GRASPING WHAT IS GRASPABLE: EVIDENCE FROM VISUAL FORM AGNOSIA

Robert D. McIntosh¹, H. Chris Dijkerman², Mark Mon-Williams³ and A. David Milner¹

(¹Department of Psychology, University of Durham, UK; ²Helmholtz Research Institute, University of Utrecht, The Netherlands, ³University of Aberdeen, UK)

Abstract

Patient DF has profound visual form agnosia. Despite this, she has no problem adjusting her finger-thumb grip aperture to the width of objects when reaching to grasp them. In a previous study, however, she was found to have great difficulty in scaling her grip aperture when attempting to grasp a transparent disc through two holes cut into it. This problem was attributed to a putative difference between the visual processing of size and distance in the brain, whereby DF retained the capacity for processing object size but not the separation between distinct elements such as holes. In the present study we have tested this idea more directly, and found no evidence to support such a distinction. Nonetheless, we replicated our earlier finding that DF is unable to produce normal prehension movements when attempting to grasp transparent stimuli by placing her digits into holes. We suggest that, whilst some simple objects offer themselves directly to the dorsal stream for grasping, an intact ventral stream is required to respond appropriately to more complex stimuli.

Key words: agnosia, size, visuomotor, grasping, distance

INTRODUCTION

Ennio De Renzi, during his long service as Chief Editor of Cortex, accepted for publication the first printed report on DF, the now well-known patient with visual form agnosia who forms the focus of the present paper (Milner and Heywood, 1989). The present study was motivated by a basic question about the nature of visuospatial processing, one implicit in much of the discussion in De Renzi's classic book (1982): are spatial relationships within an object treated by the brain in the same way as spatial relationships between objects? We have raised this question elsewhere in the context of perceptual processing in neglect (McIntosh et al., 2004). Here we raise it in relation to visual processing for action, and for this purpose DF provides a valuable test case. Despite suffering from a severe impairment in perceptually discriminating even simple visual forms, DF is adept at interacting manually with objects, showing a capacity to act upon visual information that she is unable to report consciously (Goodale et al., 1991; Milner et al., 1991). These preserved abilities reflect the capacities of the dorsal visual stream, which we now know to be functionally intact in DF, in contrast to her severely disabled ventral stream (James et al., 2003). This unique patient offers a means for exploring the capabilities, and to some degree also the limitations, of the human dorsal visual stream working in quasi-isolation.

In Milner and Goodale's (1995) model, the dorsal and ventral streams both process spatial information, but they use quite different metrics for coding that information. As a functionally specialised system for the guidance of action, the dorsal stream needs information about the location of objects with respect to the effectors that might be used to respond to them. Thus the object has to be coded in bodily (eye, head, body or limb) coordinates. In contrast, the perceptual system is more concerned with the extraction of viewerindependent properties of the environment, including the spatial layout of the world in terms of the locations of objects with respect to one another. In other words, Milner and Goodale argued that spatial information in the dorsal stream needs to be encoded in egocentric coordinates, with the analysis of 'allocentric' spatial relationships being restricted to the ventral visual pathway. It would follow from this that DF should be unable to process such allocentric relationships (Murphy et al., 1998).

Dijkerman et al. (1998) tested this idea by presenting DF with a visuomotor task designed to force the use of allocentric coding. A series of transparent discs was used, each of which had two or three circular holes cut into it. The two-hole discs were to be grasped with the forefinger and thumb, while the three-hole discs required the additional use of the middle finger. The distances between the target holes varied, and the discs were presented upright at various orientations. It was argued that, since the required grasp configurations were specified by the relative positions of the holes, subjects would need to take account of allocentric spatial relationships in order to form their grasp. DF performed very poorly at the three holegrasping tasks. Her performance was better when only two holes were present, in that her hand orientation and hand localization at the left, right, or midline of the disks were now essentially normal. She remained, however, quite unable to

adjust her grip aperture to the distance between the two holes. Given that control subjects were able to perform this task readily, it was suggested that the analysis of spatial separation requires a functioning ventral stream, even when that analysis is used to guide a visuomotor response. However, these results do not demonstrate conclusively that DF is unable to process spatial separation as a visuomotor control parameter. Several other factors could have contributed to DF's poor performance on the holegrasping tasks; for instance, the unusual visual complexity of the disc stimuli, or the high accuracy demands imposed by the task (each digit had to be inserted into a hole not much larger than the digit itself).

