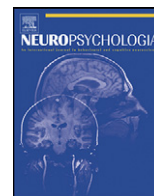




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Choosing between alternative wrist postures: Action planning needs perception

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ABSTRACT

When normal subjects grasp with their right hand a rectangular object placed at different orientations in the horizontal plane, they change from a 'thumb left' (clockwise) to a 'thumb right' (anti-clockwise) grasp when the orientation exceeds about 110°, with respect to the mid-sagittal plane. This suggests planning of the final grip orientation at, or before the start of the prehension movement. The current study assessed performance of two visual agnostic patients (SB and DF) on a grasping task requiring the planning of final grip posture. Five healthy subjects were also tested. Subjects were required to grasp a triangular-section block, which was presented at one of seven different orientations (80–140°). The healthy subjects showed a consistent relation between object orientation and hand orientation just before contact. In addition, they consistently used a clockwise grasp when object orientation was less than 100°, and an anti-clockwise grasp when it was more than 110°, with a sharply defined switch-point being identifiable for each subject. For both visual agnostic patients, hand orientation was also reliably related to object orientation. However, the selection of grasp posture was markedly abnormal: they did not consistently switch between clockwise and anti-clockwise grasps within the normal orientation range, and the switch, when it did occur, was not at all sharply defined. These results suggest that the planning of hand orientation during a grasp depends on a perceptually based judgement of the awkwardness of alternative movements. This would presumably involve ventral stream processing, which is disrupted in the visual agnostic patients.

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1. Introduction

In the last fifteen years or so, several studies have investigated the relative contribution of the two visual cortical processing streams in different visually based tasks. Early studies investigating task-dependent processing suggested that the dorsal stream is critically necessary for the immediate online control of goal-directed action, whilst the ventral stream is crucial for the recognition of objects. Evidence for this dissociation came originally from monkey neurophysiology (Sakata, Taira, Murata, & Mine, 1995) and human neuropsychological single case studies (Goodale, Milner, Jakobson, & Carey, 1991; Milner & Goodale, 1995; Milner et al., 1991), but has more recently been supported through other methodologies such as functional neuroimaging (Culham et al., 2003; James, Culham, Humphrey, Milner, & Goodale, 2003) and TMS (Desmurget et al., 1999; Rice, Tunik, & Grafton, 2006). Particularly important has been the study of visual form agnostic patient DF, whose damage includes ventral stream area LO bilaterally (James et al., 2003). This patient

could not identify the width of a rectangular shape, nor was she able to report the orientation of a slot (Goodale et al., 1991; Milner et al., 1991). Nevertheless, she was able to use the same visual information for grasping the rectangular shape or posting an object through the slot.

Other studies have confirmed her ability to use visual input about the orientation of an object for online guidance of hand orientation during a grasping movement (Carey, Harvey, & Milner, 1996; Dijkerman, Milner, & Carey, 1996). However, these studies also showed impairments in grasping behaviour under particular task conditions. Carey et al. (1996) reported that DF did not consistently grasp the appropriate part of everyday utensils, despite being able to adjust hand orientation to object orientation. This suggests that she was unable to use stored knowledge about the function of an object to guide the selection of a semantically appropriate grasp, although she could still use orientation information to execute the selected grasp efficiently. Overall, these findings suggest that ventral stream processing may be crucial for certain aspects of hand orientation during reaching and grasping, for example when recognition of the object is required.

It is well known that many aspects of a visuomotor act need to be pre-planned based on the available visual input. For example,

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Rosenbaum, Heugten, and Caldwell (1996) reported the “end-state comfort” effect when grasping an object in order to make a second movement with it. They observed that the handle was grasped with such a hand orientation that a comfortable hand configuration was achieved at the end of the second movement, even if the intermediate hand configuration at the end of the first movement was not always comfortable. The end-state comfort effect can only be achieved through planning at the start of the movement what the end posture will be. Another example comes from a study by Stelmach, Castiello, and Jeannerod (1994). When normal subjects grasp an elongated object with a triangular cross-section placed at different orientations in the horizontal plane with their right hand, they change from a ‘thumb left’ (clockwise) to a ‘thumb right’ (anti-clockwise) grip when the orientation exceeds about 110° , with respect to the mid-sagittal plane. This suggests that the final grip orientation (and thereby the direction of hand rotation during the movement) is chosen at, or before the start of the prehension movement. This type of planning is influenced by contextual visual illusions such as the rod and frame illusion (Craje, van der Kamp, & Steenbergen, 2008) and is considered to depend on visual processing within the ventral stream (Goodale & Milner, 2004; Milner & Goodale, 1995, see also Liu, Chua, & Enns, 2008), predicting that the ability should be severely disrupted by bilateral ventral stream lesions. The current study tested this prediction in two patients with visual agnosia, DF and SB, using a version of Stelmach et al’s task (1994), which requires the planning of final grip posture. Some of the data collected with SB have been reported previously in a study on visuomotor abilities of this patient (Dijkerman, Le, Demonet, & Milner, 2004). Movement execution of SB has been analyzed more thoroughly in this study and compared to that of DF and healthy controls, allowing more comprehensive results and conclusions.

