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

Robert L. Whitwell [a,b], A. David Milner [c], Cristiana Cavina-Pratesi [c], Caitlin M. Byrne [a], Melvyn A. Goodale [a,*]

[a] The Brain and Mind Institute, The University of Western Ontario, London, ON, Canada N6A 5B7
[b] The Graduate Program in Neuroscience, The University of Western Ontario, London, ON, Canada N6A 5B7
[c] Department of Psychology, Durham University, South Road, DH1 3LE Durham, UK

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ABSTRACT

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 geometries. 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). The Journal of Neuroscience, 32(6), 2013–2017; Schenk (2012b). Trends in Cognitive Sciences, 16(5), 258–259. 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 driven largely by visual feedforward processing of the geometric properties of the target. Crucially, these findings also indicate that simple 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.



## 1. Introduction

### 1.1. 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, Marc 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

* Correspondence to The Brain and Mind Institute, The University of Western Ontario, The Natural Sciences Centre, Room 205, London, ON, Canada N6A 5B7. Tel.: +1 519 661 2070; fax: +1 519 661 3961.
*E-mail address:* mgoodale@uwo.ca (M.A. Goodale).

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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 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.

### 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 previously, 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, Mine, Georgopoulos, Mutara, & Sakata 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).

### 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, 1994a). 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., 1994a).

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., 1994a). 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.

### 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 at 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 signal would maintain the status quo, whereas a larger error signal would result in 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., 1994a). 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.

In the present experiment, we explored this possibility by retesting 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 proposes, 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 visuohaptic calibration 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 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.

## 2. Methods

### 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.

### 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 ($w \times l$: 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 cm, 20 cm, and 30 cm) along their midline 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 ($w \times l$: 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. 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. 1). To 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

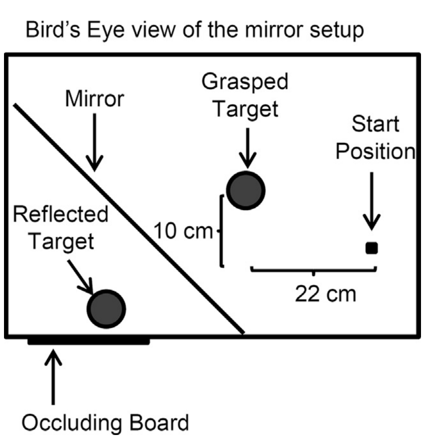


**Fig. 1.** The experimental setup for the grasping and manual estimation tasks. For the mirror tasks, a direct view of the mirror-reflected cylinder was blocked by a white board. When the goggles cleared, the participants reached out behind the mirror to grasp a second cylinder that was positioned to 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).

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.

### 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.

### 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 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 ($p_{min}=0.47$). 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 et al. (1998) test is mitigated as the sample size increases from 5 to 50 (see Crawford & 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 mentioned in Section 2.2 above, 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. Results

### 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. 2 and 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.

### 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

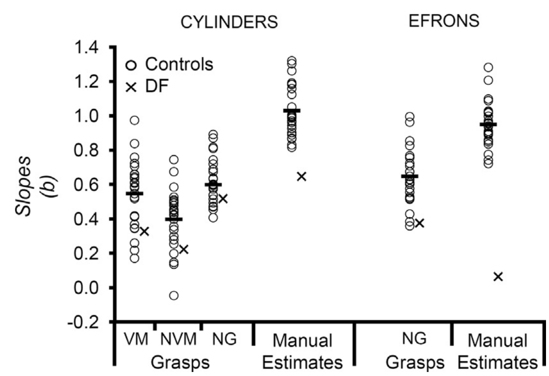


**Fig. 2.** Grip aperture scaling (as measured by slopes) for the grasping and manual estimation tasks for the controls (open circles) and DF (crosses). Control participants showed less grip-scaling in the non-veridical mirror (NVM) task than they did in the veridical mirror (VM) task, and less grip-scaling 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.

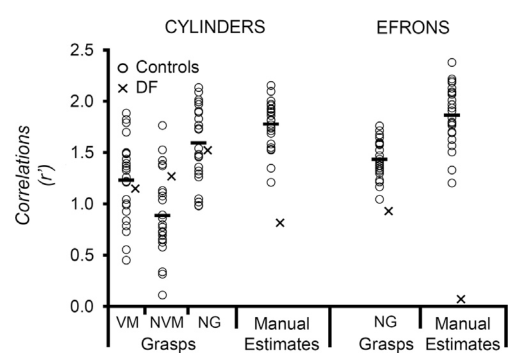


**Fig. 3.** Grip aperture scaling (as measured by Fisher-transformed correlation coefficients) for the grasping and manual estimation tasks for the controls (open circles) and DF (crosses). Similar to the results when slopes were taken as a measure of grip scaling, the controls showed weaker grip scaling 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.

