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Abstract: 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, while in a second, the feedback was of a constant intermediate width while the visual target varied trial by trial. Despite such false 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.

*Highlights (for review)

DF grasped Efron blocks across their width or manually estimated this target feature
DF's perception-action dissociation does not rely on online visual feedback
Haptic feedback does not improve DF's chance manual estimation performance
DF's grip aperture adapts to the constant, intermediate-haptic-width of the target
DF's perception-action dissociation does not rely on congruent vision and haptics

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

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Abstract

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, while in a second, the feedback was of a constant intermediate width while the visual target varied trial by trial. Despite such false 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.

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 (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, & 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). 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). For example, 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 et al. 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. 2003; Steeves, Humphrey, Culham, Menon, Milner & Goodale, 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, 1994a; Goodale et al. 1994b; Goodale et al. 1991; Whitwell et al. 2014). Despite recent evidence of bilateral damage in more posterior parieto-occipital regions of her dorsal stream (James et al. 2003; Bridge et al. 2013), 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 et al. 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). 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 (1) that 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) that 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 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). Thus, the third aim of the current investigation was 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.

2 Methods

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.

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 set 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 \times 8.3 cm, 5 cm \times 5 cm, and 4 cm \times 6.3 cm, side ratios: 2.8, 1, and 1.6; yellow set, $w \times l$: 2 cm \times 12.5 cm, 3.6 cm \times 6.9 cm, and 5 cm \times 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 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 1A).

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.

2.2.1 *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 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 described in Section 2.2.

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 towards the object to pick it up, 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. 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).

2.2.2 *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.

2.2.3 *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. 1A). The participants first performed a manual estimation task without haptic feedback as discussed in Section 2.2.1, 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, 2012; Whitwell et al. 2014).

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 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 forefinger 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.

2.4 *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 (Goodale et al. 1991; Goodale et al. 1994a; Hesse et al. 2012; Himmelbach, Boehme & Karnath, 2012; Marotta, Behrman & Goodale, 1997; Whitwell et al. 2014; Schenk 2012a). 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, 2003b, the r values were Fisher-transformed, r' , before being aggregated and submitted for inferential analysis. The second principal measure we examined was PGA.

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. Second, 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 control), we used the 'unstandardized difference test' for 'classical' or 'strong/differential' dissociations (Crawford & Garthwaite, 2005; Crawford, Garthwaite, & Gray, 2003a). This test uses on 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 et al. 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 are 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 was 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).

3 Results

3.1 Tests of the effect of online visual feedback on grasping

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 ($p < 5 \times 10^{-4}$) (see Fig. 2A) or closed loop, $p < 6 \times 10^{-6}$ (see Fig. 2B). Under open-loop conditions, her grip scaling did not differ significantly from those of the controls as measured by slopes ($p = 0.08$) (see Fig. 3A) or correlations, $p = 0.24$. Under closed-loop conditions, DF's grip scaling was significantly poorer than the controls' as measured by slopes ($p < 7 \times 10^{-3}$) (see Fig. 3A). When measured with correlations, however, DF's grip scaling in closed loop did not differ significantly from those of the controls, $p = 0.12$.

Interestingly, compared to open loop, closed loop visual feedback increased the controls' grip scaling when either slopes ($p < 3 \times 10^{-3}$) or correlations ($p < 2 \times 10^{-3}$) 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. 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.

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 ($p < 2 \times 10^{-8}$) (see Fig. 3A), and the strength of the relationship between her MEAs and target width was significantly weaker

($p < 2 \times 10^{-6}$), 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.

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 ($p < 5 \times 10^{-7}$) (see Fig. 3C) or correlations ($p < 2 \times 10^{-3}$) 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 ($p < 3 \times 10^{-4}$) (see Fig. 3C) or correlations ($p < 5 \times 10^{-3}$) 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.

