

Vision without knowledge

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SUMMARY

A brain-damaged patient (D.F.) with visual form agnosia is described and discussed. D.F. has a profound inability to recognize objects, places and people, in large part because of her inability to make perceptual discriminations of size, shape or orientation, despite having good visual acuity. Yet she is able to perform skilled actions that depend on that very same size, shape and orientation information that is missing from her perceptual awareness. It is suggested that her intact vision can best be understood within the framework of a dual processing model, according to which there are two cortical processing streams operating on different coding principles, for perception and for action, respectively. These may be expected to have different degrees of dependence on top-down information. One possibility is that D.F.'s lack of explicit awareness of the visual cues that guide her behaviour may result from her having to rely on a processing system which is not knowledge-based in a broad sense. Conversely, it may be that the perceptual system can provide conscious awareness of its products in normal individuals by virtue of the fact that it does interact with a stored base of visual knowledge.

1. INTRODUCTION

The visual system of mammals has evolved to fulfil two broad purposes. The first is to permit the organism to use information about the shape, size, orientation, motion and location of distal objects in order to guide its actions on-line in both a predictive and a reactive manner. The second function of vision, which probably evolved rather later, is to permit the acquisition and retrieval of knowledge about the more enduring properties of distal objects and other organisms, and about their interrelationships in the world. Generally speaking, the most useful way of coding visual information for the first of these purposes will be egocentric, that is, in terms of the action coordinates within which the animal operates, and it will need to have a short time constant, in order to adjust to the fleeting changes within the visual field resulting from both the animal's own movements and those of the target object. In contrast, a visual memory system needs to have representations that are comparatively long-lasting and abstracted from the transient sensory particulars that make up its raw data. Such representations would allow visual recognition of the object or place when newly encountered under different illumination or from a different viewpoint.

It has generally been assumed that these disparate needs could be satisfied by a single visual system, suitably provided with separate output channels for the different behavioural requirements of the animal. More recently, however, it has been argued that the coding needs are so different that the brain needs to keep the two kinds of processing apart, and that accordingly evolution has provided us with *two* visual

systems, one for serving action, the other for serving perception and cognition (Castiello & Jeannerod 1991; Bridgeman 1992; Goodale & Milner 1992). This idea gains support from several experimental observations that what we perceive does not always correspond with the 'real' visual information that determines our motor output. In particular, visual illusions affect perception more than action (see Milner & Goodale (1995), chapter 6). Thus the brain seems to transform its visual input differently for the purposes of perception and action, even though under most everyday circumstances the two transformations are not seriously inconsistent.

Recently we have taken this argument further (Goodale & Milner 1992; Milner & Goodale 1993) by proposing that the two broad functions of vision may be mapped on to two major cortical 'streams' of visual processing. The existence of these two streams, each emanating from the primary visual cortex (V1), was first postulated by Mishkin and his co-workers (Mishkin 1972; Ungerleider & Mishkin 1982). One pathway (the dorsal stream) was hypothesized to terminate in the posterior parietal lobe, and the other (the ventral stream) in the inferior temporal lobe. Later studies of the connective anatomy of the multitude of visual areas that we now know to exist in the primate cerebral cortex have confirmed the reality of these two systems (Morel & Bullier 1990; Baizer *et al.* 1991; Young 1992), though the two are by no means fully insulated from one another (Felleman & Van Essen 1991; Webster *et al.* 1994).

Milner & Goodale (1995) have recently assembled a wide array of evidence from neurophysiological and neurobehavioural research that supports this new

version of the 'two cortical visual systems' theory, and in particular have argued that a range of human neuropsychological findings are consistent with it. For example, patients with optic ataxia—who almost invariably have damage to the posterior parietal region—demonstrate impaired visuomotor coordination in reaching and grasping, despite often retaining comparatively normal visual discrimination (Jeannerod 1986; Perenin & Vighetto 1988; Jakobson *et al.* 1991; Jeannerod *et al.* 1994). This fits with functional imaging studies that reveal activation in these posterior parietal areas (and associated regions of secondary motor cortex) during visually guided prehension in normal individuals (Grafton *et al.* 1996b; Matsumura *et al.* 1996; Failletot *et al.* 1997).

