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Phil. Trans. R. Soc. Lond. B 1998 **353**, 1375-1384
doi: 10.1098/rstb.1998.0291

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According to recent conceptualizations, there are two separate cortical visual systems—each with its own distinctive cortical and subcortical links—and these two systems respectively serve the functions of perception and of motor control. These ideas have been arrived at through a confluence of neuroanatomical, electrophysiological, behavioural, and neuropsychological research. It is proposed that this distinction between two broad purposes of vision and their neural bases can provide useful working procedures for analysing both: (i) the nature of visuomotor processing in the normal brain; and also (ii) the abnormal patterns of visual processing that are seen in certain neurological conditions.

Keywords: visuomotor; visual perception; neuropsychology; visual streams; action

1. INTRODUCTION

The human brain appears to have two somewhat distinct visual systems operating in parallel within it (Milner & Goodale 1995). One system provides the visual contents of our perceptual experience, and codes information in an abstract form suitable for storage and for deploying in cognitive processes like imagining, recognizing, and planning. The other visual system serves the much more immediate function of guiding our actions from moment to moment, and therefore needs to code information in a quick, ephemeral and view-specific form. Its contents are probably not accessible for cognitive elaboration or conscious monitoring.

An important part of the evidence that has led to these conclusions has been provided by neuropsychology. It has been known for over 100 years that bilateral damage to the posterior parietal cortex in monkeys causes severe visuomotor difficulties in reaching for and grasping food objects (Ferrier & Yeo 1884), and it has been known for nearly 90 years that comparable damage in humans results in closely similar difficulties (Bálint 1909; see Harvey 1995). Bálint's patient had great difficulty in reaching out to take hold of objects under visual guidance; yet this was not due to a purely visual difficulty, because he only reached inaccurately when he used his right hand. Presumably, therefore, his more successful left hand must have had access to the necessary visuospatial information. In addition, Bálint's patient could touch parts of his own body quite accurately even with his right hand, showing that his difficulties were not simply motor. Bálint thus concluded that the disorder must be *visuomotor*, and he coined the term 'optic ataxia' to refer to it.

We now know that optic ataxia not only affects the visuomotor control of actions within the spatial domain, but also prevents patients from accurately forming their grip size in anticipation of grasping objects of different sizes (Jeannerod 1986; Jakobson *et al.* 1991; Jeannerod *et al.* 1994). We also know that optic ataxia causes gross visual errors in guiding the orientation of the wrist. This was first shown by asking patients to extricate a small object lodged in a groove that was presented at different angles from trial to trial (Tzavaras & Masure 1976), and later by asking similar patients to pass the hand through a large oriented slot (Perenin & Vighetto 1988). Complementary studies have shown that the visual perception of size (Jeannerod *et al.* 1994), as well as of location and orientation (Perenin & Vighetto 1988) can remain largely intact in these same patients.

Of course these findings alone would not force us to conclude that there were two separate visual processing systems, one mediating perception, and the other motor control. It was, in fact, generally inferred from the results that optic ataxia resulted from a disconnection between an intact perceptual system and an intact system for motor control. Thus perception could remain intact while visuomotor control was lost. But that hypothesis, which assumes that the visual control of action is achieved through a serial linkage between perceptual and motor systems, would not be able to explain a converse pattern of dissociations from those described by Jeannerod *et al.* (1994) and Perenin & Vighetto (1988). That is, it would not be able to account for a pattern in which perception was lost yet visuomotor control remained intact.

Yet this opposite pattern is exactly what we found a few years ago (Milner *et al.* 1991) in a patient suffering from a remarkably pure form of the condition known as 'visual form agnosia' (Benson & Greenberg 1969). Our patient, D.F., has a profound difficulty in perceiving and discriminating simple shapes, or even their size or orientation, much like previously described cases of this disorder (Goldstein & Gelb 1918; Efron 1969; Abadi *et al.* 1981). But she is far from being severely impaired in visuomotor control, as the serial processing hypothesis would predict. Instead, she is indistinguishable from normal control subjects in her ability to orient her wrist when reaching to pass her hand or 'post' a hand-held plaque through a slot placed at different orientations (Goodale *et al.* 1991;

Milner *et al*. 1991). Similarly she is quite normal in her ability to tailor her grip size during reaching movements to grasp blocks of different sizes (Goodale *et al*. 1991).

This clear double dissociation between perception and visuomotor control is difficult to account for except on the assumption that the two visual functions are mediated by separate visual processing systems. And this assumption is strengthened by a host of neuroanatomical and neurophysiological evidence which has identified two broad groupings of visual areas in the primate cerebral cortex with quite distinct neural outputs and quite distinct functional correlates (Milner & Goodale 1995). These two visual systems were first unambiguously identified by Ungerleider & Mishkin (1982), who traced a 'dorsal pathway' from primary visual cortex (V1) to posterior parietal cortex (PPC) and a 'ventral pathway' from V1 to inferior temporal cortex (ITC). Although many more cortical visual areas have since been discovered, this broad division has been bolstered by more recent studies of the cortico-cortical anatomy (Morel & Bullier 1990; Baizer *et al*. 1991; Felleman & Van Essen 1991; Young 1992).