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 [$p_{max} < 0.03$; $\overline{b} = 0.55$ 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 [$p_{max} < 0.03$; $\overline{b} = 0.60$ mm/mm ($SD = 0.16$ mm/mm); $\overline{r'} = 1.59$ ($SD = 0.38$) (see Figs. 2 and 3)]. Patient DF also reliably scaled her grasp to the diameter of the cylinders in both the VM task [$b = 0.33$ mm/mm, $r' = 1.15$, $t(26) = 7.23$, $p < 2 \times 10^{-7}$] and in the NG task, $b = 0.52$ mm/mm, $r' = 1.52$, $t(17) = 8.98$, $p < 8 \times 10^{-8}$. 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. 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 [$\overline{b} = 0.08$ (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), $t(23) = 3.75$, $p < 2 \times 10^{-3}$]. 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. 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 [$p_{max} = 0.59$; $\overline{b} = 0.40$ 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, $r' = 1.27$, $t(25) = 8.17$, $p < 2 \times 10^{-8}$]. 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: $\overline{b} = 0.15$ mm/mm ($SD = 0.20$ mm/mm), $t(23) = 3.61$, $p < 2 \times 10^{-3}$; correlations: $\overline{r'} = 0.34$ ($SD = 0.53$), $t(23) = 3.18$, $p < 5 \times 10^{-3}$]. 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 significantly 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.

### 3.4. Perceptual judgements of cylinder size

When manually estimating cylinder diameter, all of the controls showed reliable positive relationships between their MEAs and cylinder diameter [$p_{max} < 0.001$; $\overline{b} = 1.03$ mm/mm ($SD = 0.15$ mm/mm); $\overline{r'} = 1.78$ ($SD = 0.23$)]. DF also showed a reliable positive relationship between MEA and cylinder diameter, $b = 0.65$ mm/mm, $r' = 0.81$; $t(26) = 4.23$, $p < 9 \times 10^{-5}$. However, DF's slope was significantly shallower [$t(23) = 2.50$, $p < 0.01$] and her correlation significantly weaker [$t(23) = 4.09$, $p < 3 \times 10^{-4}$] than those of the control participants.

### 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.

### 3.6. 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 [$p_{max} < 2 \times 10^{-6}$; $\overline{b} = 0.65$ 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 [$b = 0.38$, $r' = 0.93$, $p < 4 \times 10^{-5}$] (see Figs. 2 and 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

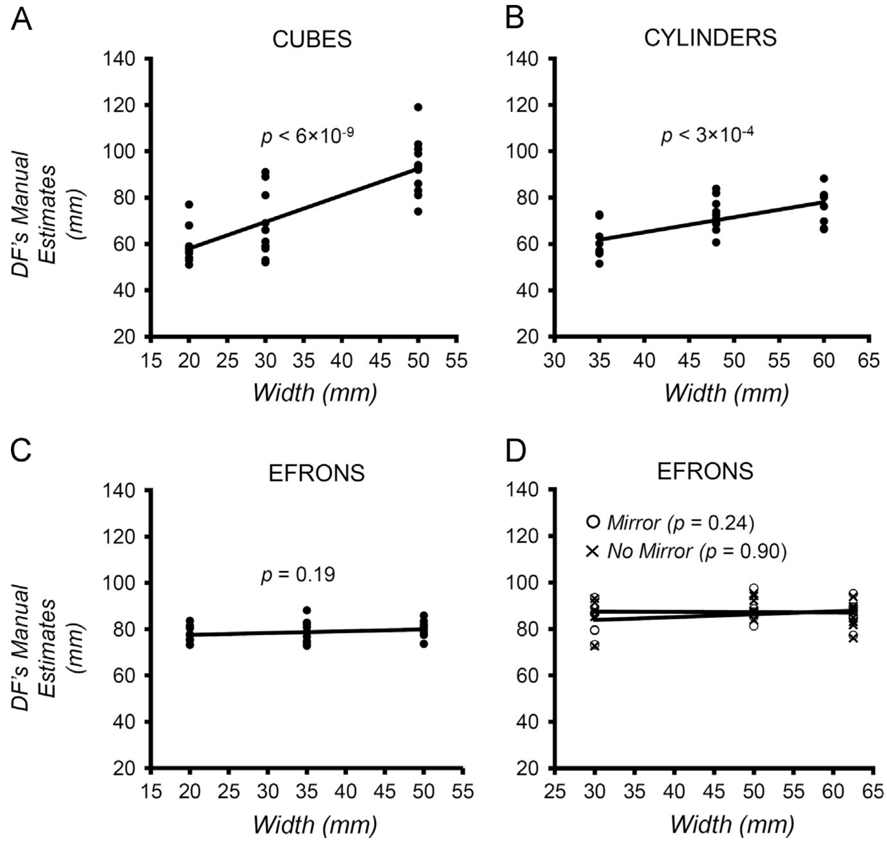


**Fig. 4.** DF's manual estimations as a function of target type (cubes vs. cylinders vs. Efron blocks) and dimension (diameter or width). (A) DF's manual estimate aperture (MEA) as a function of the width of a set of three cubes of different sizes that were pseudorandomly presented at any one of three different distances (20 cm, 30 cm, 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 distinguishing amongst 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 related to the width of the Efron blocks. In short, the mirror does not significantly affect her poor judgments of Efron width.

significantly weaker than that of the controls [$t(23)=2.70$, $p<7\times10^{-3}$].

### 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 Figs. 2 and 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 any 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. 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, $r'=0.25$, $t(28)=1.33$, $p=0.19$.]

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 gip 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.

### 3.8. 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.

## 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 significantly 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 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 Introduction (Section 1.4), 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 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 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 feedback' task than it is in the 'intermittent haptic feedback' task, 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 or not 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. Nevertheless, it remains a distinct possibility that intermittent feedback about time-to-contact in these intermittent haptic feedback tasks is enough to keep the visuomotor networks controlling grasping engaged, so that participants are less likely to resort to pantomiming.

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. 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 unappreciated aspect of dorsal stream visuomotor function. Thanks to Schenk's (2012a) 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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