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, $p < 4 \times 10^{-4}$. DF's PGA was also significantly larger when her grasps were executed in open loop than in closed loop, $p < 6 \times 10^{-3}$. This increase in DF's PGA did not differ significantly from the mean increase observed in the controls' PGA, $p = 0.45$ (see Fig 4A). In short, DF's PGA increased just as much as the controls did in the absence of online visual feedback throughout her movements.

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. 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, more extensive 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 3C).

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

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: $p < 4 \times 10^{-9}$ (see Fig. 5A); correlations: $p < 7 \times 10^{-8}$] and when it was not [slopes: $p < 2 \times 10^{-9}$ (see Fig. 5A); correlations: $p < 6 \times 10^{-5}$]. 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.5B) or correlations ($p = 0.85$) were considered.

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, $p < 4 \times 10^{-5}$. Her grip scaling, as measured by slopes, indicated an impairment ($p < 0.02$) (see Fig. 5A). When correlations were considered, however, DF's grip scaling fell within the control range, albeit towards the lower end, $p = 0.14$.

3.2.2 *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: $p < 3 \times 10^{-3}$ (see Fig. 5C); correlations: $p < 8 \times 10^{-3}$] or not [slopes: $p < 8 \times 10^{-4}$ (see Fig. 5C); correlations: $p < 0.02$].

3.3 *Tests of the effect of varying visual width while keeping haptic width the same*

3.3.1 *Grip scaling in the grasping tasks*

Patient DF ($p < 3 \times 10^{-7}$) 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 on account of the haptic width remaining the same intermediate size from trial to trial (constant haptics) (DF: $p < 5 \times 10^{-4}$). 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. 6A) or correlations (veridical haptics: $p = 0.63$; constant haptics: $p = 0.48$) were considered.

The controls' grip scaling was significantly reduced when the haptic widths of the Efron blocks were constant than when they were veridical (slopes: $p < 2 \times 10^{-4}$; correlations: $p < 7 \times 10^{-5}$). 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. 6B); correlations: $p = 0.88$].

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 ($p < 2 \times 10^{-8}$) (see Fig. 6A) and the strength of the relationship significantly weaker ($p < 3 \times 10^{-6}$) 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.

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 ($p < 2 \times 10^{-4}$) (see Fig. 6C), or correlations ($p < 6 \times 10^{-4}$) 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 ($p < 4 \times 10^{-4}$) (see Fig. 6C) or correlations ($p < 3 \times 10^{-3}$) 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.

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), $p < 2 \times 10^{-3}$. DF's PGA showed a similar, though not significant increase ($p = 0.23$). Nevertheless, the increase in DF's PGA was not 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, $p < 7 \times 10^{-4}$. A similar effect was observed for the complementary comparisons for the block with the large visual width, $p < 2 \times 10^{-3}$. 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. 7).

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 than when they were constant, $p < 2 \times 10^{-3}$. 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 **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 signalling the end of the movement would appear to be all that is required to maintain normal target-directed grasping behaviour. Goodale, Ganel, & Milner (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 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; Jakobson & Goodale, 1991; Tang, Whitwell, & Goodale, 2014; Whitwell, Lambert, & Goodale, 2008; Whitwell & Goodale, 2009).** Importantly, neither the reduction in the sharpness or strength of grip scaling nor the increase in overall peak grip aperture (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 the 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 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 (2012) 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. 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 is updated to reflect the haptic width of the object in normally-sighted individuals 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), 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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Figure Captions

Figure 1. (A) A schematic above-view of the experimental setups for (Left) the tests of online visual feedback on grasping and 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.

Figure 2. DF's peak grip aperture (PGA) as a function of the width of the target block when (A) online visual feedback was available throughout the movement and when (B) online visual feedback was not available throughout the movement. In either condition, 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 movements.

Figure 3. (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 FV) 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 perceptual width processing. (B) The effect of online visual feedback on the slopes (Δb). 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.

Figure 4. (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 visual online 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.