In the present paper, we report two experiments designed to examine the factors underlying DF's poor performance on the earlier hole-grasping task (Dijkerman et al., 1998). Experiment 1 employed a modified version of this task, using transparent rectangular blocks that had to be grasped through two square holes. The stimuli differed in surface appearance so that the required grasp points were either separated by a single visual object or appeared to belong to separate visual objects. We predicted that, if the crucial determinant of DF's grip-scaling ability was the presence of a single visual object, then she should perform well with the former class of stimuli but not with the latter. In fact, DF failed to produce recognisable prehension movements for either class of stimuli. In Experiment 2, we more directly tested the hypothesis that DF is unable to encode visual separation. Using simpler stimuli, we found that DF was as well able to scale her grasp to the spatial separation between objects as to the size of a single object. Our data have implications regarding both the flexibility and the limitations of the dorsal stream's visuomotor abilities.

METHODS

Subjects

DF 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 her dorsal stream remains functional during grasping (Culham, 2004; James et al., 2003). DF performed the present experiment 11 years after her anoxic episode, at the age of 45. Two healthy control (HC) subjects were also tested to allow representative comparison of DF's performance with that of normal individuals.

Experiment 1

The stimuli for Experiment 1 were made from rectangular 180 x 60 mm blocks of 10 mm thick transparent perspex. Each stimulus had two square holes (30 x 30 mm) cut into it, centred with respect to the width of the rectangle and evenly spaced with respect to the centre of the long axis. The inter-hole distance was 40, 60 or 80 mm. Three matched sets of stimuli were used, differing only with respect to the surface pattern, which was painted in matte black on the front surface. These patterns are shown in Figure 1. The three stimulus sets will be referred to as "I-pattern", "H-pattern" and "O-pattern".

Each stimulus was presented by slotting its base into a transparent perspex holder, which held the stimulus at a height of 20 mm above the table and tilted it backwards at an angle of 30° with respect to the vertical. The holder was fixed onto a large square of opaque white plastic. The height of the subject's chair was adjusted so that the subject gazed downwards at an angle of about 30° and viewed the stimulus rectangle face-on with the white background showing through the transparent sections of the stimulus. The room lighting was dimmed in order to encourage the impression that the black sections of the stimuli were suspended freely above the table surface. The I-pattern stimuli gave the impression of a single black rectangle against a white background; the length of this rectangle specified the inter-hole distance. The Hpattern stimuli also presented a single black object, but a more complex one; in this case, the interhole distance was specified by the height of the central portion of the black object (the cross-bar of the H). The O-pattern stimuli gave the impression of two black squares, one suspended above the other and each with a hole at its centre; the interhole distance was specified by the distance between the inner edges of the holes in the two black squares.

A green spot marked the subject's hand start position, which was 125 mm from the near edge of the table and 300 mm in front of the stimulus centre. The start position and stimulus were aligned along the subject's mid-sagittal axis. The subject began each trial with the finger and thumb of her right hand held in a pinch grip at the start position and her eyes closed. At the experimenter's signal, the subject opened her eyes and viewed the stimulus. After a delay of 3 s a tone was heard. The subject then reached out and grasped the stimulus by inserting her index finger into the upper hole, her thumb into the lower hole, and grasping the central portion of the stimulus as if intending to lift the stimulus from its holder. Following a further delay of 2 s, another tone was heard, which prompted the subject to return her hand to the start position, close her eyes and await the next trial. Each subject performed 90 trials,



Fig. 1 – The perspex stimulus sets used in Experiment 1, which differed only in the matte black pattern painted on the front surface. The lightly shaded areas indicate transparent areas and the unfilled areas indicate holes (40, 60 or 80 mm apart). The surface patterns were: (a) 'I-pattern', giving the impression of a single black shape joining the holes; (b) 'H-pattern', giving the impression of a more complex shape joining the holes, and (c) 'O-pattern' giving the impression that the holes belonged to separate objects.

with the nine stimuli presented ten times each in pseudo-random order.

