

## CRITICAL REVIEW

# The neuropsychology of object constancy

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### Abstract

There have been several proposals for the mechanism by which we are able to recognize an object across a number of viewpoints. Viewpoint-dependent accounts suggest that recognition may be based on an incremental transformation (e.g., mental rotation) strategy, while a variety of viewpoint-independent mechanisms for object recognition have also been proposed. Recent research in neurobiology, based on the two cortical visual systems account, suggest that the processes of viewpoint-dependent and viewpoint-independent object recognition may rely on separate anatomical regions, and that brain lesions may leave patients with selective access to particular types of representation. Evidence from a variety of neuropsychological disorders are reviewed to support the position that viewpoint-independent object recognition depends upon the integrity of occipitotemporal structures. In addition, it is suggested that viewpoint-dependent processes (perhaps depending on occipitoparietal structures) may supplement this primary system under nonoptimal circumstances. (*JINS*, 1997, 3, 288–298.)

**Keywords:** Object recognition, Two visual systems, Object constancy

## INTRODUCTION

A fundamental concern of the “later” stages of the object recognition process is the mechanism by which we are able to recognize an object across a number of viewpoints—often described as the problem of object constancy or stimulus equivalence. This issue is so central to models of object recognition that explaining the *entire* recognition process is often seen as largely a problem of devising a mechanism to solve this particular problem (Hummel & Biederman, 1992; Bulthoff et al., 1995). In an attempt to resolve this issue, a number of accounts of the recognition process have been developed (see Pinker, 1984; Biederman, 1987; Edelman & Bulthoff, 1992; Tanaka, 1993; Bulthoff et al., 1995; Vetter et al., 1995; Logothetis & Sheinberg, 1996 for reviews). The most theoretically useful dimension employed to classify theories of object constancy is the manner in which they deal with the critical issue of the orientation of the object with respect to the observer—more specifically, the relative *importance* of the observer's viewpoint in the recognition process (Takano, 1989; Tarr & Pinker, 1989; Edelman &

Bulthoff, 1992; Gibson & Peterson, 1994; Perrett et al., 1994; Logothetis & Sheinberg, 1996).

Theories that involve some form of mental rotation (Jolicoeur, 1985, 1990; Tarr & Pinker, 1989) assume that an image-like representation of an object in a nontypical orientation is transformed to a viewpoint that is more familiar to the observer. Once the image has been transformed to this known orientation, it can be matched to a stored description and recognized (a process that seems especially important on the first exposure to a novel exemplar of a known object; the *first trial* effect of Jolicoeur, 1985). Such accounts of object recognition rely heavily on a representation of the object that is derived from the perspective of the observer: a *viewer-centered* description (Marr, 1982). The prototypical example is Jolicoeur's (1985, 1990) model, which involves the mental rotation of an image of the object from its observed view to its canonical orientation. In such cases, where the initial viewpoint is of critical importance, the recognition process is regarded as *viewpoint-dependent* (Takano, 1989; Tarr & Pinker, 1989; Gibson & Peterson, 1994). Other models having a mental rotation component (e.g., Ullman, 1989), including those that involve mental rotation to the nearest *previously seen* orientation (Tarr & Pinker, 1989), share a similar theoretical basis.

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Other approaches deal with the problem of object constancy in a manner that is indifferent (except, perhaps, under extreme circumstances) to the object's orientation. Marr's (1982) theory is the best known of such accounts, involving a stage that requires access to a store of *object-centered* representations—which are independent of the viewpoint from which the object is observed. In Marr's scheme such a description is based on the position of component parts relative to the principal axis of the object (Marr & Nishihara, 1978; Marr, 1982). Thus, even when the observer's viewpoint changes, the central representation of the object remains the same. Because an object-centered representation does not change with viewpoint, and because the development of such a description is a mandatory stage in Marr's (1982) theory, Marr's account offers a *viewpoint-independent* route to object recognition (Takano, 1989; Tarr & Pinker, 1989; Gibson & Peterson, 1994). The influential model proposed by Biederman (1987), in which an object is described by the relative position of a limited number of elementary component parts, offers another viewpoint-independent solution to the problem. Thus, viewpoint-dependent and viewpoint-independent representations offer competing solutions to the problem of recognition across multiple views.