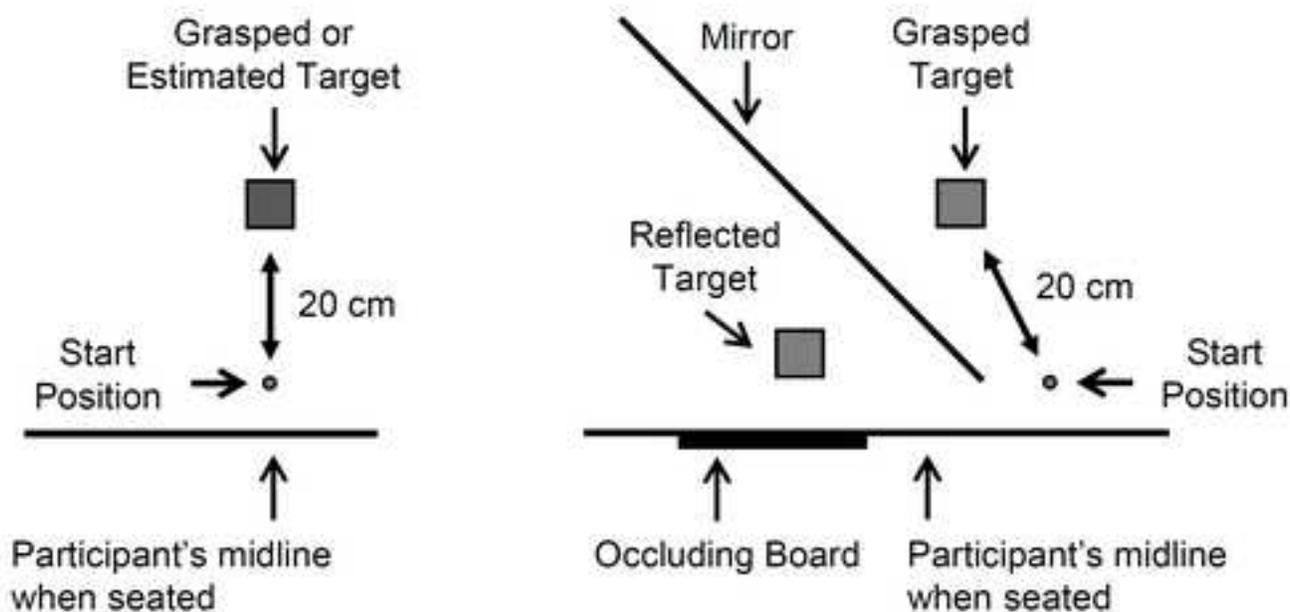
Figure 5. (A). The slopes (b) of the controls (circles) and of DF ('X's) relating either the MEAs (from the manual estimation tasks) or the PGAs (from the grasping task) to the widths of the yellow Efron blocks. For the two experimental manual estimation tasks, haptic feedback was either unavailable (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.

Figure 6. (A) 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, either 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.

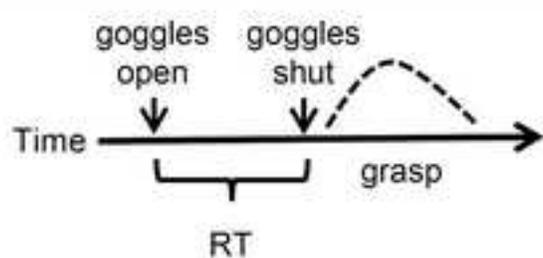
Figure 7. Adaptation in peak grip aperture (PGA) to the haptic width of the target. Adaptation was assessed by a comparison of the grasping task in which the visual and haptic width of the target were congruent (veridical haptics: VH) and the grasping task in which the haptic width (but not the visual 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'.