Experiment 2

Two sets of stimuli were used for Experiment 2. The first set (single objects) consisted of three rectangular objects made from opaque grey plastic 10 mm thick. Their dimensions were 30 x 83, 40 x 63 and 50 x 50 mm respectively. The second set (paired objects) consisted of three pairs of narrow rectangles (5 mm wide, 10 mm thick) aligned with separations of 30, 40 and 50 mm between their front and back surfaces. The lengths of the paired rectangles were matched to the lengths of stimuli from the set of single objects (i.e. the rectangles separated by 30 mm were 83 mm long, the rectangles separated by 40 mm were 63 mm long and those separated by 50 mm were 50 mm long). All stimuli were mounted rigidly on sheets of white A4 card.

A green spot, 125 mm from the near edge of the table, marked the subject's hand start position. Stimuli were centred 300 mm from the start position and aligned with it along the subject's mid-sagittal axis. Subjects were required to grasp single objects front-to-back, as if intending to lift them. For paired stimuli, subjects were required to grasp both objects at once, front-to-back, as if intending to lift them as a pair. Subjects performed 48 trials, with the six stimuli presented eight times each in pseudo-random order. The sequence of events within each trial was identical to that used in Experiment 1.

Data Recording and Analysis

An OptotrakTM system sampled the 3D positions of three infra-red-emitting markers at a frequency of 100 Hz. Markers were attached to the distal phalanxes of the index finger and thumb of the right hand, and additionally to the wrist in Experiment 2. The raw data were filtered by a dual pass through a second-order Butterworth filter with a cut-off frequency of 20 Hz. The tangential velocity of the thumb marker (Experiment 1) or the wrist marker (Experiment 2) was used to characterise the transport component of the grasping movement. The onset of the transport movement was defined as the point at which the tangential velocity first exceeded 50 mm/s; the end of the transport movement was defined as the point at which it first fell back to below 50 mm/s. The 3D separation between the index-finger and thumb markers was used to characterise the grasp component of the movement. The two dependent variables of primary interest were the maximum grip aperture (MGA) reached during the transport movement, and the time of its occurrence expressed as a percentage of the total transport duration (normalised time to maximum grip aperture: NTMGA).

Due to technical difficulties, the thumb marker was occluded for a critical portion of the movement on 36 of the 90 trials for HC2 in Experiment 1. These trials were excluded from the analysis for this subject.

RESULTS

Experiment 1

The mean MGA for each experimental condition is shown for each subject in Figures 2a-2c. Separate factorial ANOVAs by surface pattern (I, H, O) and inter-hole distance (40, 60, 80 mm) were performed for each subject. Both healthy control subjects showed a reliable influence of inter-hole distance on MGA regardless of the surface pattern painted on the stimuli [HC1: F (2, 81) = 280.96, p < 0.0005. HC2: F (2, 45) = 133.44, p < 0.0005]. In contrast, the effect of inter-hole distance failed to reach significance for patient DF [F (2, 81) = 2.73, p < 0.1]. Also unlike the control subjects, DF showed a reliable main effect of surface pattern [F (2, 81) =10.14, p < 0.0005]. Scheffé post-hoc tests indicated that her MGA was smaller for the O-pattern stimuli than for the I-pattern (p < 0.05) or H-pattern stimuli (p < 0.0005). A further indication of the nature of grip formation in each subject may be gleaned from Figure 2d, which shows the NTMGA for each stimulus type. It is well documented that maximum grip aperture occurs during the second half of the movement (Jeannerod, 1986), typically at between 60% and 80% of transport duration (Smeets and Brenner, 1999). Both control subjects conformed to this pattern, but patient DF reached MGA very late in the movement, at about 95% of the total transport time, regardless of surface pattern.

The data summarised in Figure 2 suggest that both control subjects produced relatively normal



Fig. 2 – The scaling and timing of the MGA attained during the primary transport movement in Experiment 1 (standard errors indicated): (a) MGA for patient DF by surface pattern and inter-hole distance; (b) MGA for HC1 by surface pattern and inter-hole distance; (c) MGA for HC2 by surface pattern and inter-hole distance, and (d) NTMGA for each subject by surface pattern.



