as reaching and grasping – and that in DF’s brain such pathways would also be at work.

In summary, the demonstration that DF has a remarkable ability to use information about object form and orientation to control skilled actions despite having a massive deficit in form vision has stood the test of time. Although a number of critics have tried to argue otherwise, it appears that she is able to use visual information about the shape of objects in a feedforward manner to guide her hand and fingers as she reaches out to grasp them – and her spared ability to do this does not depend on some sort of abnormal recruitment of haptic information to augment her compromised visual processing. Instead, it appears that vision-for-action in DF, at least as it applies to the control of grasping, depends on the recruitment of relatively intact visuomotor networks in her dorsal stream, and that these networks are engaged in much the same manner as they are in the normal healthy brain.

6.6 Future Directions

As foreshadowed in Section 6.2.3, the literature lacks an examination of the role that explicit expectancy of haptic feedback plays in the programming of grasping movements. According to the account offered in Chapter 5, purposeful, simulated grasps require more cognitive supervision and are less ‘automatic’ than natural ones – pretending to grasp imaginary or visible ones we cannot feel takes more focus and effort. Knowledge of the availability of haptic feedback on an upcoming trial should, therefore, modulate the effect of haptic feedback on grasp kinematics. Interestingly, Schenk (2012a) found no distinction between the slopes for grasps with and without haptic feedback when the two were randomly interleaved and the participants were provided advance notice of the presence/absence of the matching cylinder behind the mirror. However, Schenk’s analysis was restricted to the slopes. As Chapter 5 details, many additional measures of the grasp kinematics are affected by the removal of haptic feedback when these two conditions are blocked separately, including the time taken to plan the movement, the speed of the movement (as indexed by peak hand velocity), and the extent the hand opens throughout the movement. Thus, it remains unknown whether any of these other measures were affected. Furthermore, there are always two factors to be concerned with when comparing blocked and randomized trial orders: the consistency of the trial order (and therefore the nature of possible carry over effects) and the predictability of the upcoming condition. Blocking haptic and no haptic feedback conditions into separate blocks of trials not only renders the availability of haptic feedback on any given trial highly predictable but it also admits a homogeneous trial order and, therefore, a homogeneous source for sensorimotor memory; Randomly interleaving haptic and no haptic feedback trials, independent of any predictability, imposes a heterogeneous trial order and, therefore, a heterogeneous source for sensorimotor memory. Thus, a future study should examine the influence of predictive knowledge of the availability of haptic feedback on grasp kinematics under blocked trial orders and randomized ones *with and without* knowledge of the presence/absence of haptic feedback. This would afford the investigator a more comparable set of conditions to contrast the effects of the predictability (expectancy or predictive knowledge) of the presence/absence of haptic feedback on grasping when sensorimotor memory is and is not equivalently heterogeneous.

As was discussed in Chapter 5, although tactile feedback from the surface of the table appears to be enough to keep DF’s grip scaling within the normal range, it does not result in a complete shift to natural grasps. For example, in neurologically intact participants, unlike natural grasps, pantomimed ones that are directed at the surface of the table appear to obey so-called ‘relative’ psychophysical laws that are intrinsic to target magnitude (Weber’s law) and those that rely on the magnitude of an irrelevant dimension of the target object (so-called ‘holistic processing’). Important future work could explore these influences on DF’s grasps. If these object and magnitude related effects are driven by the same processes that drive perceptual estimates of target size, then DF’s real-time pantomime grasps when directed at the surface of the table should not obey Weber’s law nor should they be influenced by holistic processes. In contrast, a positive result on either test would strongly suggest that object processing is more fractionated than even the TVSH suggests.