A. Schematic bird's eye view of the setups

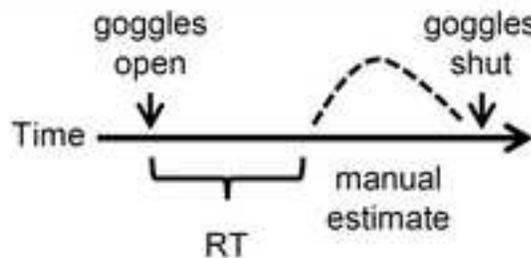


B. Protocols for the experiments

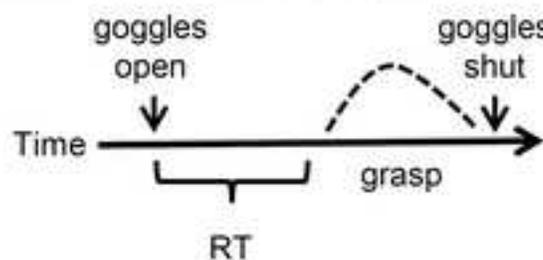
Online Visual Feedback Removed



Manual Estimates without Haptic Feedback



Online Visual Feedback Available



Manual Estimates with Haptic Feedback

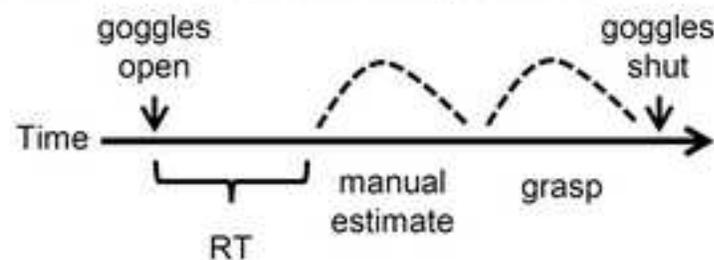
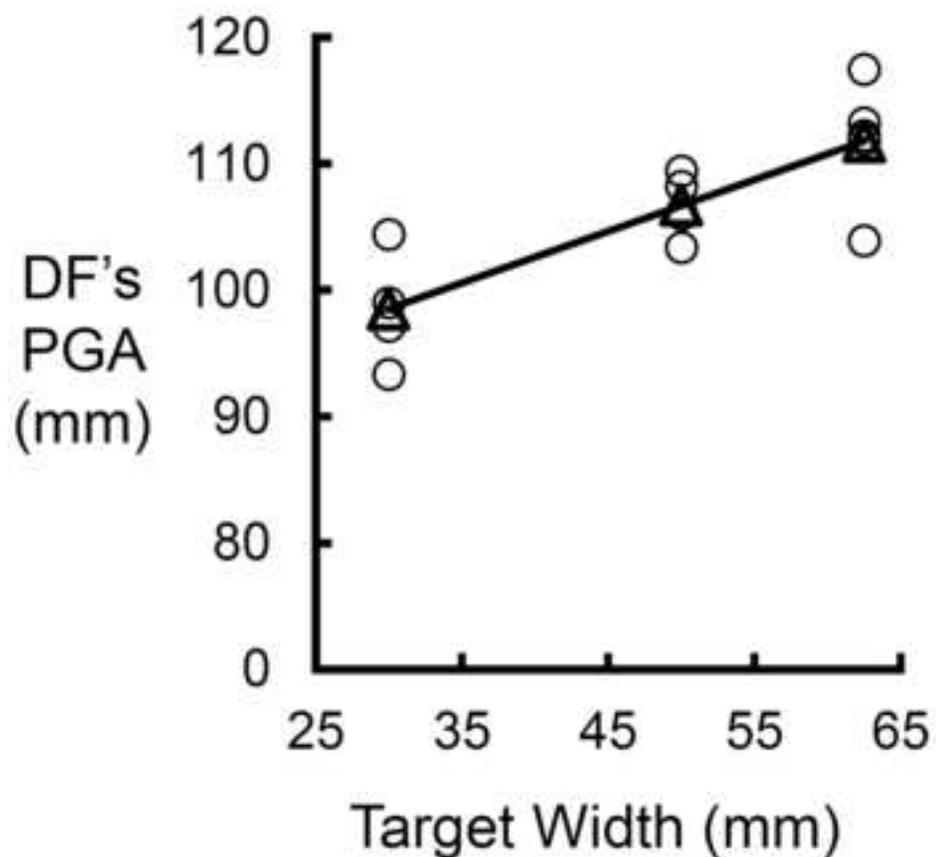