2. Methodology

2.1. Participants

DF: This patient experienced carbon monoxide poisoning in 1988, resulting in a severe visual form agnosia (Milner et al., 1991). Recent high-resolution structural MRI has confirmed a dense bilateral lesion in lateral prestriate cortex, which functional MRI has shown to coincide with the lateral occipital area (LO), an area in the ventral stream that is implicated in object perception (James et al., 2003). Functional MRI also shows that the anterior intraparietal area (AIP) in DF’s dorsal stream remains functional during object grasping. DF performed the present experiment twice, once at the age of 45 and a second time at the age of 48.

SB: This patient, a right-handed man, suffered from an attack of viral meningoencephalitis at the age of 3 years. At the time of testing, at the age of 31 years, SB retained a severe object, letter and face recognition deficit. Although he can describe the contours of a visually presented object, he cannot identify the object in most cases. SB’s perceptual capacities and pattern of brain damage have already been described in detail in an earlier paper (Le et al., 2002). For more extensive descriptions of SB’s visuomotor abilities see Dijkerman et al. (2004). MRI structural scans revealed large lesions of occipito-parietal and occipito-temporal regions in the right hemisphere, and at the occipito-temporal junction in the left hemisphere (Le et al., 2002). The right-hemisphere lesion includes complete or partial damage to the human counterparts of the monkey’s V2, V3, V4 and MT, and also to area LO. In addition there is limited damage to the right inferior parietal lobule in the region of the supramarginal gyrus. The spared regions in the right occipital pole include the calcarine fissure (primary visual cortex, V1) at least in its rostral and superior aspects. In the left hemisphere, the lesions involve mainly the ventrolateral visual cortex, including a complete destruction of the fusiform gyrus and area LO. In summary, the lesions seem to have all but destroyed the visual ventral stream bilaterally, while sparing the occipital pole and the left dorsal stream.

Five healthy female control subjects (mean age 30.8 years, range 24–41 years) with normal (or corrected to normal) vision were also tested.

2.2. Procedure and experimental set up

Following a task devised by Stelmach et al. (1994), we asked participants to grasp, without lifting, a triangular-section prism block (6 cm long by 2.5 cm wide), made out of dark grey plastic. Because its section was an equilateral triangle, the object offered only one effective grip pattern, with the thumb and fingertips in opposition at the two ends: it could not be picked up sideways, without it slipping out of one’s

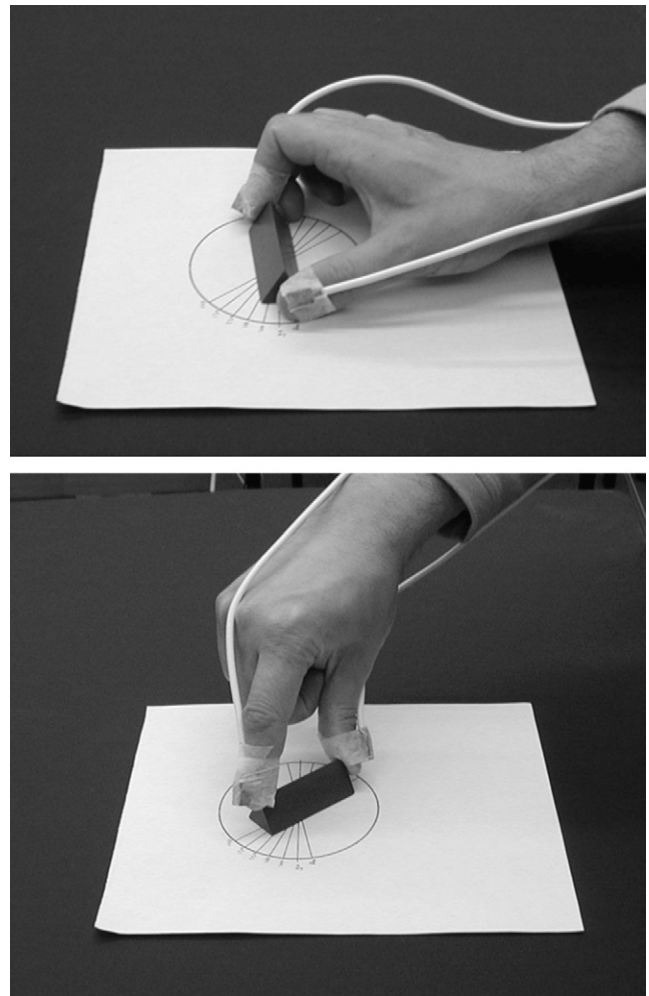


Fig. 1. The two different ways of orienting the finger opposition space in the present grasping task. Normal subjects grasp objects that are placed at orientations less than 90° (with 0° being aligned parallel to the midsagittal axis) with their thumb on the left and their index finger on the right (clockwise, top picture). They switch to an ‘anti-clockwise’ grasp when the object is placed at 110° or higher (bottom picture).

grip (see Fig. 1). The object was placed on a white table top, with its centre 30 cm away from the starting position along the subject’s midsagittal axis. The starting position was 5 cm away from the table edge. The target object was presented at one of seven different orientations ($80\text{--}140^\circ$ in steps of 10° , with 0° being with its main axis parallel to the mid-sagittal axis). Each target orientation was presented ten times in a pseudo-randomized order.