Ungerleider & Mishkin (1982) reviewed the contrasting effects of experimental lesions to these two systems, and also the contrasting physiological properties of single neurons in the two systems. They took the evidence overall as supporting their working hypothesis that the two pathways processed different aspects of the visual array, specifically that 'the ventral or occipitotemporal pathway is specialized for object perception (identifying *what* an object is) whereas the dorsal or occipitoparietal pathway is specialized for spatial perception (locating *where* an object is)' (p. 549). But in that same year, Glickstein & May (1982) also wrote an important review, starting with a different emphasis and reaching a rather different conclusion as to the functions of the two systems. Instead of contrasting the visual inputs the ventral and dorsal areas received, they contrasted the output connections of the two systems. They reported that several dorsal visual areas send profuse neuronal projections to the superior colliculus and to motor nuclei in the pons, while none of the ventral visual areas do this. These brainstem target structures in turn supply visual information to the cerebellum (the superior colliculus doing so via the pontine nuclei). Glickstein & May therefore proposed that 'The behavioral, anatomical, and physiological evidence suggests that the parietal lobe visual areas are especially concerned with the visual guidance of movement' (1982, p. 136).

More recent evidence confirms the differential outputs of the two systems and thereby gives further clues to their respective functions. It transpires that areas in the dorsal system project not only to sensorimotor areas in the brainstem, but also to specific premotor areas in the frontal lobe, each related to different action domains such as saccadic eye movements, arm reaching movements, and hand grasping movements (Cavada & Goldman-Rakic 1989; Boussaoud *et al*. 1996; Wise *et al*. 1997). On the other hand, the ITC has strong reciprocal connections with the amygdala (see, for example, Baizer *et al*. 1993), a structure with which the PPC in contrast has very few if any interconnections. The amygdala is implicated in processes of learning to associate visual stimuli with reward (see, for example, Mishkin 1982; Gaffan *et al*. 1988) and also with social and emotional cues (Kling & Brothers 1992; Brothers & Ring 1993). Thus, whereas the dorsal system has direct and rapid access to motor-related systems, the ventral stream seems to provide the visual route to associative learning, and can thereby mediate more flexible and long-term visual effects on behaviour.

Recent neurophysiological evidence also favours Glickstein & May's (1982) interpretation, and at the same time allows us to extend the scope of their hypothesis. Although their emphasis was on visuomotor control rather than on visuospatial perception, nevertheless they saw the main role of the dorsal system as supplying visual information for the guidance of actions in space. At that time it was already known from the work of Hyvärinen & Poranen (1974), Mountcastle *et al*. (1975), and others, that out of six categories of visually driven neurons in the monkey's PPC, five would require visual coding of the egocentric spatial location of the stimulus: (i) visual saccade neurons; (ii) visual tracking neurons; (iii) arm-projection neurons; (iv) visual fixation neurons; and (v) light-sensitive neurons (cells that did not appear to have any selective association with a particular kind of behaviour on the part of the animal). None of these categories of cells seemed to have any selectivity for stimulus shape or orientation. But Mountcastle *et al.* (1975) did identify a sixth group of visual neurons, albeit without exploring them in detail: 'manipulation' neurons. It was not until 1990 that Sakata, one of the original co-authors in the Mountcastle *et al*. (1975) paper, began to publish more detailed studies of these cells (see Sakata *et al*., this issue).

The first of these reports from Sakata's laboratory was by Taira *et al.* (1990). By showing that many neurons in the anterior part of the intraparietal sulcus (an area now known as AIP) are not only selectively associated with specific visual stimuli, but are very non-selective with regard to the location of those stimuli, these authors refuted the notion that visual processing in PPC is restricted to an analysis of visual space. Most of the cells they recorded from were associated with particular motor acts (grasping, pulling, pushing, and so on), rather like a group of neurons that Rizzolatti *et al.* (1988) had previously found in area F5 of the premotor cortex. It is surely not coincidental that areas F5 and AIP are heavily and reciprocally interconnected (Godschalk *et al*. 1984; Matelli *et al*. 1986). Sakata and his colleagues have recently gone further, revealing neurons in a more posterior part of the intraparietal sulcus selective for visual object properties such as stimulus orientation in three dimensions, and the height:width ratio of elongated shapes (Shikata *et al.* 1996).

In short, the balance of evidence from both electrophysiological and neuropsychological sources has now shifted decisively in favour of viewing the dorsal visual stream as dedicated to the guidance of movements rather than to the analysis of space (Milner & Goodale 1995). Furthermore, although visual space clearly does have to be analysed to provide guidance for movements of the eyes, head, arm, wrist, and the body as a whole, it is now quite certain that this spatial analysis is not done by a single all-purpose system in the PPC. There is a growing range of evidence from monkey electrophysiology (see, for example, Colby & Duhamel 1997; Andersen *et al.* 1997;

Snyder *et al.* 1997) for several visuospatial coding systems in PPC, each associated with a different response modality (e.g. saccades versus arm reaches). Neuroimaging studies show that the same is true in the human posterior parietal cortex: there are separate visual representations for guiding eye and hand movements towards the same stimulus locations (Kawashima *et al.* 1996). In the case of stimulus motion, the neuronal signals are beginning to be analysed separately for different oculomotor purposes even within the monkey's 'purely visual' area MT (V5). As would be expected, microstimulation at a given locus within MT generally influences pursuit and saccadic eye movements in consistent ways, as if there was a real perturbation of the visual stimulus velocity (Gruh *et al.* 1997). But occasionally such stimulation affects the two oculomotor responses in quite different, inconsistent, ways. Presumably therefore, different outputs regarding visual motion are already being processed in MT for transmission on to separate saccadic and tracking systems in such PPC areas as 7a and LIP.