Conversely, a patient with visual form agnosia (D.F.) is able to reach for and grasp visual targets flawlessly, despite having a devastating inability to perceive or discriminate their shape or size (Milner *et al.* 1991; Goodale *et al.* 1991). Given structural imaging evidence that D.F.'s parietal and frontal lobes remain largely intact, it seems reasonable to suggest that the parietal visuomotor systems revealed by lesion and functional-imaging data are what provide her with the means to control her actions visually. The complementary assumption is made that her visual agnosia itself is caused by a disconnection of area V1 from processing systems for contour and form perception within the ventral stream. The scan evidence of dense damage in lateral occipital cortex in D.F. is consistent with this (see below, and see also Sparr *et al.* (1991)), and positron emission tomography (PET) studies indicate that occipito-temporal regions are severely underactivated in other cases of apperceptive agnosia (Grossman *et al.* 1996).

2. THE VISUAL WORLD OF D.F.

Patient D.F. suffered from accidental carbon monoxide poisoning in 1988, at the age of 34. A structural magnetic resonance imaging (MRI) scan carried out a year later showed that despite this pathology, there was a remarkably concentrated region of bilateral cortical damage in the lateral prestriate cortex, mainly in areas 18 and 19 (Milner *et al.* 1991). A series of perceptual tests have shown that D.F. has a profound and persisting failure to discriminate and identify contour orientation and simple geometric shapes, whether these are defined by luminance boundaries or by colour, motion or depth boundaries. For example, she performs at chance level in discriminating a square from an oblong pattern of equal area (Efron 1969) up to an aspect ratio of 1:2 (Milner *et al.* 1991; Carey *et al.* 1996). Although she performs better than chance with more elongated rectangles, she never reaches 100% correct. She also performs at or near chance level when asked to indicate the orientation of a single line (Milner *et al.* 1991; Dijkerman & Milner 1997).

Despite these problems, D.F. is able to detect high-spatial-frequency gratings with normal contrast thresholds (Milner *et al.* 1991; Milner & Goodale 1995), although unable to report reliably whether the

gratings are horizontally, vertically or obliquely oriented. She is also able to see colour, performing creditably on formal tests of colour discrimination (Milner & Heywood 1989), and can see motion and stereoscopic depth within random-dot patterns, though without recognizing the shape that she sees in motion or in depth. Thus D.F. does have visual experience, but it is limited to a narrow range of stimulus domains, and does not include shape or orientation.

Yet D.F. can successfully perform visuomotor tasks using these very dimensions for which she lacks visual awareness. For example, when she is asked to reach out and pass her hand (or a hand-held plaque) through a slot cut into a disc placed at different orientations in front of her, she does so unhesitatingly and accurately. Video recordings show that she begins to turn her hand appropriately as soon as she raises it from the table, well before it reaches the target (Milner *et al.* 1991). Yet despite this normal visuomotor control, D.F. is quite unable to report or reproduce the orientation of the slot. Even when she was asked to make such a judgement manually, for example by rotating the plaque at a distance from the slot so as to match the target orientation, her responses did not differ significantly from chance (Milner *et al.* 1991; Goodale *et al.* 1991).

A similar picture emerges when D.F. is asked to reach out and pick up solid rectangular blocks of different widths but each with an identical surface area (cf. Efron 1969). Her grip is perfectly pre-calibrated during mid-reach so as to permit a skilled grasp, the aperture between her index finger and thumb correlating closely with the width of the object (Goodale *et al.* 1991), exactly as found in studies of normal individuals (Jeannerod 1981; Jakobson & Goodale 1991). Indeed she can grasp these objects with ease even when they are presented at a range of different orientations, requiring her simultaneously to adjust both her wrist orientation and her grip size (Carey *et al.* 1996). Furthermore, just like normal subjects, D.F. distributes her grasp points systematically in favour of the narrower of the two dimensions of the oblong blocks in this task: the more elongated the block, the fewer grips she makes along the long dimension (Carey *et al.* 1996). Thus the programming of her arm and wrist movements is governed in part by a covert appreciation of the gross shape of the object. Yet in all these grasping tasks she experiences her performance as guesswork; and she demonstrates her inability to *perceive* width by failing to use her forefinger and thumb in a demonstrative way to indicate the width of the blocks (Goodale *et al.* 1991).