The *Minibird* (Ascension Technology Corporation) magnetic recording system was used for recording the reaching and grasping movements. The positions of markers attached to the nails of the thumb and forefinger of the right hand were tracked for 3 s at a sampling rate of 103 Hz. Start and end times of the grasping movement were determined by using a velocity based criterion (5 cm/s for the thumb marker).

2.3. Data analyses

Grasp orientation was determined throughout the movement. This was achieved by calculating the angle of a straight line drawn through the markers on the index finger and thumb, with respect to the sagittal plane, for each frame. Several variables were extracted from the grasp orientation data. First, the reaching movements were normalized with respect to time, with each movement being divided into 100 samples. The grasp orientation measured at 2 normalized samples before the end of the movement was examined as a function of the object orientation. Second, the grasp posture was classed as clockwise if this orientation was signed positively (with 0° being the index finger-thumb axis being aligned parallel to the midsagittal axis), and as anti-clockwise if it was signed negatively (see Fig. 1). For each participant, the percentage of anti-clockwise grasps was calculated for each object orientation. In order to describe the dependence of grasp posture on object orientation in a manner analogous to a psychophysical analysis, the best-fitting sigmoid curve was calculated for each participant’s data. Provided that a reliable fit was obtained, two (pseudo-psychophysical) parameters were derived. The ‘switch-point’ was calculated as the

object orientation at which the frequency of anti-clockwise grasps was equal to 50% (analogous to the point of subjective equality in a standard psychophysical analysis). The 'switch-sharpness' was calculated as the range of object orientations between anti-clockwise frequencies of 25 and 75% (analogous to one just noticeable difference in a standard psychophysical analysis).

We also assessed whether hand orientation was reliably related to object orientation 2 samples before the end of the movement. For this we calculated hand orientation irrespective of whether a clockwise or anti-clockwise grip was used. We further divided the grasps into 'natural' or 'awkward' depending on whether control subjects performed a grasp for that particular object orientation using a clockwise or anti-clockwise grip. This meant that all clockwise grasps were classed as 'natural' when performed for object orientations between 80 and 110°, while anti-clockwise grasps were considered to be natural when object orientation was between 100 and 140°. All other grasps were considered to be 'awkward'. The 'awkward' grasps were excluded from the analysis as biomechanical constraints when performing these uncomfortable grasps might have influenced hand orientation. A linear regression analyses was performed for each participant only using data from the 'natural' grasps with object orientation as independent variable and hand orientation as dependent variable.

To assess whether the grasp posture had been pre-planned, we examined the change of hand orientation over the course of each reach. Hand orientation was plotted as a function of normalized time. Hand orientation at 0, 10, 30, 50 and 70% of movement duration was calculated in relation to object orientation and to final grip posture (clockwise, anti-clockwise). The data were analyzed for each subject using *t*-tests to determine the stage in the movement at which hand orientation began to differ according to whether the final grasp posture on that trial was to be 'clockwise' or 'anti-clockwise'. The *t*-tests were carried out on hand orientation measured at 0, 10, 30, 50 and 70 percent into the movement, with final hand position (clockwise–anti-clockwise) as the independent variable.

Finally, standard kinematic measures such as movement time (MT), maximum grip aperture (MGA), time to maximum grip aperture (TMGA), and time to maximum grip aperture as percentage of total movement time (%TMGA) were calculated.

3. Results

3.1. Relation between hand posture and target orientation

Fig. 2 depicts the percentage of clockwise grasps for each orientation per subject. It is clear from this figure that the control subjects consistently switch from a 'clockwise' (positive values) to an 'anti-clockwise' (negative values) grip at 100–110°. The 'switch-point' for the control subjects varied between 98.9 and 111.6°. The 'switch-sharpness' (range of object orientations between anti-clockwise

frequencies of 75 and 25%) varied between 0.49 and 3.89°, showing that the control subjects changed quite sharply between clockwise and anti-clockwise grips.