2. THE DORSAL STREAM UNCOVERED

A felicitous coherence between recent electrophysiological and neuropsychological findings has thus allowed us to decide between two equally promising interpretations of (at that time) ambiguous data on dorsal stream function (Glickstein & May 1982; Ungerleider & Mishkin 1982). Remarkably, in fact, the visuomotor function discovered in patient D.F. matches very closely what one would expect from a person with an intact but isolated dorsal system, given the physiological evidence from neurons in the monkey PPC. For example, Shikata *et al.* (1996) have observed that the selectivity of neurons in the monkey intraparietal sulcus to the orientation of a surface lying in depth is very sensitive to binocular input. When one eye is covered, most of the neurons lose their orientation selectivity. In precisely the same way, we have found that although D.F. is qualitatively and quantitatively indistinguishable from normal controls when reaching to grasp a 5 cm^2 plaque that is tilted in the sagittal plane when she uses binocular vision, her performance declines dramatically when she views the shape monocularly (Dijkerman *et al.* 1996; Milner 1997*b*).

In another set of experiments, D.F. has been tested with a variety of patterns presented on sheets of paper at different orientations, and asked to 'stamp' them with an inked elongated block, as if 'posting' the block into a slot. From this it has been possible to explore the cues to contour that she can use to guide the orientation of her manual responses. As one might expect, D.F.'s accuracy when responding to oriented luminance contours is good (Goodale *et al.* 1994*a*). She can respond well above chance to the 'columns' in a dot matrix whose column–row dot spacing has a ratio of 1:6 or 1:4, thus exploiting the Gestalt principle of 'grouping by proximity' (E. Ashbridge and D. I. Perrett, unpublished data). D.F.'s responses, however, were not improved by the addition of 'grouping by similarity' cues such as colour (alternating red and green columns of dots). Furthermore, for displays eliminating proximity cues (i.e. with a column–row ratio of 1 : 1), she was unable to use grouping by colour similarity to guide her responses. Yet D.F. is not achromatopsic: she could identify verbally, and point to, individual coloured spots among an array of spots of different colours. She was also well able to direct her stamping responses to the orientation of patterns of abutting bars alternating in colour (E. Ashbridge and D. I. Perrett, unpublished data). These results fit well with what is known of colour coding in the dorsal stream: whereas MT neurons are unselective for particular wavelengths, many of them continue nevertheless to respond to the orientation of a wavelength defined boundary, even at equiluminance (Saito *et al.* 1989).

The extent to which D.F.'s visuomotor control in everyday situations resembles that of normal control subjects encourages us to treat her as an 'experiment of nature' which might help us to delineate the visual limits of the human dorsal visual system. This approach gains still further encouragement from the two described instances where her performance breaks down under conditions where, from our knowledge of primate electrophysiology, we would expect the system to break down. We have therefore examined the limits of D.F.'s visual processing for motor control in a variety of other task situations, with a view to erecting hypotheses as to the operating characteristics of the normal human dorsal stream. These hypotheses would be difficult, of course, to test directly in humans, but they would make falsifiable predictions as to the upper-limit properties of neurons within the monkey dorsal stream.

Previous demonstrations of both temporal and spatial limits on D.F.'s visuomotor control have been summarized in a previous paper (Milner 1997*b*). Thus she is able to scale her grip size appropriately to grasp blocks of different sizes when they are immediately present to her eyes, but her grip scaling falls to chance when a delay of 2 s or more is imposed on her response. This indicates that a short visual 'memory' is characteristic of the visuomotor system underlying D.F.'s grasping.

In more recent studies, we have found that delays of a few seconds also severely reduce the spatial accuracy of both D.F.'s saccadic eye movements (Dijkerman *et al.* 1997), and her manual reaching movements (Milner *et al.* 1998*b*). Yet her immediate saccades and immediate reaches to the identical visual targets are both of normal accuracy. These new results indicate that there are low limits on the time for which useful visuospatial information is retained within the posterior parietal systems governing both saccadic eye movements and manual reaches in D.F. Future work may allow us to determine whether the time constants are the same in these three domains of visuomotor control (grasping, reaching and saccades).

The *spatial* limits on D.F.'s visuomotor system are obvious from her poor performance in copying or matching tasks. A response made at a site shifted away from the stimulus loses its accuracy quite dramatically. For example, if she is shown a single line drawn on a piece of paper she is initially unable to copy its orientation on a separate piece of paper (Dijkerman & Milner 1997). Yet she is able to trace over a single oriented line, and even 'cheat' in the copying task by tracing the presented line 'in the air' before then promptly drawing her copy. In fact, she can even deploy the strategy of imagining herself tracing over the line while holding the pencil to the paper and then transform this imagined movement into a fairly successful copying response (Dijkerman & Milner 1997). Interestingly, D.F.'s introspection when doing this is that if she delays more than a second or two before committing the pencil to paper when using this motor imagery strategy, then she 'loses it'.