Figure2

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A. Without online visual feedback
(visually open loop)



B. With online visual feedback
(visually closed loop)

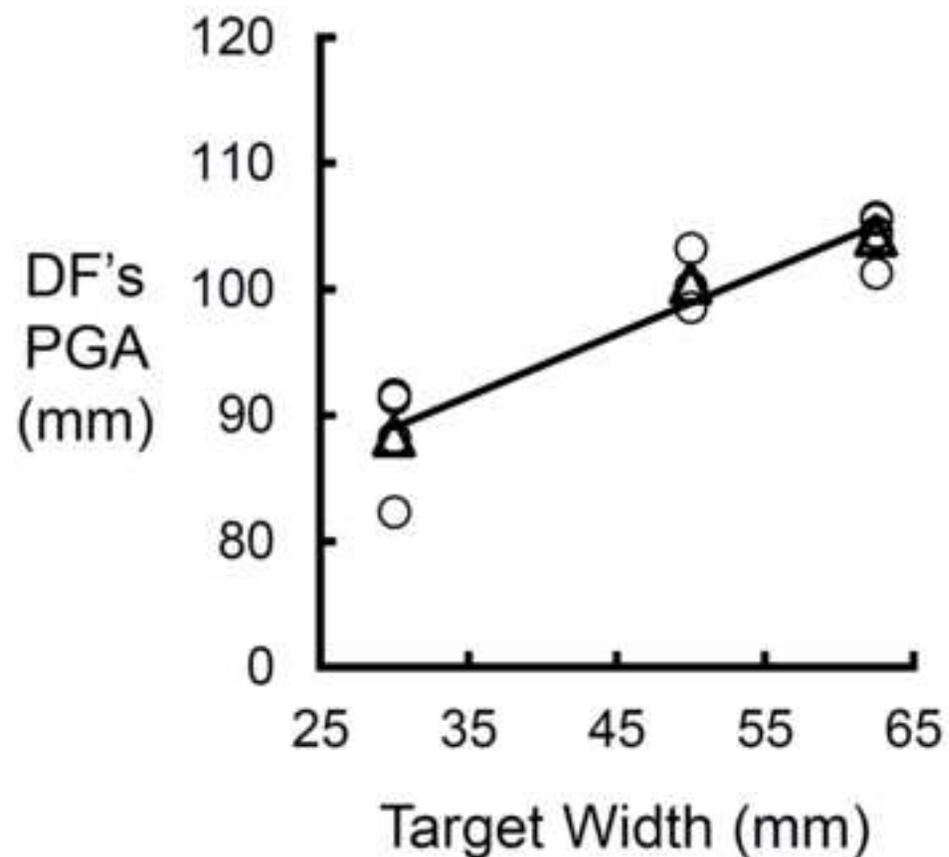


Figure 3