Finally, on the issue of the unconscious visual processing of object form, one interesting and potentially quite fruitful investigative endeavor would examine the role that ‘shape skeletons’ or the ‘medial axis’ of objects (Blum, 1973; Blum & Nagel, 1978; Psotka, 1978) might play in mediating DF’s spared visuomotor ability. A point within a shape is part of the shape’s medial axis provided a single radius line touches two (and only) two points along the shape’s boundary. Recent evidence suggests that neurologically intact participants at the population level show sensitivity to the medial axis of pictorial shapes when asked to reach out to touch any spot they choose within the shape. Interestingly, participants do not appear to be able to explicitly report or describe the medial axis: when they are asked to indicate which of several different images of the same shape each with a different ‘cloud’ of ‘touch-points’, the vast majority fail to identify the version that identifies the medial axis (Firestone & Scholl, 2014). This latter observation when combined with the visuomotor nature of the response that reveals sensitivity to the medial axis in the first place, suggests that dorsal visual pathways might be mediating the effect. Thus, a future investigation could examine DF’s touch-points for sensitivity to the medial axis of shapes that she cannot discriminate amongst through button-press or through verbal report. A positive finding would open up an entirely new area for further exploration which would include possible avenues for advances in robotics and the rehabilitation of patients with deficits in object form processing. Similar experiments could also test for sensitivity to shape skeletons in patients deemed to be cortically blind and in patients with damage to the dorsal visuomotor structures of the posterior parietal cortex. These future experiments, when considered as a whole seem well-positioned to identify the locus of an unconscious sensitivity to shape. Indeed, neuropsychological research has been integral in enriching our current understanding of object processing in the human visual system and this fruitful field of research shows no signs of slowing down.

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James, T. W., Culham, J. C, Humphrey, G. K., Milner, A. D., and Goodale, M. A. (2003). Ventral occipital lesions impair object recognition but not object-directed grasping: An fMRI study. *Brain*, 126, 2463–2475.

Johansson, R. S. and Flanagan, J. R. (2009). Sensory control of object manipulation. In J Hermsdörfer, DA Nowak (Eds) *Sensorimotor Control of Grasping: Physiology and Pathophysiology*, pp 141-160, Cambridge University Press: Cambridge.

Karnath, H. O., Ruter, J., Mandler, A. Himmelbach, M. (2009). The Anatomy of object recognition – Visual form agnosia caused by medial occipitotemporal stroke. *The Journal of Neuroscience*, 29, 5854–5862.

Króliczak, G., Cavina-Pratesi, C., Goodman, D. A., and Culham, J. C. (2007). What does the brain do when you fake it? An FMRI study of pantomimed and real grasping. *Journal of Neurophysiology*, 97, 2410–2422.

Marcel, A. J. (1998). Blindsight and shape perception: deficit of visual consciousness or of visual function? *Brain*, 121, 1565–1588.

Milner, A. D., Ganel, T., and Goodale, M. A. (2012). Does grasping in patient D.F. depend on vision? *Trends in Cognitive Sciences*, 16, 256–257.

Milner, A. D., and Goodale, M. A. (2006). The visual brain in action (2nd ed.). New York: Oxford.

Perenin, M. T., and Rossetti, Y. (1996). Grasping without form discrimination in a hemianopic field. *Neuroreport*, 7, 793–797.

Psotka, J. (1978). Perceptual processes that may create stick figures and balance. *Journal of Experimental Psychology: Human perception and performance*, 4, 101–111.

Safstrom, D., and Edin, B. B. (2004). Task requirements influence sensory integration during grasping in humans. *Learning and Memory*, 11, 356–363.

Safstrom, D., and Edin, B. B. (2008). Prediction of object contact during grasping. *Experimental Brain Research*, 190, 265–277.

Sanders, M. D., Warrington, E. K., Marshall, J., and Weiskrantz, L. (1974). "Blindsight": Vision in a field defect. *Lancet*, 303, 707–708.

Schenk, T. (2010). Visuomotor robustness is based on integration not segregation. *Vision Research*, 50, 2627–2632.

Schenk, T. (2012a). No dissociation between perception and action in patient DF when haptic feedback is withdrawn. *The Journal of Neuroscience*, 32, 2013–2017.

Schenk, T. (2012b). Response to Milner et al.: Grasping uses vision and haptic feedback. *Trends in Cognitive Sciences*, 16, 258–259.

Schenk, T., and McIntosh, R. D. (2010). Do we have independent visual streams for perception and action? *Cognitive Neuroscience*, 1, 52–78.

Whitwell, R. L., Striemer, C. L., Nicolle, D. A., and Goodale, M. A. (2011) Grasping the non-conscious: Preserved grip scaling to unseen objects for immediate but not delayed grasping following a unilateral lesion to primary visual cortex. *Vision Research*, 51, 908–924.