Fig. 3 – Examples of transport velocity (solid line) and grip aperture (dashed line) profiles, with the end of the primary transport movement indicated (dotted vertical line), for Experiment 1: (a) Patient DF grasping an I-pattern stimulus with a 40 mm inter-hole distance; (b) Patient DF grasping an I-pattern stimulus with an 80 mm inter-hole distance; (c) HCl grasping an I-pattern stimulus with an 80 mm inter-hole distance. Note that patient DF shows no grip scaling during the primary transport movement but makes a series of secondary corrective movements during which she adapts her grip aperture to the stimulus. The control subject shows normal prehension behaviour, with grasp formation occurring during the transport movement.

reach-to-grasp movements, whilst patient DF performed the task altogether differently, reaching a MGA unrelated to inter-hole distance and at the very end of the transport movement. This impression is confirmed by a closer examination of DF's responses, which reveals that, typically, she did not begin to scale her grasp until after the end of the main transport movement. On 72 of the 90 trials, DF produced clear secondary corrective movements, during which she adjusted her finger-thumb aperture to the inter-hole distance after making contact with the target object (presumably under visual and/or tactile guidance). Examples of this behaviour are shown in Figure 3.

There are at least two ways of accounting for DF's abnormal behaviour. First, her late grasp formation might reflect a serial strategy of guiding a single digit to its hole during the main movement, and then positioning the other digit during the secondary adjustment phase. If this were the case, we would expect one digit to receive less secondary adjustment than the other (provided that DF was consistent in the digit that she selected for primary guidance). The second hypothesis would be that she was unable to identify the target holes reliably. In this case, the position of both digits would need to be adjusted after contacting the object. To evaluate these alternatives, we performed an analysis of the secondary adjustment received by each digit for the 72 trials in which clear secondary movements were made. The 3D displacement of the final digit position from its position at the end of the transport movement was calculated for the index finger and thumb separately, providing a measure of the magnitude of the secondary adjustment for that digit. Figure 4 shows the mean magnitude of adjustment for the thumb and index finger, broken down by surface pattern.

A mixed-design ANOVA by surface pattern (I, H, O) and digit (thumb, finger), with repeated measures on the last factor, found significant effects of surface pattern [F (2, 69) = 6.51, p < 0.005] and digit [F (1, 69) = 4.15, p < 0.05] and a significant interaction [F (2, 69) = 5.44, p < 0.01]. Scheffé *post-hoc* tests confirmed that more adjustment overall was made for O-pattern stimuli than for I-pattern (p < 0.01) or H-pattern stimuli (p < 0.05). The interaction term was explored with paired t-



Fig. 4 – The magnitude of secondary adjustment for the finger and thumb by surface pattern for patient DF in Experiment 1 (standard errors indicated). The data are collated from the 72 trials in which DF made clear secondary adjustments following the primary transport movement.

tests performed separately for each surface pattern. Significantly more secondary adjustment was made to the thumb position than to the finger position for I-pattern [t (20) = 3.74, p < 0.005] and H-pattern stimuli [t (24) = 2.70, p < 0.05], whilst both digits received a comparably large amount of adjustment for O-pattern stimuli [t (25) = -1.18, p = 0.25]. These results suggest that our two explanations of DF's abnormal performance may apply differentially to the different stimuli. For I-pattern and H-pattern stimuli, DF may have adopted a strategy of guiding the index finger toward its target hole during the main movement and subsequently adjusting the thumb position to fit into the second hole. For O-pattern stimuli, the initial positioning of both digits was highly inaccurate, suggesting that DF had difficulty in identifying the target holes correctly.

Experiment 2

The results of Experiment 2 were much more straightforward than those of Experiment 1, with all subjects showing apparently normal reach-to-grasp movements. Figures 5a-5c illustrate the highly reliable scaling of MGA to stimulus size for all subjects [DF: F (2, 42) = 42.34, p < 0.0005. HC1: F (2, 42) = 40.53, p < 0.0005. HC2: F (2, 42) = 35.79, p < 0.0005]. Stimulus type had no influence on MGA or on the scaling of MGA to stimulus size in any subject. Figure 5d shows that the relative timing of occurrence of MGA for patient DF was also normal, with MGA occurring at about 80% of the total transport time, independent of stimulus type

(single or paired). The large corrective secondary movements made by DF in the hole-grasping tasks of Experiment 1 were not observed in Experiment 2.