In another experiment, Goodale *et al.* (1994b) presented D.F. with smoothly-curved random shapes to pick up, one at a time. These shapes had a small number of optimal 'grasp points' at which normal subjects would position their forefinger and thumb when picking up the object so as to ensure a stable grip. D.F.'s grasp points were indistinguishable from those of normal control subjects. Yet she was quite unable to make same/different judgements at an above-chance level when the shapes were presented to her in like or unlike pairs. This study provides

additional evidence that D.F.'s visuomotor system is able to analyse certain action-related aspects of shape, despite the failure of her perceptual system to make the same discriminations.

These various studies show that D.F. is able to govern many of her actions using visual information of which she has no awareness. But it is clear that this is only true of actions that are targeted *directly at the visual stimulus*. She cannot successfully use the same visual information to guide an identical but displaced response—a response using the same distal musculature but at another location. Presumably the difference is that a response displaced in this way is necessarily an arbitrary or symbolic one—not one that would fall within the natural repertoire of a hard-wired visuomotor control system. Thus D.F. seems to be using a visual processing system dedicated for motor control, which can only come into play when she carries out 'natural' goal-directed actions.

There are temporal as well as spatial limits on D.F.'s ability to drive her motor behaviour visually. After showing her a rectangular block, Goodale *et al.* (1994a) asked D.F. to delay for either two or 30 seconds with eyes closed, before allowing her to reach out as if to grasp it. Even after a 30 second delay, the preparatory grip size of normal subjects still correlated well with the object width. In D.F., however, all evidence of grip scaling during her reaches had evaporated after a delay of even two seconds. This failure was not due to a general impairment in short-term memory. Instead, it seems that a delayed reach is no longer a 'natural' movement, and indeed this is so even for normal subjects. A detailed kinematic analysis of the control subjects showed that they moved their hand abnormally in the delay conditions, as if their apparently normal grip scaling was actually generated 'artificially' by imagining the object and then 'pantomiming' the grasp. This pantomiming strategy would not have been open to D.F., since she could not have generated a visual image of something that she failed to perceive in the first place. Presumably the visual processing that *is* available to her has a very short time constant, because it is designed to deal with present or imminent states of the visual world, and to disregard past states that may no longer be relevant (for example as a result of self-motion).

3. APPREHENSION THROUGH PREHENSION

Having lived with her profound visual disability for several years, it is not surprising that as an intelligent person, D.F. has developed strategies to help her to cope with the everyday world. For example, Murphy *et al.* (1996) have suggested that D.F. might be able to perform above chance in discriminating squares from the more elongated rectangles by making ocular scanning movements along (say) the horizontal extent of each shape and thereby cueing herself kinaesthetically. But they discovered that D.F. did best of all when asked to *reach out and pick up* one of the shapes (say the square), rather than just to say which was which. Closer examination of D.F.'s behaviour revealed that

she often made a partial movement towards one of the blocks before then correcting herself and directing her hand to the other. The proportion of her *initial* reaches that were made in the correct direction was significantly lower than her final choice performance; in fact it was at a level indistinguishable from her verbal judgements. The authors argued that D.F. might have been using her own anticipatory grip size to tell her which object she was approaching, so that if it was the wrong one she could then change direction.

This result significantly extends previous reports of self-cueing in patients with visual form agnosia (Goldstein & Gelb 1918; Landis *et al.* 1982). Those earlier patients spontaneously developed tracing habits with the hand or eye which allowed them to identify simple shapes and letters that they were otherwise unable to recognize. Evidently they too could monitor their own actions kinaesthetically so that a non-visual route to recognition could be used.