Other limits on D.F.'s spared visual coding have become apparent by exploring in various ways her ability to process visual form. For example, we have extended the 'posting task' mentioned earlier to see whether she could post a T-shaped object into a T-shaped aperture presented in the frontal plane in front of her. We found that she divided her responses almost 50 : 50 between two kinds of hand orientation: one in which the shape correctly corresponded to the orientation of the T-shaped aperture, and the other in which the orientation was approximately 90° away from the target orientation (Goodale *et al.* 1994*a*). In other words, she was able to rotate her wrist correctly with respect to one of the two orientations of the T-shaped aperture, but was not able to take the orientations of both segments of the T into account in turning her wrist.

In another attempt to explore the shape processing capacity of D.F.'s visuomotor system, we used a grasping task. She was presented with a solid cross shape in the frontal plane, the two bars of the cross being 7.5 cm in length and 1.6 cm in width. We found in this task that normal control subjects consistently reached out to grasp the cross using the thumb and three middle fingers, tailoring the orientation of the wrist such that each of the four digits engaged with the spaces between the arms of the cross. Thus, for example, the orientation of the forefinger–thumb axis immediately prior to contact changed in a linear relation as a function of the orientation of the cross. In contrast, D.F. maintained the same default orientation of the hand whatever the orientation of the cross (Carey *et al*. 1996).

Clearly, although her behaviour was different in the two experiments, D.F. showed no evidence in either of these experiments for an appreciation of the shape formed by two oriented contours presented in combination. But of course the nature of 'shape' or 'form' is not easy to define in a universally agreed way, and the idea that it requires an appreciation of the orientation of two or more contours in combination is only one possible conceptualization.

Informally, we have been aware for some time that D.F. has no difficulty in combining more than one feature from different domains in guiding her actions: for example, she can catch a ball (requiring an integration of space, size and motion-in-depth). Those observations are perhaps not surprising given that Sakata and co-workers (1997) have recently described visual-fixation neurons in monkey PPC that are specifically active during tracking of a target moving in depth. But D.F. can even catch a thrown lightweight 35 cm × 1.5 cm wooden dowel quite competently, a feat requiring an integration of space, size, orientation, and motion-in-depth (Carey *et al*. 1996). In a formal experimental test, we examined whether D.F. was able simultaneously to combine the width and orientation of singly presented rectangular blocks of different width (but all with identical surface area). We found that her visual control of grip size as well as the orientation of her hand were both completely normal when reaching out to grasp the blocks (Carey *et al*. 1996).

What was more interesting, from the point of view of shape processing, was that D.F. distributed her grasps between the long and the short dimensions of these rectangular blocks in a completely normal way. That is, she did what all normal subjects do quite unconsciously, which is to grasp the narrower of the two dimensions of an elongated block; and again like normal subjects, the more elongated the block, the higher her ratio of 'narrow' grasps to 'wide' grasps (though even the longest block could be grasped either way). This simple observation indicates that like some of the neurons described by Shikata *et al.* (1996) in the monkey's PPC, D.F.'s visuomotor system is able to compute the aspect ratio of rectangular shapes (and act accordingly). Independent evidence confirms that D.F. can extract the gross shape of an object to determine her grasp points when picking it up. Goodale *et al.* (1994*b*) tested her with randomly contoured smooth flat shapes that permitted only two or three stable precision grasp locations for the opposed forefinger and thumb. D.F. performed well on this task, selecting grasp points similar to those chosen by normal control subjects. Yet she performed at chance level, of course, when asked to match pairs of the shapes as 'same' or 'different'. D.F.'s choice of stable grasp points in this task may indicate that her visual system is able to compute relative curvature at different points around the circumference of the shapes used in the study.

We are beginning to discern from studies such as these some of the visual coding limitations of D.F.'s visuomotor system, and accordingly to construct hypotheses as to the limitations built in to the normal human dorsal stream. So far the results are consistent with the work of Sakata and his colleagues on the properties of individual neurons in the monkey's PPC. But we can go further, and make certain predictions from what we have found in D.F.—such as that it is unlikely that visual neurons will be found in PPC that are selective for two-component shapes like T or X. On the other hand, neurons that can compute and discriminate the curvature of object contours would be predicted to exist.

3. COVERT VISION: ACTIONS SPEAK LOUDER THAN WORDS

In normal clinical practice, as in normal visual psychophysics, it is tacitly assumed that people's visual capacities can be assessed by asking them to say what they can or cannot see. It is assumed that if brain damage causes a visual problem, then patients should be able to introspect about it, and what they say they can or cannot see should correspond with their level of visual functioning in everyday active life. D.F. gave the lie to this, when she startled us with her excellent visuomotor control despite the most profound perceptual disability. The converse dissociation between perception and visuomotor control, while not quite so sharp, had already been reported by using similar visual tests of perception and motor control in patients with optic ataxia (Perenin & Vighetto 1988; Jeannerod *et al*. 1994). If we (Milner & Goodale 1995) are right in our argument that this striking double dissociation can be reified with reference to the human homologues of the dorsal and ventral cortical streams of visual processing, then the tasks that reveal the dissociations should provide us with a diagnostic tool for trying to understand other neurological disorders of vision. While the conventional approach may tell us a great deal about the deficits that follow disruption of the ventral stream and its input channels, the use of visuomotor tasks may tell us not only whether there is a disruption of the dorsal stream, but also may reveal unexpected covert visual function, as seen in D.F.