As can be seen in Fig. 2, SB and DF showed a different pattern. In the first testing session DF did not change hand orientations at a particular object orientation. Instead she used both grips over a range of object orientations (90–120°) and only showed a consistent grip for the extreme object orientations (80° clockwise; 130–140° anti-clockwise). Indeed, although her 'switch-point' was within the normal range for this session (110.10°), the 'switch sharpness' was not (8.50°). In the second session, the 'switch-point' as well as the 'switch sharpness' are outside the normal range (129.9° and 6.2°, respectively) suggesting that DF only changes to an anti-clockwise grasp for the object orientations 130 and 140°. As we already described previously (Dijkerman et al., 2004), SB also did not change between grips at a certain object orientation. Instead, he always grasped the object in an anti-clockwise manner, except for three trials at 80 and 90°. It was not possible to calculate the 'switch-point' or 'switch sharpness' for his data, since no sigmoid function could be fitted reliably to his data.

Fig. 3 depicts hand orientations at two frames before the end of the movement irrespective of whether the grip was clockwise or anti-clockwise. A linear regression analysis for each individual performed on the 'natural' grasps showed that, for all participants, including the agnostic patients, hand orientation just prior to the end of the movement was reliably related to object orientation (minimum $r^2 = 0.70$). This suggests that visual input about the object orientation was used to adjust the hand orientation during the grasping movement. Thus, although the agnostic patients adjust their hand orientation during the grasping movement to the object orientation, they do not consistently pre-select a particular hand-grip posture, in contrast to all control subjects.

Next we determined the point during the grasping movement at which it became clear that the object was going to be grasped with a clockwise or anti-clockwise grip. Control subjects presumably pre-plan this decision. If the agnostic patients, however, are impaired in planning the grasping movement, the decision to adopt a certain grip may be deferred until after the movement has started.

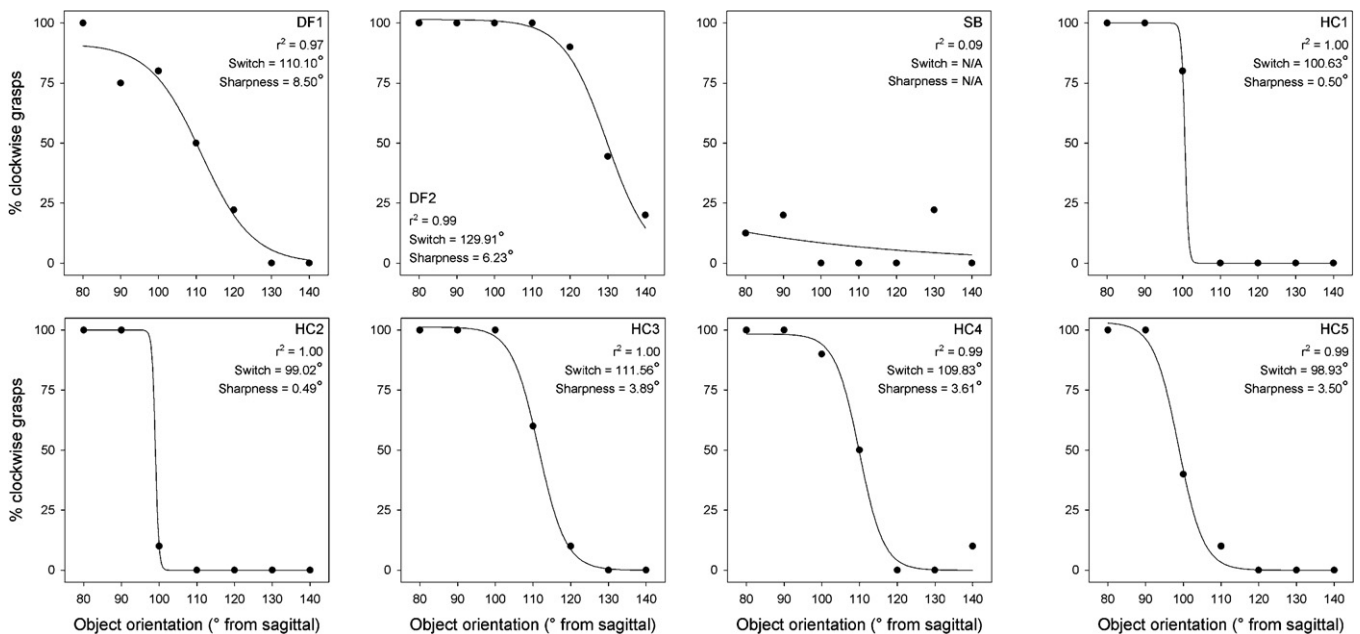


Fig. 2. The best-fitting sigmoid curves for grasp posture across object orientations plotted in a manner analogous to a psychophysical analysis for each participant. Two (pseudo-psychophysical) parameters were derived. The 'switch-point' was calculated as the object orientation at which the frequency of anti-clockwise grasps was equal to 50% (analogous to the point of subjective equality in a standard psychophysical analysis). The 'switch-sharpness' was calculated as the range of object orientations between anti-clockwise frequencies of 25 and 75% (analogous to one just noticeable difference in a standard psychophysical analysis).