We have recently observed an even more impressive self-cueing phenomenon in D.F. (Dijkerman & Milner 1997). We asked her simply to copy an oriented straight line presented to her on a circular piece of paper, by drawing it on another piece of paper. Her performance was unexpectedly good, with a highly significant majority of her responses lying within 45 degrees of the correct orientation (figure 1 and figure 2, top). But she required latencies of several seconds to perform the task, and she confessed when questioned afterwards that on each trial she had *imagined* herself tracing over the original line, prior to drawing her copy. We therefore asked D.F. to repeat the copying task under conditions where she was allowed no time for such self-cueing (figure 2, bottom). It is obvious that she performed no better than chance, and in fact her errors were statistically no more likely to be within ± 45 degrees than beyond 45 degrees. We also found in separate tests that even without time constraint her copying would fall to chance if she was given a concurrent distracting task—either tapping the table with her other hand in an imaginary square, or counting backwards in twos.

These new observations take us into a qualitatively new realm of self-cueing in apperceptive agnosia. It seems that D.F. is not only able to monitor her own *overt* actions in order to derive information to help her make 'perceptual' discriminations (cf. Murphy *et al.* 1996), but that she can also monitor her internally generated *motor imagery* for the same purpose. This is an intriguing notion, since it implies that *non-visual* imagery—indeed imagery generated in response to a visual feature that was not consciously perceived—can be used to inform a 'perceptual' choice.

D.F. told us that she had to keep her pencil on the paper while forming her motor image, and then to make an immediate drawing before the image faded. This fits well with the evidence summarized in the previous section on delayed grasping (Goodale *et al.* 1994a). Both are consistent with the idea that D.F. is using a visuomotor system designed for on-line control, and one which therefore has a very brief memory span. It also fits well with recent theoretical approaches which assume that motor imagery is