Curriculum Vitae

Degrees Completed or In-Progress

- Doctorate of Philosophy, Cognitive Behavioural Neuroscience (expected completion Spring 2015)
  The University of Western Ontario, London, ON, Canada
  Visual and Haptic Contributions to the Grasp Kinematics of Precision and Pantomimed Ones in Visual Form Agnosia and Normally-Sighted Populations
- Master of Science, Cognitive Behavioural Neuroscience (2010)
  The University of Western Ontario, London, ON, Canada
  Preserved Grip Scaling to Unseen Objects Following a Unilateral Lesion to V1 for Immediate but not Delayed Grasping
- Bachelor of Science, Physiology and Psychology (2005)
  The University of Western of Ontario, London, ON, Canada.

Current Position

Sep 2010 – Present
Doctoral Candidate, Graduate Program in Neuroscience
The University of Western Ontario, London, ON, Canada.

- Supervisor: Dr. Melvyn A. Goodale

Previous Training

Sep 2004 – Aug 2008 Research Assistant, Psychology Department, UWO, London, ON, Canada.

- Supervisor: Dr. Melvyn A. Goodale
- Designing, implementing, analysing, summarizing, and disseminating experiments in cognitive behavioural neuroscience

Sep 2004 – Apr 2005 Independent studies, Psychology, UWO, London, ON, Canada.
  - Iconic Masking: The meta-spatiotemporal account and the coherent percept
  - Supervisor: Dr. Patrick Brown

Awards & Scholarships

Sep 2013 – Aug 2014 Ontario Graduate Scholarship with Distinction
  - $16500 per year for one year.

Sep 2010 – Aug 2013 Post-Graduate Scholarship Doctoral Level Scholarship (PGS-D), Natural Sciences and Engineering Research Council of Canada (NSERC).
  - $21000 per year for three years

Sep 2009 – Aug 2010 Canadian Graduate Scholarship Postgraduate Masters Level Award (CGS-M), NSERC.
  - $17500 for one year

Sep 2008 – Aug 2014 Western Graduate Research Scholarship, UWO
  - $7515 current academic year

Sep 2009 – Aug 2010 Ontario Graduate Scholarship, UWO
  - $15000 for one year (declined)

Sep 2008 – Aug 2009 Keith Humphrey Memorial Award, UWO
  - $500

Sep 1999 – Apr 2000 Entrance Scholarship, UWO
  - $750

Proficiency and Growing Expertise

Experimental Tools

- Motion capture systems (eye, hand, and limb kinematics)
- Anatomical and Functional Magnetic Resonance Imaging
- Transcranial Magnetic Stimulation (functional disruption)
- ATI Transducers (for measuring grip and load forces applied during object lifting

Subject Populations

- Normally-sighted and neurologically intact
- Visually impaired and/or neurologically damaged patients

Software Tools

- Analysis of Brain Function and Structure (Brain Voyager QX)
- Programming languages (Matlab, R, Java)
- Other software (Microsoft Office, SPSS, BrainSight – TMS neuronavigation)

Current Professional Affiliations

- Vision Sciences Society (2006 – Present)
- Society for Neuroscience (2011 – Present)

Published, In Press, or Submitted Articles (16)

*Undergraduate students I have supervised are underlined

1) Foley R, **Whitwell RL** (Submitted) How do the spatial contents of experience in the ventral visual pathway contribute to goal-directed action. *Cognitive Science*

2) Foley RT, **Whitwell RL**, Goodale MA (*in press*) The two-visual-systems hypothesis and the perspectival features of visual experience. *Consciousness and Cognition*

3) **Whitwell RL**, Ganel T, Byrne CM, Goodale MA (*in press*) Real-time vision, tactile cues, and visual form agnosia in pantomimed grasping: removing haptic feedback induces a switch from natural to pantomime-like grasps. *Frontiers in Human Neuroscience*

4) **Whitwell RL**, Milner AD, Cavina-Pratesi C, Barat M, Goodale MA (*in press*) Patient DF's visual brain in action: Visual feedforward control in a patient with visual form agnosa. *Vision Research.*

5) **Whitwell RL**, Tang R, Goodale MA (2015) The influence of visual feedback from the recent past on the programming of grip aperture is grasp-specific, shared between hands, and mediated by sensorimotor memory not task set. *Cognition*, 138, 39–63.

6) **Whitwell RL**, Milner AD, Goodale MA (2014) The Two Visual Systems Hypothesis: New challenges and insights from visual form agnosic patient DF. *Frontiers in Neurology*, 5, 1–8.