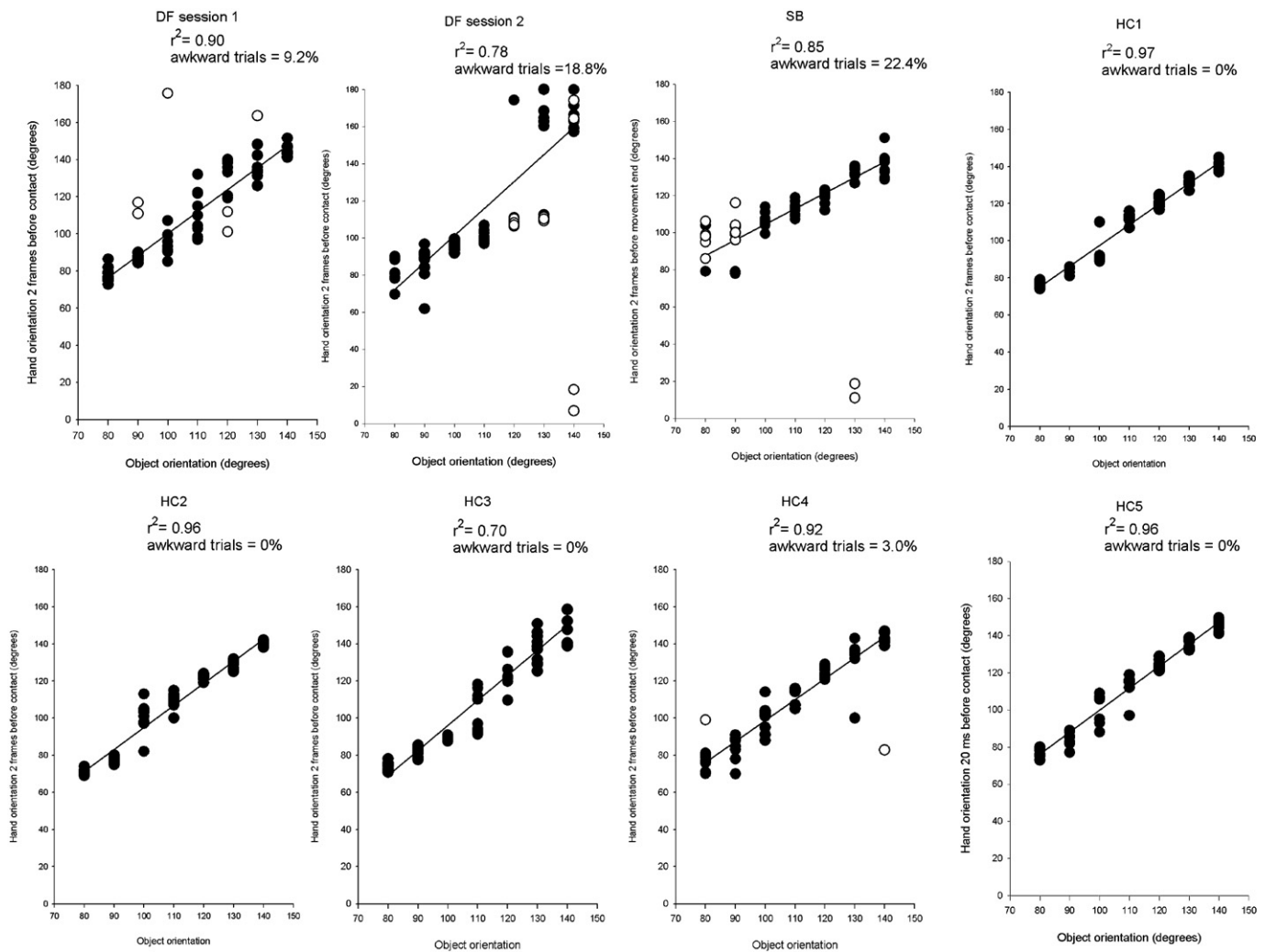


Fig. 3. Hand orientation two normalized frames before the end of the movement as a function of object orientation, irrespective of whether the grasp was clockwise or anti-clockwise. Visual agnostic participants DF (two sessions) and SB are depicted in the first three graphs on the top row. The healthy control subjects are shown in the remaining graph on the top row and in the bottom four graphs. The hand orientations are coded according to whether they are natural (e.g. 'clockwise' grip for object orientations 90–110 or 'anti-clockwise' grip for object orientations 100–140, filled circles) or awkward (all other trials, open circles). A linear regression was performed for natural trials only. Hand orientation just before the end of the movement was highly related to object orientation for all participants including DF and SB.