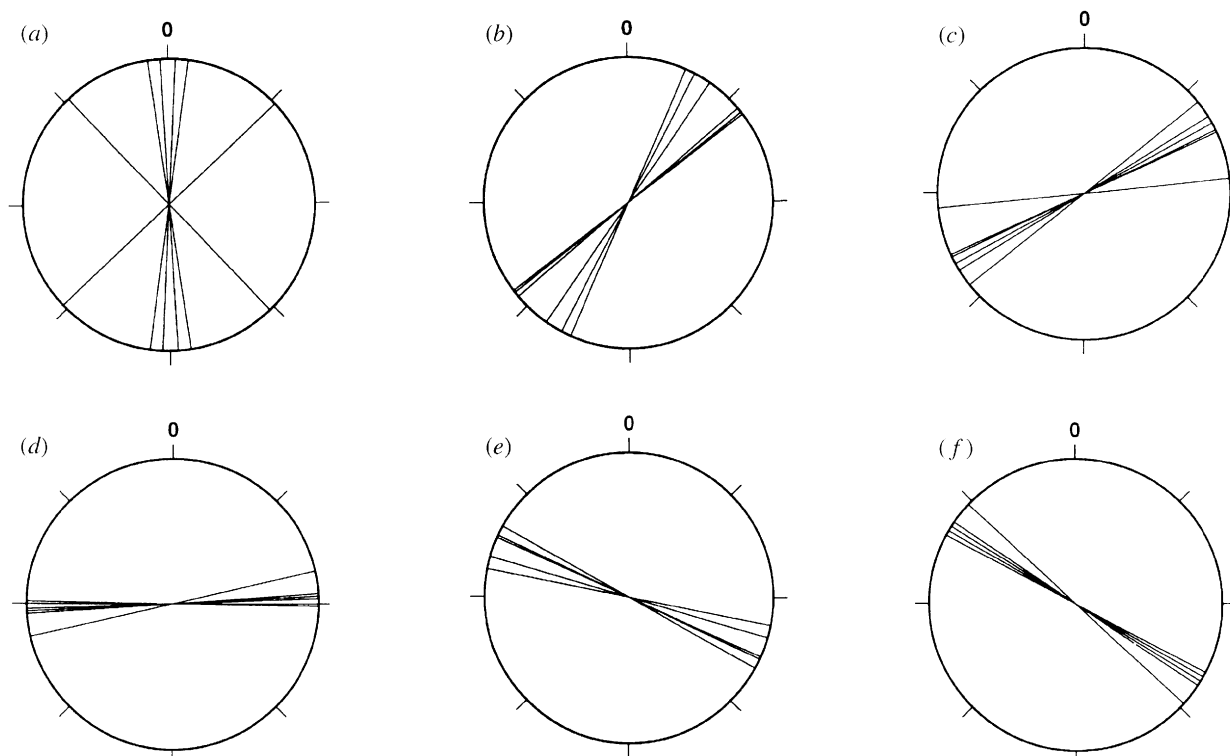


Figure 1. Polar plots of the responses of patient D.F. when asked to draw a copy of an oriented line in each of six orientations.

mediated by systems designed for the preparation of motor acts (Jeannerod 1994), an assumption that is supported by recent PET studies of normal individuals. For example, Grafton *et al.* (1996a) found activation in the parietal lobe and secondary motor areas (but no significant activation of ventral structures in occipitotemporal cortex) in volunteers who were shown a series of cylinders and asked to imagine grasping them. These critical structures appear to be intact in D.F.

It follows that D.F.'s above-chance scores in other avowedly 'perceptual' tasks might be explicable in the same way. For example, she has been tested recently for her ability to discriminate the orientation of a square plaque tilted away from her in the depth dimension, either by reaching to grasp the plaque or by reproducing its orientation with a hand-held plaque (Dijkerman *et al.* 1996). Under binocular viewing conditions, D.F. orients her hand in the sagittal plane with an accuracy indistinguishable from control subjects when reaching to grasp the plaque (figure 3). The correlation drops under monocular conditions, perhaps because D.F. is reliant on posterior parietal coding systems that depend crucially on stereoscopic cues (Sakata *et al.* 1997). And as would be expected, D.F. also performs less well when asked to *match* the orientation of the target plaque in depth, her performance falling fully to chance under monocular conditions (figure 4). But interestingly, D.F. performs significantly above chance on the matching task when tested binocularly. Clearly we must therefore entertain the possibility that when matching, she imagines herself *grasping* the plaque, and translates the imagined tilt of her hand and forearm into an actual tilt of the hand-held plaque. Monocular conditions would

presumably impoverish this motor imagery, just as they reduce her overt grasping accuracy.

4. KINDS OF KNOWLEDGE

D.F. has no explicit knowledge (i.e. awareness) of the shapes and sizes that she is able to grasp by virtue of her remaining visual apparatus. And there is some evidence to suggest that this residual system possesses no 'knowledge' base derived from perceptual experience. For example, if D.F. is shown a household implement whose nature and function she fails to recognize, she can still pick it up quite proficiently; but the lack of recognition may cause her to grasp the object at the wrong end (Carey *et al.* 1996). Generally a normal individual's grasping behaviour will be determined by the 'semantics' of an object as well as by its physical structure. Presumably, our grasping of a familiar object is achieved by virtue of (i) a successful act of object recognition through the ventral stream of processing, leading to a retrieval of the object's functional semantics, which (ii) will determine in part the programming of an act of prehension by secondary motor systems. Not until after that point will (iii) the dorsal stream come into play, to ensure that the action is executed smoothly with the benefit of relevant information about the location, size, orientation, gross shape and motion of the object. I would argue that the dorsal stream has no need to be privy to the functional identity of the object in order to do this last job successfully.