DISCUSSION

The present experiments were designed to test the tentative hypothesis that the visual form agnosic patient DF has a specific difficulty in encoding spatial separation as a visuomotor control parameter due to her ventral stream damage (Dijkerman et al., 1998). The current data provide clear evidence against this idea. Experiment 2 demonstrated that DF can make normal grasping movements to enclose pairs of spatially separated objects. Of course, this ability may not require allocentric coding of the location of one object with respect to the other. It is possible that two spatial location can combine to form the common target of a grasping movement (as when grasping the front and the back surface of a wine glass) and are functionally grouped as a whole so that normal mechanisms of object size processing can be engaged. Accordingly, our data do not contradict Milner and Goodale's (1995) proposal that spatial information in the dorsal stream is encoded solely in egocentric coordinates. They do, however, suggest that the dorsal stream is more flexible in its visuomotor capacities than has sometimes been assumed.

On the other hand, our results also suggest some interesting *limitations* to the visuomotor abilities of an isolated dorsal stream. In agreement with our



Fig. 5 – The scaling and timing of the MGA attained during the primary transport movement in Experiment 2 (standard errors indicated): (a) MGA for patient DF by stimulus type and size; (b) MGA for HC1 by stimulus type and size; (c) MGA for HC2 by stimulus type and size, and (d) NTMGA for each subject by stimulus type.

previous study (Dijkerman et al., 1998), Experiment 1 found that DF had great difficulty when attempting to grasp objects by holes cut into them. On the majority of trials, DF adapted her grip aperture to the stimulus only after transporting her hand and making contact with the object. The initial positioning of both digits was particularly inaccurate for the O-pattern stimuli. We suggest that the visual complexity of these stimuli may have made it difficult for DF to target the correct points on the object. This inference is supported by video recordings showing that DF often attempted to insert one or other digit into the transparent middle section of the O-pattern stimulus, apparently mistaking it for a target hole. These observations highlight the vital role for perceptual analysis in 'flagging up' relevant goals and locations for action (Milner and Goodale, 1995; Goodale, 1998) and are

consistent with the notion that DF is impaired in selecting appropriate grasp points for complex objects (Carey et al., 1996).

DF performed slightly better with the visually simpler I-pattern and H-pattern stimuli, making smaller secondary adjustments. This was particularly true for the index finger, suggesting that this digit was often aimed correctly during the initial transport movement. However, although DF may have been able to discern the correct grasp points for these stimuli, she still showed little evidence of preparatory grip formation. Despite her adept grasping abilities (evident in Experiment 2), DF was unable to produce normal prehension in our hole-grasping tasks. Why do these tasks cause her such problems? Our data do not give us a firm answer to this question, but we can offer some testable hypotheses.

One obvious factor distinguishing the holegrasping tasks from typical grasping tasks is their higher accuracy requirements. Grasping an object by placing the digits inside two 3 cm holes is akin to grasping an object flanked closely by obstacles. The positioning of the digits during the approach phase needs to be carefully controlled to avoid a collision. It is possible that such stringent accuracy requirements force the subject to monitor the whole act of prehension consciously and deliberately. DF's perceptual impairment may have compromised her ability to engage in such monitoring, leading her to adopt an alternative strategy to solve the task. Although this hypothesis seems plausible, we do not believe that high accuracy demands alone can explain DF's failure in Experiment 1. Indeed, we have independently observed that she can readily execute skilful grasping movements to objects flanked by obstacles as little as 3 cm away (McIntosh et al., 2000), implying that the visuomotor abilities of the dorsal stream include the avoidance of obstacles (see also Milner and McIntosh, 2004). An additional factor would seem to be required to explain the present results.

We suggest that the critical factor may again be related to the visual complexity of the stimuli, in this case their subtlety. The I-pattern (and H-pattern) stimuli of Experiment 1 were designed to encourage the impression of single black objects suspended in space. DF's problem may have been that our illusion worked too well, in that she was unable to discern the transparent portions of the stimuli at all. (Our observation that she sometimes attempted to insert a digit into transparent sections of the stimuli indicates that this was the case.) Unlike normal subjects, DF would not have had a rich perceptual representation to supplement the visual processing carried out in the dorsal stream. The dorsal stream may lack the capacity for processing the fine surface detail necessary for a complete description of an object's properties. In other words, ventral stream participation may be required for a sufficiently detailed stimulus representation to guide grasping responses to complex objects such as those used in Experiment 1. This idea that strategically appropriate skilled behaviour requires some degree of collaboration between the two visual streams is, of course, explicit in Milner and Goodale's model (1995).