We used independent samples *t*-tests to assess at what part of the movement a reliable difference between hand orientations leading to a 'clockwise' and an 'anti-clockwise' grasp could be observed. This was done for DF only, as SB performed only three grasps with a 'thumb to the left' grip. The results show that for four out of five control subjects a difference between 'clockwise' and 'anti-clockwise' grip can already be detected after 10% of the movement (see Table 1 and Fig. 4). For the remaining control subject, the difference becomes significant at 30% into the movement. For DF, the difference between the two types of grip is also significant at 10% of the total movement in both sessions. DF therefore performs sim-

ilarly to the control subjects in that she selects her grip prior to, or early during, the movement, in a normal fashion. However, a significant difference was also found in both sessions for DF's initial hand orientation at the first frame of the movement (see Table 1). This was not the case for any of the control subjects and suggests that DF's final grip may partly be determined by her initial hand orientation. Inspection of SB's changes in hand orientation over time suggests that he too planned his grip before, or early in, the movement on almost all trials. However, it is also clear from Fig. 4 that although grasp posture was usually pre-selected, there are occasional instances where participants change between one and

Table 1
 Independent samples *t*-test, assessing at which stage of the movement a significant difference could be detected between 'clockwise' and 'anti-clockwise' grips.

	At start of the movement	After 10%	After 30%	After 50%	After 70%
HC1	$T(64) = 1.46, p = .19$	$T(64) = 1.56, p = .12$	$T(64) = 19.60, p < .001$	$T(64) = 56.24, p < .001$	$T(64) = 64.33, p < .001$
HC2	$T(68) = 1.61, p = .12$	$T(68) = 4.08, p < .001$	$T(68) = 16.62, p < .001$	$T(68) = 30.15, p < .001$	$T(68) = 63.40, p < .001$
HC3	$T(68) = 1.73, p = .09$	$T(68) = 3.30, p = .002$	$T(68) = 18.57, p < .001$	$T(68) = 32.81, p < .001$	$T(68) = 39.39, p < .001$
HC4	$T(64) = .07, p = .94$	$T(64) = 3.11, p = .003$	$T(64) = 15.05, p < .001$	$T(64) = 40.74, p < .001$	$T(64) = 49.35, p < .001$
HC5	$T(68) = 1.17, p = .25$	$T(68) = 5.54, p < .001$	$T(68) = 24.02, p < .001$	$T(68) = 35.45, p < .001$	$T(68) = 41.12, p < .001$
DF	$T(60) = 5.23, p < .001$	$T(60) = 8.71, p < .001$	$T(60) = 22.04, p < .001$	$T(60) = 22.85, p < .001$	$T(60) = 21.52, p < .001$
DF2	$T(65) = -3.89, p < .001$	$T(65) = -6.30, p < .001$	$T(65) = -9.89, p < .001$	$T(65) = -11.38, p < .001$	$T(65) = -11.61, p < .001$