According to the present interpretation, then, D.F.'s brain damage has uncovered a visual processing system (specifically the human dorsal stream) that can operate in relative isolation within the domains of

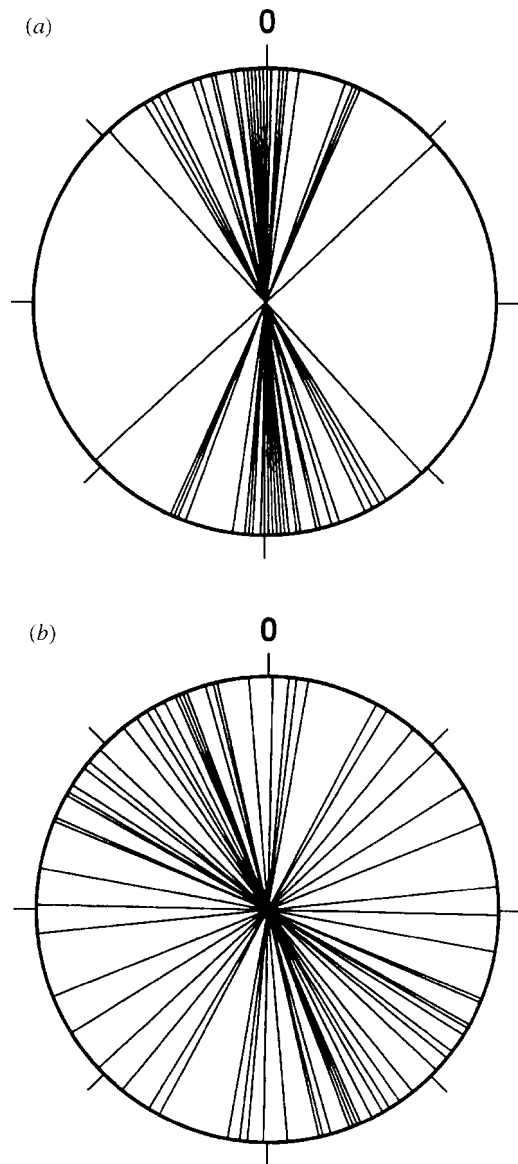


Figure 2. Top: summary polar plot of the data in figure 1, normalized to the vertical. Bottom: summary polar plot of the responses of patient D.F. when asked to make an *immediate* copy of an oriented line; data again normalized to the vertical.

size, shape and orientation. This interpretation is fully consistent with our knowledge of the functional properties of visually-responsive neurones within the monkey's dorsal stream (Milner & Goodale 1995; Sakata *et al.* 1997). This animal evidence, like the human evidence we can glean from studying D.F., is consistent with the idea that visual processing in the dorsal stream is bottom-up rather than top-down. This is not to deny that dorsal processing will guide actions that have been planned and set in train as a consequence of knowledge-based visual processing within the ventral stream.

I suggest that in providing visual guidance for our actions the dorsal stream acts in large part alone and independent of any knowledge base, and I interpret this in a broad sense to include what Gregory (1996, 1997) has called 'operating rules'. These rules include Gestalt laws of organization and perspective. To the extent that they depend on edges, such rules are

absent from D.F.'s visual experience. Thus she can not see depth represented through contour, though she is able to see depth through shading, which *is* present in her visual awareness (Humphrey *et al.* 1996). The idea that Gregory's 'operating rules' are not obeyed by the dorsal stream is consistent with several dissociations that have been demonstrated in normal observers faced with visual illusions. Gregory (1980, 1997) has argued over many years that higher-level visual illusions, including geometric illusions, deceive the perceptual system because the system makes (false) assumptions about the structure of the world based on prior knowledge (including operating rules). These include, for example, assumptions about perceptual stability and spatial constancy (Bridgeman *et al.* 1979, 1981; Wong & Mack 1981; Goodale *et al.* 1986). It seems that the dorsal system, by and large, is not deceived by these illusions, perhaps because evolution has taught it that a little knowledge can be quite literally a dangerous thing. Instead, it directs our saccadic eye movements and our hand movements to where a target really is, which is not always where our perceptual system tells us it is. Similarly, under appropriate circumstances geometric illusions can be seen to affect visually guided reaching (Gentilucci *et al.* 1996) and grasping (Agloti *et al.* 1995; Brenner & Smeets 1996) far less than they affect our perceptual judgements. We may perceive an object as bigger than it really is, but we open our finger-thumb grip veridically when reaching for it.