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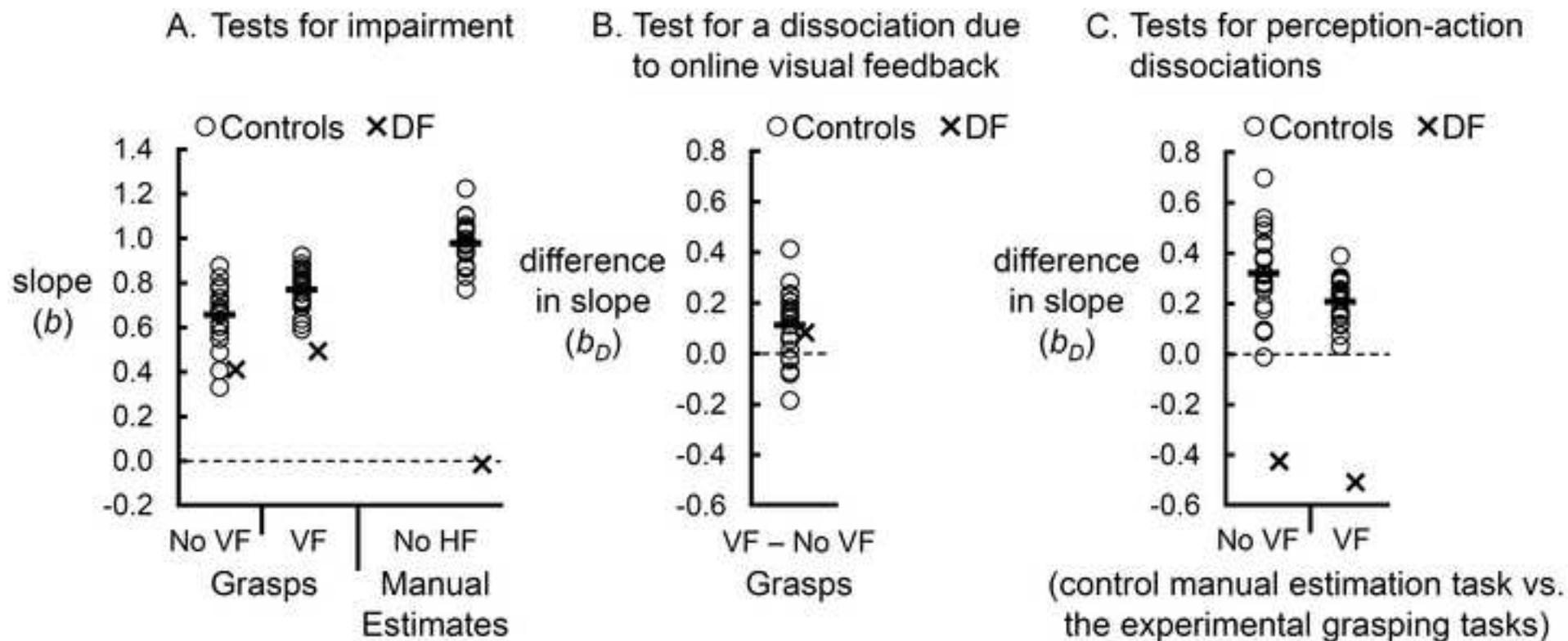
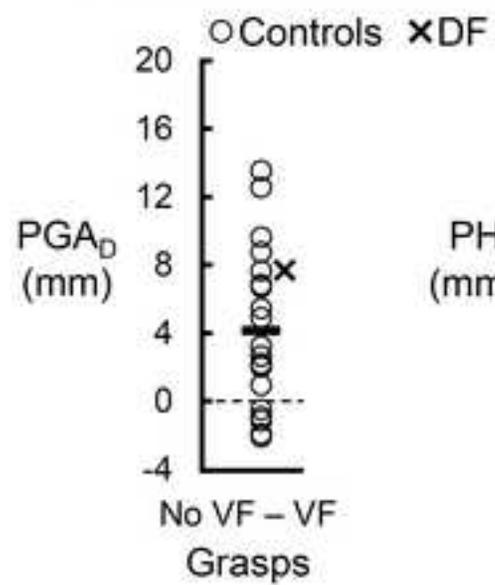


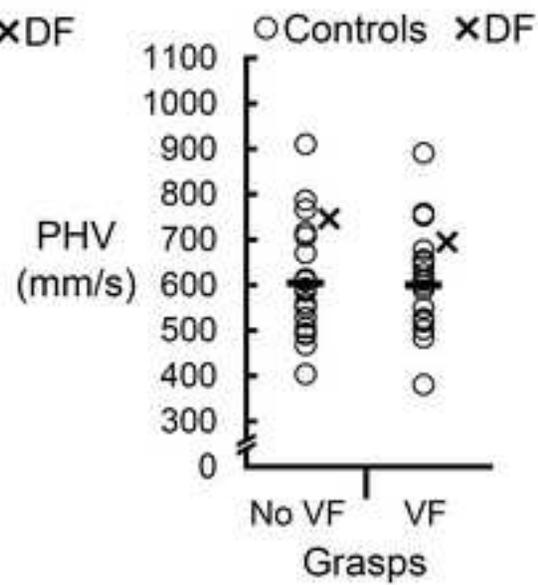
Figure 4

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A. Test for dissociation due to online visual feedback