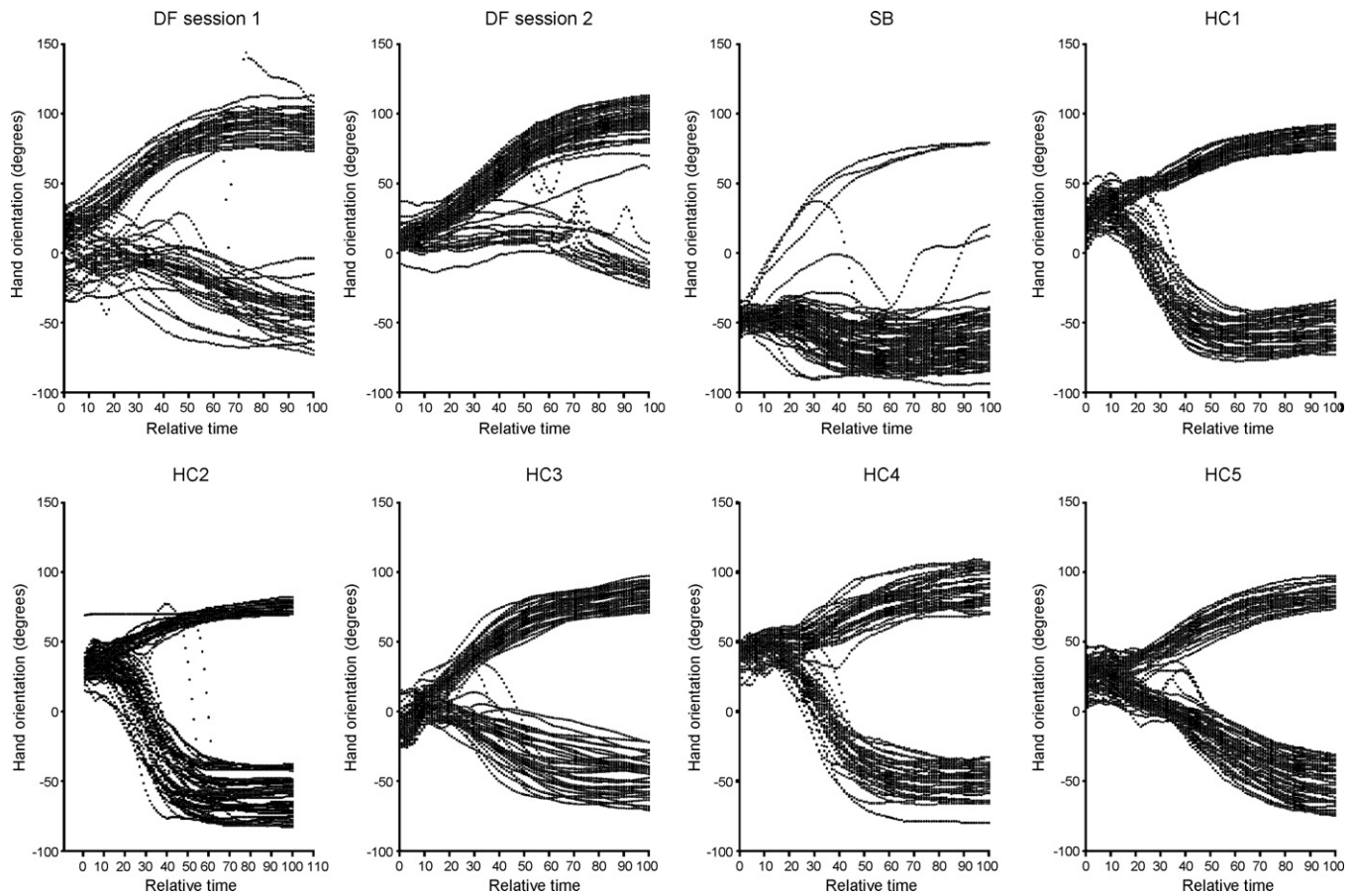


Fig. 4. Hand orientation during the course of the movement for each individual trial. Note that for all participants, including the two agnostic patients, the clockwise and anti-clockwise grips are clearly distinguishable very early in the movement.

Table 2

Mean and standard error (between brackets) of movement time (MT), maximum grip aperture (MGA) and time to maximum grip aperture (TMGA) and time to maximum grip aperture as a percentage of total movement time (%TMGA).

	MT	MGA	TMGA	%TMGA
HC1	829 ms (13.04)	104.98 mm (0.47)	545 ms (10.74)	66.21% (1.30)
HC2	1142 ms (21.95)	105.42 mm (0.80)	781 ms (30.15)	68.13% (2.47)
HC3	768 ms (15.25)	103.10 mm (0.76)	572 ms (10.24)	76.05% (1.70)
HC4	1013 ms (24.05)	111.67 mm (0.69)	587 ms (17.87)	59.25% (1.88)
HC5	952 ms (12.40)	104.43 mm (0.77)	780 ms (14.37)	82.79% (1.74)
SB	778 ms (23.65)	114.45 mm (0.97)	568 ms (12.91)	75.67% (1.98)
DF	1163 ms (18.89)	106.39 mm (0.88)	898 ms (26.16)	78.08% (2.24)
DF2	1087 ms (24.23)	101.96 mm (1.22)	886 ms (19.38)	82.60% (1.49)

another grip online. This tendency was not notably more marked in the patients than amongst the controls.

3.2. Standard kinematic measures

The means and standard errors of the MT, MGA, TMGA and %TMGA are shown in Table 2. DF and SB perform within the normal range on most measures. SB was slightly outside the normal range in terms of MGA (3 mm) and DF on TMGA. However %TMGA and MT were similar to those of the control subjects.

4. Discussion

In this study, the prediction that planning of the final, comfortable hand orientation would be impaired after bilateral damage to the ventral stream was tested in two patients with visual agnosia. Both DF and SB fail to show the normal sharp switch of wrist posture

between clockwise and anti-clockwise as the orientation of a centrally placed elongated object changes with respect to the subject (Stelmach et al., 1994; see Dijkerman et al., 2004 for an earlier report of this finding for SB). In healthy subjects this switch in posture occurs at approximately 100–110° clockwise from the sagittal axis. Of course all subjects can generally still grasp the object even when they have chosen the ‘wrong’ wrist posture to adopt, but doing so is uncomfortable, and often results in poorer orientation scaling (see Fig. 3, DF session 2) and fumbling movements to secure the grasp. Indeed, informal observations during the testing of both DF and SB revealed awkward grasps during several trials. Healthy subjects therefore usually pre-emptively avoid this problem by planning the more appropriate posture of the hand before initiating the reach.