As already mentioned, visual processing via the ventral stream may access stored knowledge that will then inform the programming of actions. However, it is possible that this knowledge could differentially affect separate elements within an action sequence. One interesting example of stored knowledge is our internal metric relating sizes to weights, which determines our expectations when lifting objects (this knowledge itself gives rise to a well-known perceptual illusion). If it is through the ventral system that visual information about size gains access to this knowledge, and if a geometric illusion can deceive that system, then we could be tricked into miscalibrating our grip force when lifting an object we see. There is in fact evidence that such grip-force miscalibration does occur, in circumstances where observers are deceived about the size of solid objects under the influence of the Ponzo 'train-lines' illusion (Brenner & Smeets 1996). The evidence from that experiment also suggests, however, that the opening movements of the fingers prior to contact with the object are *not* miscalibrated. These results indicate that visual information can guide action in both a direct, perhaps hard-wired, way, which is not subject to illusions, but also in an indirect and malleable way which is. I would argue that the former route—the dorsal stream—is neither informed nor misinformed by top-down influences, while the latter—the ventral stream—is.

5. CONCLUSION

I am suggesting that D.F.'s visuomotor system (and *ex hypothesi* the primate dorsal stream of processing)

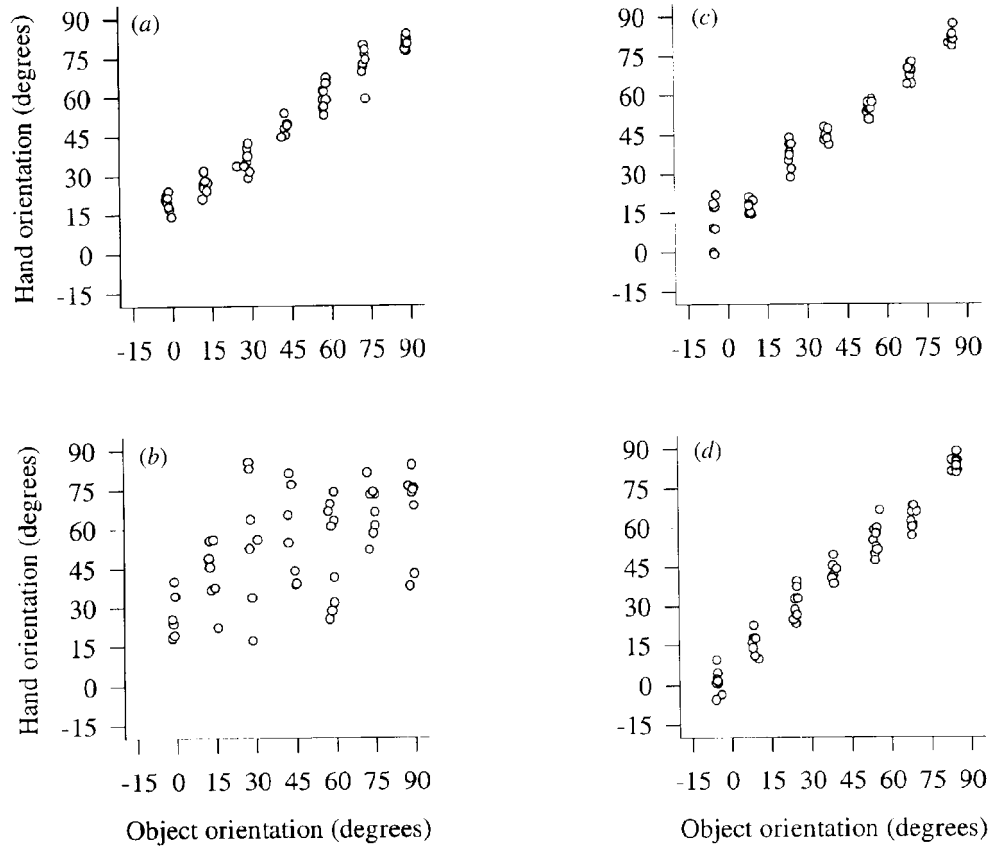


Figure 3. Correlation diagrams showing the performance of patient D.F. (left) and a typical normal control subject (right) on a task requiring the subject to grasp front-to-back a plaque tilted in depth. The orientation of the forefinger–thumb axis in the sagittal plane is plotted against the actual orientation of the target. Upper: binocular viewing conditions; lower: monocular viewing conditions.