7) **Whitwell RL**, Milner DA, Cavina-Pratesi C, Byrne CM, Goodale MA (2014) DF's Visual Brain in Action: the role of tactile cues. *Neuropsychologia*, 55:41–50.

8) Tang R, **Whitwell RL**, Goodale MA (2014) Explicit knowledge about the availability of visual feedback affects grasping with the left but not the right hand. *Experimental Brain Research*, 232:293–302.

9) **Whitwell RL**, Goodale MA (2013) Grasping without Vision: Time normalizing grip aperture profiles yields spurious grip scaling to target size. *Neuropsychologia*, 51:1878–1887.

10) **Whitwell RL**, Buckingham G (2013) Re-framing the Action and Perception Dissociation in DF: Haptics matter, but how? *Journal of Neurophysiology*, 109:621–624.

11) **Whitwell RL**, Striemer, CL, Nichols, D, Goodale MA (2011) Grasping the non-conscious: Preserved grip scaling to unseen objects for immediate but not delayed grasping following unilateral lesions to primary visual cortex. *Vision Research*, 51:908–924.

12) Chouinard PA, **Whitwell RL**, Goodale MA (2009) The lateral-occipital and the inferior-frontal cortex play different roles during the naming of visually-presented objects. *Human Brain Mapping,* 30:3851–3864.

13) **Whitwell RL**, Goodale MA (2009) Updating the programming of a precision grip is a function of recent history of available feedback. *Experimental Brain Research*, 194:619–629.

14) **Whitwell RL**, <u>Lambert L</u>, Goodale MA (2008) Grasping Future Events: explicit knowledge of the availability of visual feedback fails to reliably influence prehension. *Experimental Brain Research* 188:603–611.

15) Gonzalez CLR, Ganel T, **Whitwell RL**, Morrissey B, Goodale MA (2008) Practice Makes perfect, but only with the right hand: Sensitivity to perceptual illusions with Awkward grasps decreases with practice in the right but not the left hand. *Neuropsychologia* 46:624–631.

16) Gonzalez CLR, **Whitwell RL**, Morrissey B, Ganel T, Goodale MA (2007) Left handedness does not extend to visually guided precision grasping. *Experimental Brain Research* 182:275–279.

Conference Talks (2)

*Undergraduate students I have supervised are <u>underlined</u>

1) **Whitwell RL**, Milner DA, Cavina-Pratesi C, <u>Barat M</u>, Goodale MA. Patient DF’S visual brain in action: The role of visual and tactile feedback [Meeting] *Satellite Symposium: Linking primate brain circuits to behaviour: advancements and applications. 8th Annual Meeting of the Canadian Association for Neuroscience* (Montreal, Quebec, Canada) May 2014

2) **Whitwell RL**, Milner DA, Cavina-Pratesi C, Barat M, Byrne CM, Goodale MA. Visual feedforward grasping and motor adaptation to actual target width in visual form agnosic patient DF. [Meeting] *14th Annual International Meeting of the Vision Sciences Society* (Naples, Florida, USA) May 2014

Published Refereed Conference Abstracts

*Undergraduate students I have supervised are underlined.

1) **Whitwell RL**, Milner AD, Cavina-Pratesi C, Barat M, Goodale MA. DF's Visual Brain in Action: The role of tactile and visual feedback. [Meeting] *8th Annual Meeting of the Canadian Neuroscience Association for Neuroscience* (Montreal, Quebec, Canada) May 2014.

2) Merritt KE, **Whitwell RL**, Buckingham G, Chouinard P, Goodale MA. The Debate is Over: Action and perception dissociate using a 3D variant of the Sanders parallelogram illusion while controlling for visual and haptic feedback. [Meeting] *8th Annual Meeting of the Canadian Neuroscience Association for Neuroscience* (Montreal, Quebec, Canada) May 2014.

3) **Whitwell RL**, Milner DA, Cavina-Pratesi C, Barat M, Byrne CM, Goodale MA. Visual feedforward grasping and motor adaptation to actual target width in visual form agnosic patient DF. [Meeting] *14th Annual International Meeting of the Vision Sciences Society* (Naples, Florida, USA) May 2014

4) Merritt KE, **Whitwell RL**, Buckingham G, Chouinard P, Goodale MA. Dissociating action and perception using a 3D variant of the Sanders Illusion while controlling for visual and haptic feedback. [Meeting] *14th Annual International Meeting of the Vision Sciences Society* (Naples, Florida, USA) May 2014

5) **Whitwell RL**, Tang R. & Goodale MA. Anticipatory knowledge of visual feedback and cognitive supervision affect grasping with the left but not the right hand. [Meeting] *Canada-Israel Symposium: Brain Plasticity, Learning, and Education* (London, Ontario, Canada) Jun 2013.