B. Tests for impairment



C. Test for dissociation due to online visual feedback

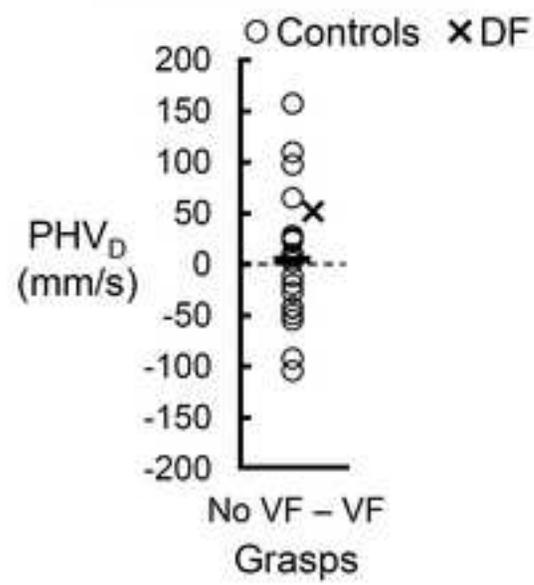


Figure 5

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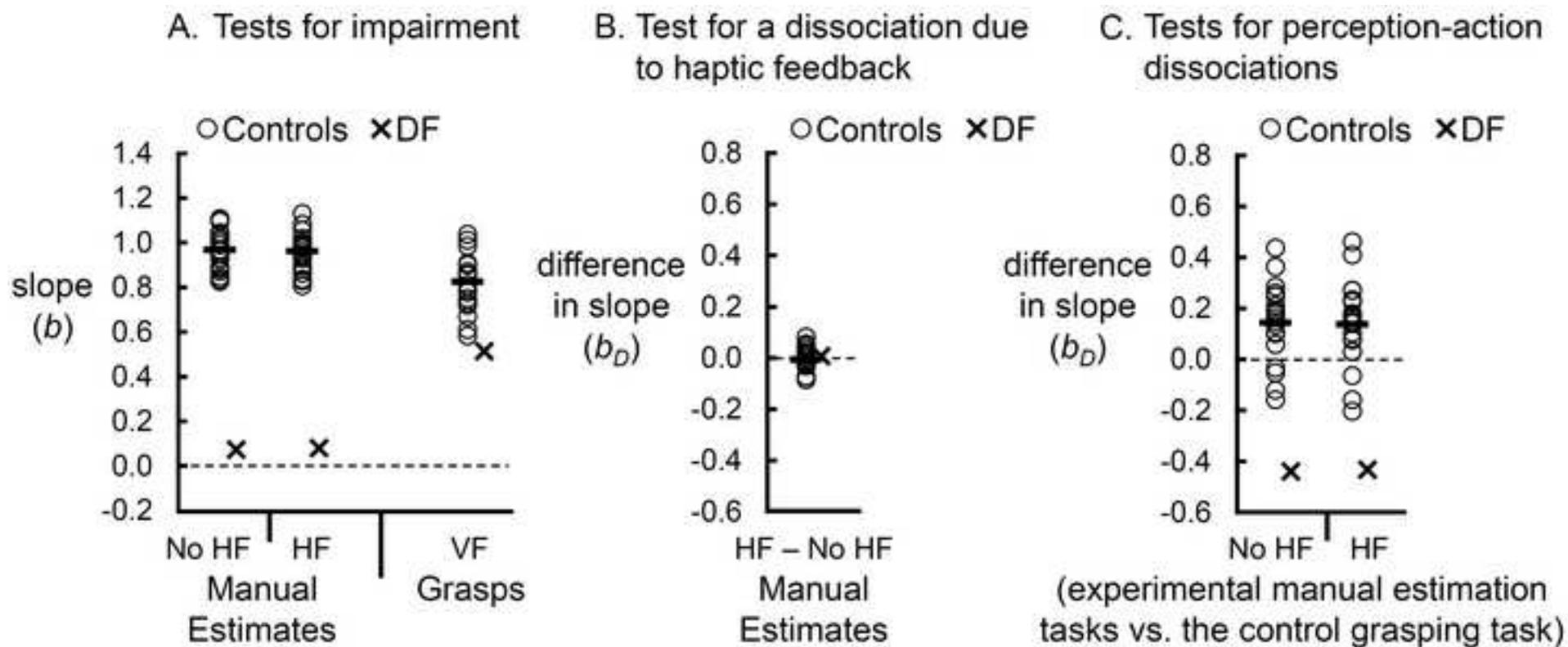