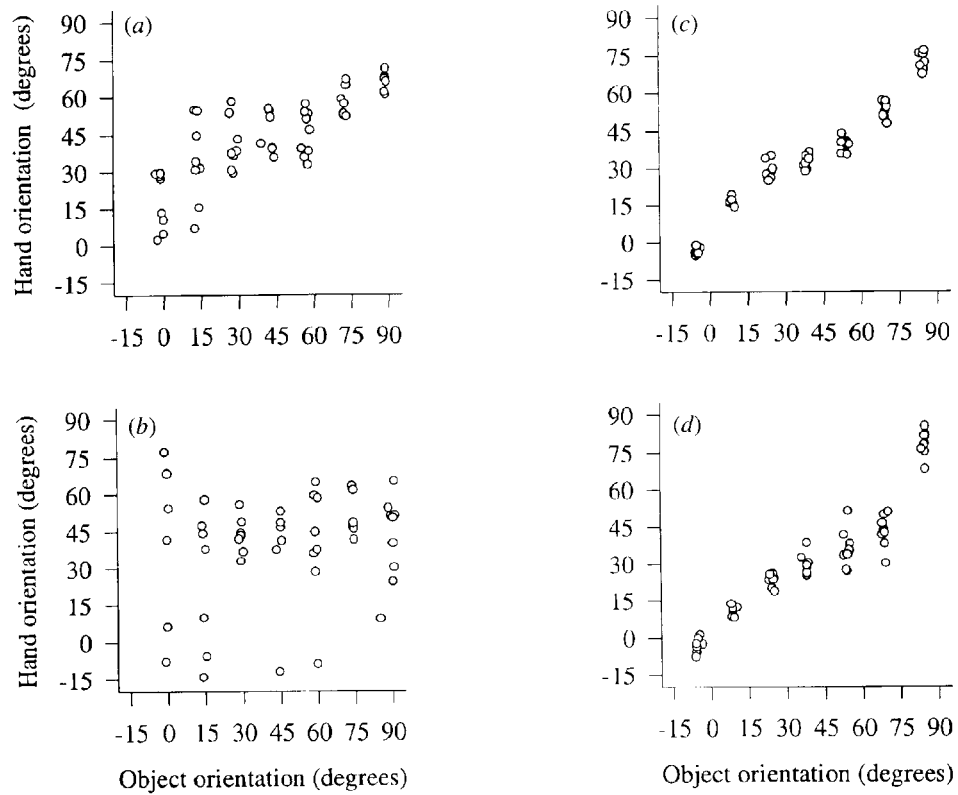


Figure 4. Correlation diagrams showing the performance of patient D.F. (left) and a typical normal control subject (right) on a task requiring the subject to *match* the orientation of a plaque oriented in depth, using a hand-held plaque. The orientation of the hand-held plaque in the sagittal plane is plotted against the orientation of the target plaque. Upper: binocular viewing conditions; lower: monocular viewing conditions.

not only operates (i) without yielding explicit knowledge of the visual information it processes, but also (ii) without the benefit of a stored knowledge base. These two propositions may be related, and not merely through a lexical accident of the English language. I tentatively suggest that (i) conscious awareness of what one sees is available only in association with visual processing within the higher reaches of the ventral stream (Milner 1995); and that (ii) these ventral-stream systems are specialized for the generation of abstract visual representations whose *raison d'être* is in part to provide a knowledge base for perception and recognition.

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