6) **Whitwell RL**, Cavina-Pratesi C, Milner DA, Byrne CM, Goodale MA. Preserved grip scaling to visual size despite non-veridical haptic feedback in a patient with visual form agnosia. [Meeting] *7th Annual Meeting of the*

Canadian Association for Neuroscience (Toronto, Ontario, Canada) May 2013.

7) **Whitwell RL**, Cavina-Pratesi C, Milner DA, Goodale MA. Preserved grip scaling to visual size despite non-veridical haptic feedback in a patient with visual form agnosia [Meeting] 13*th Annual International Meeting of the Vision Sciences Society* (Naples, Florida, USA) May 2013.

8) Striemer CL, **Whitwell RL**, Goodale MA. Implicit facial emotion recognition in a case of cortical blindness grasps [Meeting] 13*th Annual International Meeting of the Vision Sciences Society* (Naples, Florida, USA) May 2013.

9) Byrne CM, **Whitwell RL**, Ganel T, Goodale MA. Can't Touch This: Removing haptic feedback of the goal object during visually-guided grasping induces pantomime-like grasps [Meeting] 13*th Annual International Meeting of the Vision Sciences Society* (Naples, Florida, USA) May 2013.

10) **Whitwell RL**, Sperandio I, Garach M. Goodale MA. Grasping the Ebbinghaus Illusion: Perception and action dissociate but overt attention does not. [Meeting] *22nd Annual Meeting of the Canadian Society for Brain, Behaviour and Cognitive Science* (Kingston, Ontario, Canada) Jun 2012

11) **Whitwell RL**, Buckingham G, Chouinard PA, Mikkila JM, Fortunato SF, Goodale MA. Practice reduces the effect of a Ponzo illusion on precision grasping but not manual estimation [Meeting] *12th Annual International Meeting of the Vision Sciences Society* (Naples, FL, USA) May 2012.

12) Sperandio I, **Whitwell RL**, Chouinard PA, Goodale MA. Preservation of size constancy for action, but not perception, in a patient with bilateral occipital lesions [Meeting] *12th Annual International Meeting of the Vision Sciences Society* (Naples, Florida, USA) May 2012.

13) **Whitwell RL**, Striemer CL, Goodale MA. The functional correlates of action blindsight: Evidence for a functioning fronto-parietal network in the absence of phenomenological vision [Meeting] *41st Annual International Meeting of the Society for Neuroscience* (Washington, D.C., USA) Nov 2011

14) Striemer CL**, Whitwell RL**, Goodale MA. Preserved grip scaling for immediate but not delayed grasping in the absence of conscious vision [Meeting] *14th Annual International Meeting of the Association for the Scientific Study of Consciousness* (Toronto, ON, Canada) June 2010.

15) **Whitwell RL**, Chouinard PA, Goodale MA. Visual feedback modulates BOLD activity in the posterior parietal cortex more so for visually-guided grasping than for visually-guided reaching [Meeting] *10th Annual International Meeting of the Vision Sciences Society* (Naples, Florida, USA) May 2010.

16) Chouinard P, **Whitwell RL**, Goodale MA. Role of LOC and pIFG in processing physical features of objects and semantics during object naming [Meeting] *38th Annual Meeting of the Society for Neuroscience* (Washington, DC, USA) Nov 2008.

17) Chouinard PA, **Whitwell RL**, Goodale MA Role of the lateral-occipital complex and of the posterior inferior-frontal gyrus in naming objects [Meeting] *1st North American Symposium on TMS and Neuroimaging in Cognition and Behaviour* (Montreal, QC, Canada) Sep 2008.

18) Culham JC, Wolf ME, **Whitwell RL**, Brown LE, Khan SA, Cant JS, Monaco S, Dutton GN, Goodale MA. fMRI and behavioral testing reveal preserved motion processing and visuomotor control in a patient with extensive occipitotemporal lesions. [Meeting] *18th Annual Meeting of the Canadian Society for Brain, Behaviour and Cognitive Science* (London, ON, Canada) June 2008.