Figure6

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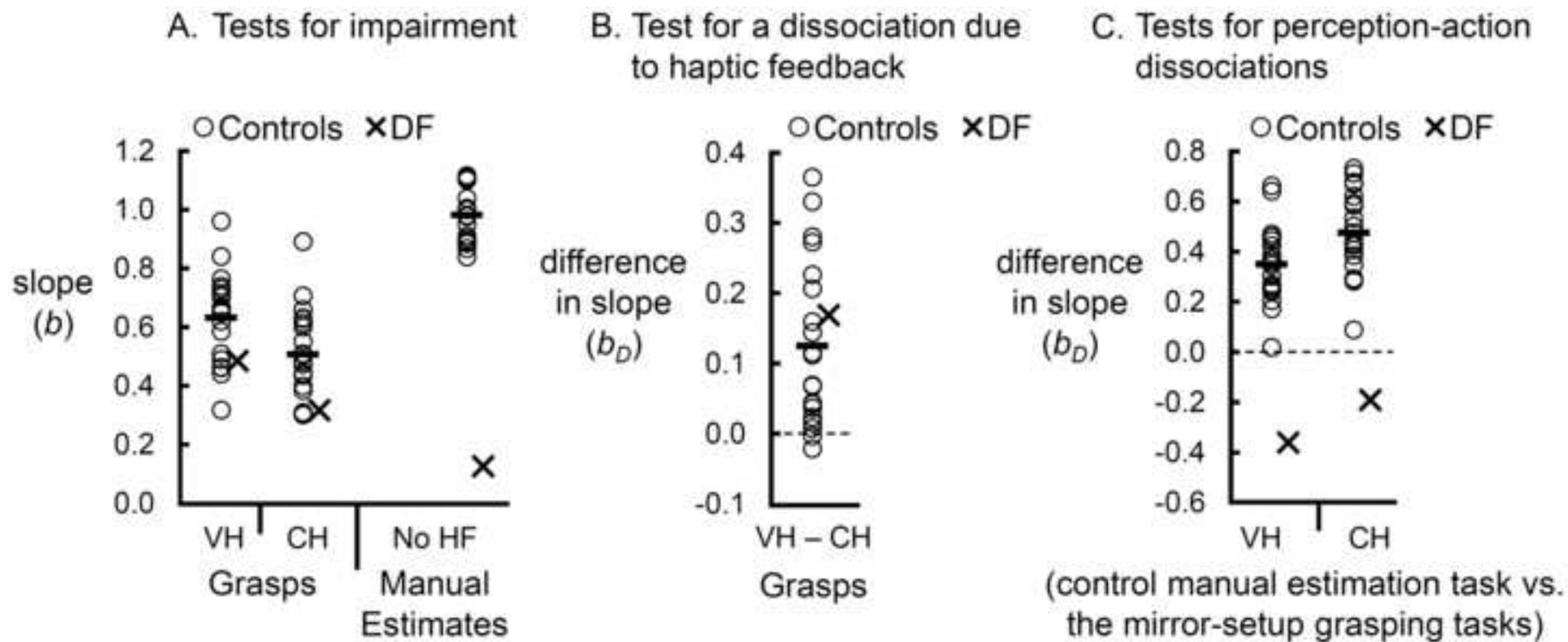


Figure 7

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Tests for adaptation in PGA to the intermediate haptic width