In summary, the dorsal stream seems to provide a dedicated sub-system for the visual guidance of action but it appears that it cannot operate fully successfully in isolation. Certain simple objects, even irregular ones (Goodale et al., 1994), may offer the clear affordance of 'dorsal graspability'. In these cases, the ventral stream may do little more than facilitate the selection of the object as the target of a grasping movement, and even DF's severely compromised level of visual awareness is sufficient for this. However, other more complex stimuli do not seem to afford grasping in the absence of an intact ventral stream, since a more detailed perceptual analysis is required to identify suitable grasp points (e.g. Carey et al., 1996; Dijkerman et al., 1998) or to interpret other subtleties of the situation (e.g. the parts of an object to grasp and the parts to avoid). On the other hand, once the target of a prehension movement has been specified, the dorsal stream appears to be equally capable of completing the grasp whether the target is single, double or, perhaps, multiple.

Acknowledgements. The authors are grateful to the Wellcome Trust (grant 048060) and Leverhulme Trust (grant F/268/T) for their financial support, and as always to DF and her partner for their tolerance and co-operation.

References

- CAREY DP, HARVEY M and MILNER AD. Visuomotor sensitivity for shape and orientation in a patient with visual form agnosia. *Neuropsychologia*, 34: 329-338, 1996.
- CULHAM JC. Neuroimaging investigations of visually-guided grasping. In Attention and Performance XX: Functional Brain Imaging of Human Cognition. Oxford: Oxford University Press, 2004, pp. 415-436.
- DE RENZI E. Disorders of Space Exploration and Cognition. New York: John Wiley and Sons, 1982.
- DIJKERMAN HC, MILNER AD and CAREY DP. Grasping spatial relationships: Failure to demonstrate allocentric visual coding in a patient with visual form agnosia. *Consciousness and Cognition*, 7: 424-437, 1998.
- GOODALE MA. Visuomotor control: Where does vision end and action begin? *Current Biology*, 8: R489-R491, 1998.
- GOODALE MA, JAKOBSON LS, MILNER AD, PERRETT DI, BENSON PJ and HIETANEN JK. The nature and limits of orientation and pattern processing supporting visuomotor control in a visual form agnosic. *Journal of Cognitive Neuroscience*, 6: 46-56, 1994.
- GOODALE MA, MILNER AD, JAKOBSON LS and CAREY DP. A neurological dissociation between perceiving objects and grasping them. *Nature*, 349: 154-156, 1991.
- JAMES TW, CULHAM J, HUMPHREY GK, MILNER AD and GOODALE MA. Ventral occipital lesions impair object recognition but not object-directed grasping: a fMRI study. *Brain*, 126: 2463-2475, 2003.
- JEANNEROD M. The formation of finger grip during prehension: a cortically mediated visuomotor pattern. *Behavioural Brain Research*, 19: 99-116, 1986.
- McINTOSH RD, DIJKERMAN HC, MON-WILLIAMS M, MILNER AD. Visuomotor processing of spatial layout in visual form agnosia. Presented at Experimental Psychology Society. Cambridge, July 2000.
- MCINTOSH RD, MCCLEMENTS KI, DIJKERMAN HC and MILNER AD. 'Mind the gap': The size-distance dissociation in visual neglect is a cueing effect. *Cortex*, 40: 339-346, 2004.
- MILNER AD and GOODALE MA. *The Visual Brain in Action*. Oxford: Oxford University Press, 1995.
- MILNER AD and HEYWOOD CA. A disorder of lightness discrimination in a case of visual form agnosia. *Cortex, 25:* 489-494, 1989.
- MILNER AD and MCINTOSH RD. Reaching between obstacles in spatial neglect and visual extinction. *Progress in Brain Research*, 144: 213-226, 2004.
- MILNER AD, PERRETT DI, JOHNSTON RS, BENSON PJ, JORDAN TR, HEELEY DW, BETTUCCI D, MORTARA F, MUTANI R, TERAZZI E and DAVIDSON DLW. Perception and action in "visual form agnosia". *Brain*, 114: 405-428, 1991.
- MURPHY KJ, CAREY DP and GOODALE MA. The perception of spatial relations in a patient with visual form agnosia. *Cognitive Neuropsychology*, 15: 705-722, 1998.
- SMEETS JBJ and BRENNER E. A new view on grasping. Motor Control, 3: 237-271, 1999.

AD Milner, Wolfson Research Institute, University of Durham, Queen's Campus, Stockton-on-Tees TS17 6BH, UK. Email: a.d.milner@durham.ac.uk