19) **Whitwell RL**, Lambert L, Goodale MA. Visuomotor planning cannot take advantage of conscious knowledge of future events. [Meeting] *8th Annual International Meeting of the Vision Sciences Society* (Naples, Florida, USA) May 2008.

20) Wolf ME, **Whitwell RL**, Brown LE, Cant JS, Chapman C, Witt JK, Khan SA, Chouinard PA, Culham JC, Dutton GN, Goodale MA. Preserved visual abilities following large bilateral lesions of the occipitotemporal cortex. [Meeting] *8th Annual International Meeting of the Vision Sciences Society* (Naples, Florida, USA) May 2008

21) Wolf ME, **Whitwell RL**, Han T, Goodale MA. Evidence that grip scaling, but not perceptual estimation, resists the ponzo illusion. [Meeting] *1st Annual National Meeting of the Canadian Association for Neurosciences* (Toronto, ON, Canada) June 2007.

22) **Whitwell RL**, Morrissey B., Gonzalez CLR, Ganel T, Goodale MA. Left handedness does not extend to visually guided grasping. [Meeting] *6th Annual International Meeting of the Vision Sciences Society* (Sarasota, Florida, USA) May 2006.

Supervisory Experience: senior honours thesis students

- Masihula Barat *Does visual feedback explain the action-perception dissociation in visual form agnosic patient DF?* (2013–2014)
- Kate Merritt *The Role of Cognitive Supervision in Visually Guided Action* (2013–2014)
- Deiter Meena *Neural substrates of visual form and orientation processing* (2012–2013)
- Mehul Garach *The role of eye movements and overt attention in illusions* (2011–2012)
- Elysa Jeria *Trial history effect of object size on action and perception exert distinct perseverative and sequential size-contrast effects* (2010–2011)
- Amanda Wilhelm *Points in space or points on an object? The influence of object visual properties of extent and shape on visually guided grasping* (2009–2010)
- Thida Han *Vision for Action and Perception* (2006–2007)
- Lisa Lambert *The Effects of the Sequence of Availability of Visual Feedback on Movement Planning* (2006–2007)

Supervisory Experience: laboratory volunteers and research assistants

- Nathan Katz (2014–present)
- Nicole Stokes (2012–2014)
- Adora Whitney (2012–2013)
- Caitlin Byrne (2012–2013)
- Jessica Mikkila (2011–2012)
- Stefanie Fortunato (2010–2011)

Academic Service

- Adjudication committee for the Schulich School of Medicine and Dentistry Leadership Award (2014)
  - The graduate student adjudicator among four faculty members and one post-doctoral fellow in the committee
- Reviewer for the following journals
  - Acta Psychologica
  - Experimental Brain Research
  - Experimental Psychology: Learning, Memory, and Cognition
  - Frontiers in Human Neuroscience
  - Human Brain Mapping
  - Neuroimage
  - Neuropsychologia
  - Transactions on Neural Systems and Rehabilitation Engineering

Volunteerism

- Schulich Graduate Representative Council (2013–2014)

  - Neuroscience Graduate Program representative. Advocated on behalf of the students in the neuroscience graduate program on issues ranging from Western Graduate Research Scholarship and TA-ships to international conference travel allowances. Implemented the first student vote for my replacement at the end of my tenure.
- Assistant Marshal, The University of Western Ontario summer 2014 convocation ceremony
- Adjudication committee for the Schulich School of Medicine and Dentistry Leadership Award (2014)
  - The graduate student adjudicator among four faculty members and one post-doctoral fellow in the committee
- London Ontario Brain Bee (2014)
  - Led group demonstrations of the experimental techniques involved with motion-tracking, educating high school students about studies that have shown that the human visual use of vision for conscious report and for skilled actions.
- Usher, The University of Western Ontario summer 2013 convocation ceremony
- London Ontario Brain Bee (2013)
  - Led groups of high-school students in interactive demonstrations of the size-weight illusion and the rubber hand illusion.
- Philosophy of Mind, Language, and Cognitive Science graduate conference (2011)
  - Transcranial magnetic stimulation (TMS) and frameless stereotaxy demo for groups of conference attendees. Explored the strengths and weaknesses of using TMS and some of its basic principles, including motor thresholding.
- Fire Marshal, department of psychology, The University of Western Ontario (2008-2010)
  - Responsible for ensuring that the 6th floor of the Social Sciences Centre was clear of personnel in the event that a fire alarm sounds.