The absence of a normal ‘switch’ point in DF and SB’s data is presumably due to the need for a perceptually based anticipatory judgement of the awkwardness of the alternative movements, and then a postural decision based on this analysis. Both SB and DF

therefore would be expected to have difficulty because they are impaired in the necessary perceptual analysis that must inform such a decision (Le et al., 2002; Milner et al., 1991). Both DF and SB have suffered severe damage to the ventral-stream systems that underlie the perception of shape and pattern, causing visual form agnosia (James et al., 2003; Le et al., 2002; Milner et al., 1991). We may infer that both patients would therefore have an imperfect or impoverished perceptual representation of the solid shape that was presented to them on each trial, including its orientation on the table. It may be assumed that their well-documented perceptual deficits prevent adequate action selection.

Although both patients are impaired when selecting their grip, they manifest their deficits differently. While SB almost always grasps with an anti-clockwise grip, DF shows a more variable response, which nevertheless does not show the sharp switch point as observed in the control subjects. Several factors may contribute to this difference between the two patients. First, although both SB and DF suffered bilateral damage to the ventral stream, the lesion was more extensive in SB, which may have resulted in his qualitatively different pattern of grasp selection (e.g. very few switches between clockwise and anti-clockwise grasps). A second explanation may be that the two patients, though both faced with an inability to select the correct grip on a perceptual estimate of the object orientation, resorted to different strategies to deal with this; for example adopting a 'default' selection based either on the hand orientation at the start of the movement (DF), or their own preference for one type of grip over the other (SB).

Yet however inappropriately selected their actions are, both patients still proceed to program their grasps (as evidenced by standard kinematic measures) and particularly their finger-thumb grip orientation to the object orientation, with considerable skill, in agreement with previous studies (Carey et al., 1996; Dijkerman et al., 2004; Goodale et al., 1991; Milner et al., 1991). Indeed as Fig. 4 shows, DF and SB executed grasps comfortably in most of the trials, with pre-programming of the movement from the outset (cf. Milner et al., 1991). The data thus reveal a dissociation between two different requirements for the successful performance of a visuomotor action. Each patient has a preserved ability to execute a visually guided grasp, despite performing abnormally on planning the appropriate overall posture for the action in the first place. To put it another way, our patients cannot successfully use visual orientation information to make an initial action selection, but are able to use visual information to calibrate their actions once the action has been selected, despite partial damage to dorsal stream visual areas in both patients.

Carey et al. (1996) showed that DF was impaired when required to select appropriate parts of everyday utensils for grasping, again despite normal grip orientation. Grip selection in this task presumably requires recognition of the object and retrieval of semantic information about the function of the tool. In the current study, object recognition and semantic information were not required to select the correct grip. This suggests that ventral stream involvement in grasp selection does not depend necessarily on object recognition or semantic processing but may also be required when predicting the final posture of a grasp. In general, the ventral stream may be critically involved in visuomotor behaviour whenever anticipatory mental simulation of an action is required for selection of the form of the action. Previous studies have shown that patient DF is impaired in grasping, pointing, or making saccades based on memorized visual input (Goodale, Jakobson, & Keillor, 1994; Milner, Dijkerman, & Carey, 1999). In contrast, after posterior parietal lesions, optic ataxic patients improve their visuomotor performance after a delay between target presentation and grasping or pointing response (Milner et al., 2001; Milner, Paulignan, Dijkerman, Michel, & Jeannerod, 1999). The current study suggests the ventral stream is also involved when planning a grasp depends

on predictions about its consequences. Thus, based on the assumption that the performance of DF and SB show the dorsal stream operating in isolation, the current findings reveal another limitation to visuomotor processing in this stream. Whereas it is capable to adjust hand orientation to the object orientation during the grasp, the dorsal stream is not able to predict the awkwardness of the final posture and adjust the grasp accordingly. Similarly, the ventral stream and frontal areas appear to be required for the control of new as opposed to overlearned visuomotor skills, again illustrating the limitations of dorsal-stream processing (Gonzalez, Ganel, Whitwell, Morrissey, & Goodale, 2008; Grol, de Lange, Verstraten, Passingham, & Toni, 2006).

A critical distinction has been made elsewhere between the planning and programming of an action (Goodale & Milner, 2004; Milner & Goodale, 2008). Programming of an action involves pre-specification of movement parameters based on visual information about the object's size, shape, orientation and egocentric position. These movement parameters bear a direct relation to the visual characteristics, e.g. maximum grip aperture depends on size of object, and hand orientation on object orientation. As such there is a relatively direct translation of visual parameters in motor parameters. In contrast, planning of an action does not involve direct visual to motor transformations, but rather relates to the initial selection of higher order aspects of the movement such as the type of grip with which the object is grasped, or whether to grasp it with one or with two hands (van Doorn, van der Kamp, & Savelsbergh, 2007). This can be influenced by previous motor experience, but also by stored knowledge about the object to be grasped (Carey et al., 1996). This distinction between planning and programming has been blurred by some writers, who have conflated both aspects of action preparation as "planning" (Glover, 2004). It is clear that the unfolding of DF and SB's actions, as shown in Fig. 4, must be based on intact action programming, despite faulty action planning.

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