(a) *Hemianopia*

The first and best known example of 'covert' visual capacity was of course provided by certain patients with hemianopic field defects following damage to the primary visual cortex (V1) or to the optic radiations passing from the lateral geniculate nucleus (LGNd) to V1. The phenomenon of 'blindsight' was first studied in detail by Weiskrantz and his colleagues (see Weiskrantz *et al.* 1974; Weiskrantz 1986, 1997), and the tasks they first used to demonstrate it were visuomotor tasks. It is now generally accepted that although hemianopic patients (by definition) are unable to perceive a light in the affected parts of the contralesional visual hemifield, some of them are nonetheless able to surprise themselves by directing their gaze or their hand at well-above chance levels towards the location of the light.

The usual interpretation of these preserved saccadic and pointing abilities (see, for example, Weiskrantz 1986) has been that in the absence of a viable geniculostriate visual pathway, the patient has to rely on the older colliculo-pulvinar route from the eye to the brain. The superior colliculus in itself is an ancient sensorimotor structure that appears to have the machinery necessary to guide shifts of gaze in response to visual stimuli (Robinson & McClurkin 1989; Sparks & Hartwich-Young 1989) and even to guide arm reaching responses to visual stimuli (Werner 1993; Werner *et al.* 1997). In a recent functional MRI experiment, Sahraie and co-workers (1997) have found that there is an increased level of activation in the superior colliculus during unconscious detection of motion (i.e. in blindsight) as compared with conscious detection of motion (obtained by using different stimulus parameters) in the same patient's impaired field.

But on the other hand, it is possible that the visuomotor structures of the cortical dorsal stream are necessary for blindsight as well, and indeed it would be difficult to explain why the extent and nature of blindsight varies so much from one hemianopic patient to another if extrastriate visual cortex played no role. In addition, electrophysiological studies have shown that dorsal stream structures maintain neuronal activity in response to visual stimuli following the ablation or inactivation of V1, whereas this is not the case for ventral stream areas (Gross 1991; Bullier *et al.* 1994). This preserved cortical activity in dorsal stream areas may thus plausibly be proposed as a critical physiological correlate of visuomotor control in blindsight.

Recent research with hemispherectomized patients is consistent with such a proposal. In contrast with earlier studies, it now seems that if cortical damage is not restricted to primary visual cortex but also includes the rest of the cerebral hemisphere, then there is no true blindsight (King *et al.* 1996; Stoerig *et al.* 1996). It seems that any residual detection in the contralesional visual field following hemispherectomy can be attributed to the use by the patients of scattered light spreading within the ocular medium into the good hemifield, where it can of course be detected consciously by the patient (see Stoerig & Cowey (1997) for review).

If then, extrastriate cortex is necessary for blindsight, can we go further and argue that the dorsal stream in particular has a crucial role? Perenin & Rossetti (1996) have now provided good evidence for this idea, by using the same tasks that revealed covert visual function in patient D.F. They have reported that a V1-damaged patient shows qualitatively just the same dissociation between perception and visuomotor control as D.F. When asked to post a card into a slot presented at different orientations in the hemianopic field, the patient performed significantly above chance (though his spatial accuracy was not sufficient for him to actually insert the card), and when asked to reach out and grasp blocks of different sizes, the patient calibrated his grip at statistically above-chance levels. In contrast, however, he performed randomly when asked to indicate the orientation of the slot or the size of the blocks, either manually or verbally. The same result has now been found with another patient. Her spatial accuracy was better, allowing her to post the card successfully on several trials (Rossetti 1998). Interestingly, Rossetti found that this second patient suffered severe interference with her posting behaviour when asked to make simultaneous verbal guesses of the orientation of the slot while making her reaches.

This work confirms that blindsight is demonstrable for intrinsic as well as extrinsic (location and motion) visual properties of objects, and the clear contrast between the perceptual and motor versions of the tasks strongly suggests that blindsight patients are able to use the same visuomotor structures as D.F. Of course, D.F. has the additional advantage of a functioning area V1 (as shown by her good acuity and relatively intact visual fields, as well as by structural magnetic resonance imaging). This presumably provides her with a much higher-resolution visual input into the dorsal stream structures mediating these visuomotor functions.

Of course, it must be conceded that not all blindsight can be comprehended in terms of dorsal stream function, although we have argued (Milner & Goodale 1995) that most of it can. In particular, the unconscious discrimination of wavelength that has been recorded in a number of patients requires a different account, most probably in terms of intact LGN neurons projecting through an extrastriate route direct to cortical areas V2 and/or V4 (Cowey & Stoerig 1992).

(b) *Visuospatial neglect*

A tendency to ignore stimulus items in the left half of extrapersonal space is not unusual after right middle cerebral artery strokes that affect the region of the parietal lobe bordering the temporal lobe (Bisiach & Vallar 1988). Curiously, such leftward neglect is not restricted to purely retinocentric, or even head-centred visual coordinates, as quite often items even on the right side of space will be neglected if they fall on the left side of objects or other perceptually segregated regions of the visual field (Walker 1996).

One of the more intriguing, and most easily demonstrated, features of visuospatial neglect is the tendency of patients to make rightward errors when asked to bisect a

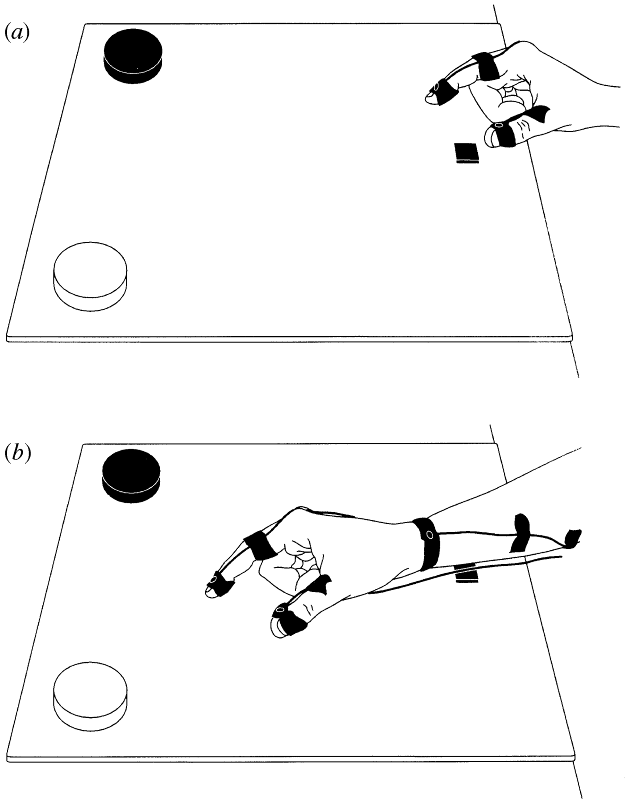

Figure 1. Visual neglect: size estimation and grasping tasks. (*a*) In the size estimation task, the subject did not reach out, but merely opened his or her finger and thumb to indicate how wide one of two identical-size cylinders (the white one) was judged to be. In some trials the white cylinder was on the right, in others it was on the left. (*b*) In the grasping task, the subject reached for the white cylinder in each trial and picked it up.

horizontal line at its midpoint. These errors can often be of several centimetres in magnitude. We have investigated the cause of these errors by showing patients lines that have been pre-bisected at various points, and asking them to point to whichever end of the line appears to be closer to the bisection mark. We have found that most patients who make bisection errors show a leftward bias when asked to point in this way, even when the prebisection mark is located at the exact midpoint of the line (Milner *et al.* 1993; Harvey *et al.* 1995). This suggests that most neglect patients make bisection errors because they misperceive the line, rather than because they have a motor bias to respond rightwards (in which case they should point rightwards, if anything, in our prebisected-lines task, an outcome that we have seen only in rare cases).

We have explored directly this apparent tendency in neglect patients to perceive the left half of lines as shorter than the right half, by presenting pairs of stimuli of the same or different length for them to make larger–smaller judgements. We have found that the most of the neglect patients judge the leftward of two horizontal lines or rectangles to be shorter than an identical stimulus on the right (Milner & Harvey 1995; Pritchard *et al.* 1998). This tendency is not present in right-hemisphere patients without neglect, nor in healthy controls.

One possibility is that there is a rather high-level visual representational system located in the right parieto-temporal lobe region which when damaged gives rise to these perceptual distortions. We have therefore begun to investigate which cortical stream provides this putative system with its visual inputs. We have tested a neglect patient (E.C.) by using an arrangement whereby she is presented with two plastic cylinders of identical size, one white and one black (figure 1), varying the location of the white stimulus between left and right from trial to trial (Pritchard *et al.* 1997). The patient was asked in one test condition to reach out and grasp the white object in each trial using her forefinger–thumb precision grip, and in the other condition not to reach out, but instead to show us how big the white object is simply by opening her finger and thumb. In the grasping task, we measured the maximum grip size achieved during the reach, which typically occurs about two-thirds of the way along the trajectory. In both tasks, an Optotrak 3020 system was used to measure the vectored distance between infrared markers attached to the finger and thumb.

We found that E.C. was able to grasp the target stimulus skilfully, whichever side it was placed on. She always opened her finger–thumb grip in proportion to the size of the object ahead of time when reaching to grasp it. Indeed E.C.'s finger–thumb aperture showed a highly significant linear relationship with the actual size of the object, whichever side it was presented on. Furthermore, as shown in figure 2, there was no significant difference between the maximum grip apertures attained when reaching to the left and when reaching to the right. Her grasps were similar, for a given size object, whichever side the object appeared on. (Although there was a slight tendency for the gain to be higher on the right side of space, the interaction did not approach statistical significance.)

In contrast, when E.C. was asked to estimate the size of the target objects, it is clear from figure 3 that her judgements were very different on the two sides. Although once again her finger–thumb aperture correlated highly significantly with the actual size of the object, on either side of space, there was nonetheless a consistent difference between the two sides. In agreement with her size-matching data, she underestimated the size of the target cylinders when they were placed on her left, often by as much as 1 cm relative to the right. This left–right difference was highly significant, a result never yet found in any of the control subjects (brain-damaged or healthy) we have tested.

We conclude that the use of comparable tests of visual perception and visuomotor control can reveal something about neglect, just as it has done about other conditions such as visual form agnosia and hemianopia. In particular, it appears that neglect can influence the visual perception of size without affecting visuomotor control in relation to the very same stimuli. We conclude that neglect is a perceptual phenomenon rather than one which relates all-pervasively to visual processing. We believe that our finding lends indirect support therefore to the view that the representational system that is damaged in neglect is probably much more closely linked to the ventral stream of processing than to the dorsal (Milner 1995, 1997*a*; Milner *et al.* 1998*a*).

(c) *Williams' syndrome*

Another recent example where investigators have contrasted performance on tests of perception and action

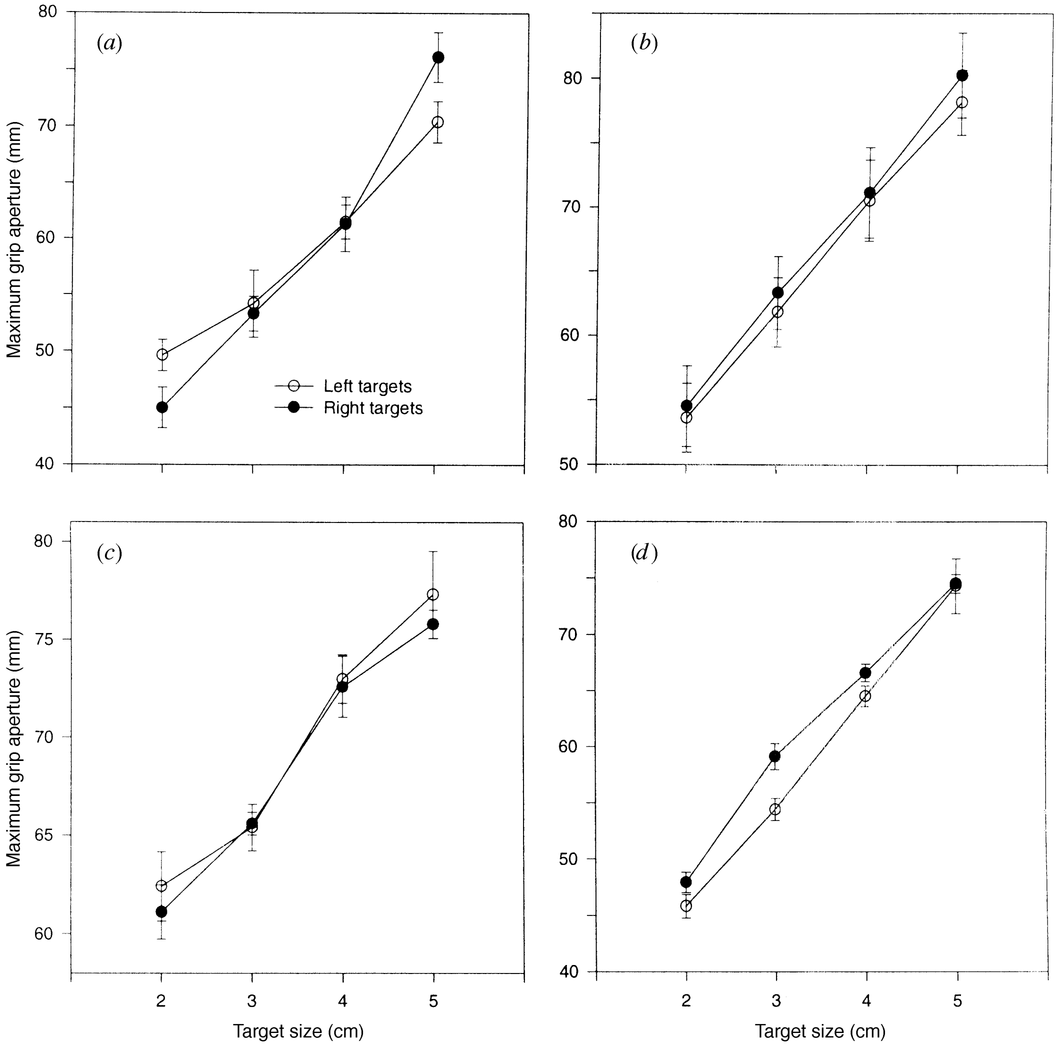

Figure 2. Grip scaling during grasping, in a patient with visuospatial neglect (*a*, E.C.), along with data for two right-hemisphere lesion controls (*c*, RCVA control JM; *d*, RCVA control WR) and a group of eight healthy controls (*b*). The diameter of the target cylinder is shown on the abscissa. The ordinate represents the maximum separation in millimetres between two infrared-emitting diodes (IREDs), one attached to the forefinger and the other to the thumb, attained during reaches. E.C. scaled her grip size accurately when reaching out to grasp a cylinder, with no consistent under-scaling on the left relative to the right. (From Pritchard *et al.* 1997.)

to help clarify the nature of a neurological disorder is the work of Atkinson and her collaborators (1997) with children suffering from Williams' syndrome. In this congenital disorder, children have a severe deficit in spatial cognition, but relatively spared visual perception. To investigate the possible visual pathways that might be compromised in this condition, Atkinson and co-workers tested a group of affected individuals first on their thresholds for seeing coherent motion in patterns of dots. As would be predicted if the dorsal stream area MT (V5) was damaged, elevated thresholds were found. But in addition, they tested the children on posting a card into an oriented slot, and showed that there was a selective deficit in this task relative to a perceptual matching version of the task. This would suggest that dorsal stream areas well within the posterior parietal cortex are compromised, as well as area MT (which lies more posteroventrally in the human brain than in the monkey).

It appears that like adults (and children: H. C. Dijkerman, E. Isaacs, S. R. Jackson, A. D. Milner, R. Newport and A. Shaw, unpublished data) with damage to the dorsal stream, Williams' syndrome children have a visuomotor impairment that cannot be explained in perceptual terms. Thus, as well as helping to further our understanding of a particular disorder, these results add further support to the idea of separate visual processing systems in the brain.

4. CONCLUSIONS

The view has developed from electrophysiological and behavioural studies in the monkey, as well as from studies of optic ataxia and normal visually guided behaviour in humans, that there are two rather separate visual processing systems in the cortex, each with different functional endpoints and operating characteristics, and that they correspond to the monkey's dorsal and ventral streams. An intensive series of studies of one particular patient with pure visual form agnosia (D.F.) is strongly consistent with this idea, and seems to provide a rather pure example of a selective disruption of the ventral (perceptual) system without serious damage to the dorsal system.

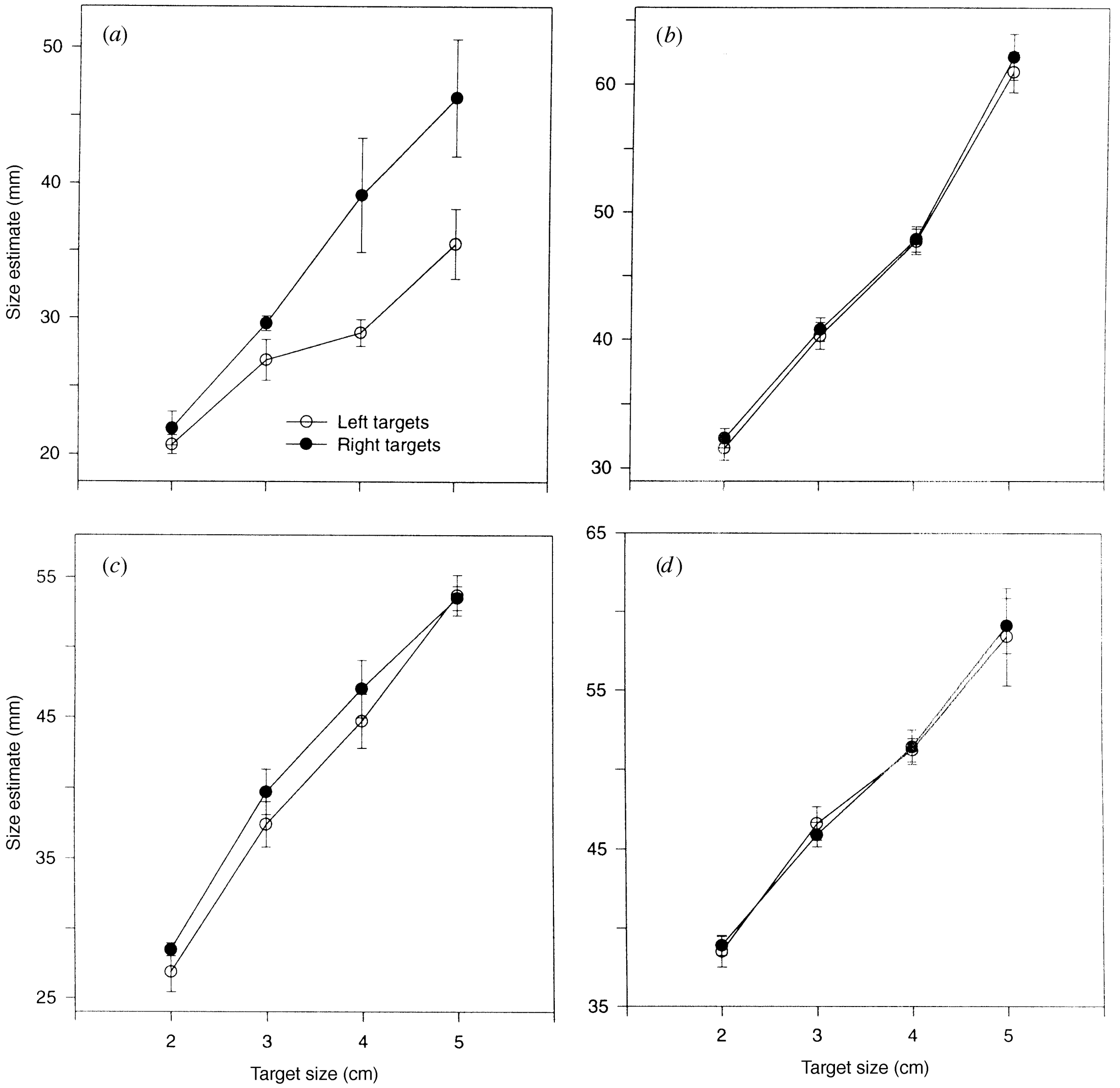

Figure 3. Size estimation data in the same neglect patient, E.C. (*a*). In contrast to the grasping data shown in figure 2, she underestimated the size of cylinders presented on her left (open circles), relative to the same cylinders when presented on her right (closed circles). The ordinate represents the mean asymptotic separation in millimetres between IREDs attached to the forefinger and the thumb while the subject attempted to match the diameter of a cylinder. Conventions as in figure 2. (From Pritchard *et al*. 1997.)

One can work backwards from this proposition in two ways. First, one can determine the limits of D.F.'s visual skills in guiding her motor acts, to construct hypotheses about the parameters of the normal human dorsal system. Second, one can apply tasks that have been developed to establish these neuropsychological dissociations to try to understand the visual pathways that are disrupted in other forms of neurological disorder.

I thank the Wellcome Trust for financial support of the research described here, and Catrin Pritchard for allowing me to reproduce her data on patient E.C.

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