In recent years, it has been possible to bring neurobiological evidence to bear on the problem of object constancy. The traditional neuropsychological understanding of the breakdown of object recognition has been one of a bewildering variety of disorders, almost all of which had been demonstrated (by double dissociation techniques) to be functionally independent (Damasio et al., 1989; McCarthy & Warrington, 1990; De Haan & Newcombe, 1992; Humphreys & Riddoch, 1993; Farah & Ratcliff, 1994). The general category of object recognition disorders appears to fractionate into a variety of object agnosias, including specialized losses of face and word recognition.

Classical neuropsychology also describes a variety of neuropsychological disorders that are more clearly *spatial* than perceptual, but which also have a bearing on the nature of representation in the visual system (De Renzi, 1982; Newcombe & Ratcliffe, 1989; McCarthy & Warrington, 1990; Ellis & Young, 1993; Halligan & Marshall, 1993). These include loss of topographical orientation and impairments in domains such as attention, reaching, and voluntary gaze. In many patients with such disorders, object recognition (at least as assessed clinically) seems relatively intact.

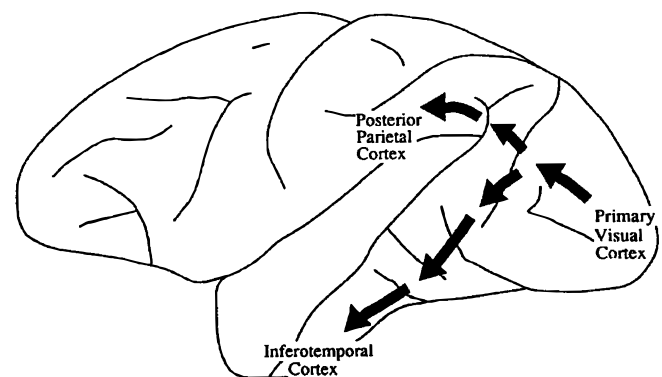
An influential attempt to unify perceptual and spatial disorders in a model that might account for the neuropsychological findings (as well as findings with normal subjects), has grown out of the idea that there are two "cortical visual systems"—specialized for spatial and object perception. The original formulation was presented by Ungerleider & Mishkin (1982), based on work in monkeys (although see Grüsser & Landis, 1991, for some precursors in the German neurological literature), and had few points of contact with the work on cognitive models of the recognition process in normal humans. More recently, the two visual systems account

has been highly influential in relating work on the neural substrate of recognition to issues of object representation (Kosslyn et al., 1990, 1994; Biederman & Cooper, 1992; Farah, 1992; McCarthy, 1993; Milner & Goodale, 1993; Haxby et al., 1994).

## Two Cortical Visual Systems

The key hypothesis of the Ungerleider and Mishkin (1982) account can be summarized by the simple idea that the many areas of extrastriate cortex are organized into two relatively independent pathways. One system (the so-called dorsal stream) runs from occipital to parietal cortex, and is primarily concerned with the perception of spatial information, in particular the spatial location of the object. The second (ventral stream) system runs from occipital to inferotemporal cortex, and is concerned with the recognition of objects as members of a familiar class (see Figure 1).

One problem with Ungerleider and Mishkin's (1982) scheme is the fact that the two visual systems hypothesis is a generalization about the *monkey* visual system, and cannot be applied indiscriminately to human vision. This seems particularly germane because it is claimed that the human homologue of several key areas of the ventral and dorsal systems have yet to be identified or clearly specified (Eidelberg & Galaburda, 1984; Ungerleider & Haxby, 1994; see also Courtney et al., 1996). The most problematic claim would be that there is *no* monkey homologue for the regions of recent evolutionary development of great importance to human visual cognition, in particular the human inferior parietal lobule. However, it has recently been suggested that STP (in the monkey superior temporal cortex) may be the monkey homologue of the human inferior parietal lobule (Morel & Bullier, 1990; Watson et al., 1994; Milner, 1995). It has also been suggested that, in humans, the inferior parietal lobule is involved in the "binding" of information from the two visual systems (Watson et al., 1994; see Boussaoud et al., 1990, and Morel & Bullier, 1990 for similar suggestions about macaque visual cortex).



**Fig. 1.** The two streams of visual processing in macaque monkey visual cortex, described by Ungerleider & Mishkin (1982). Reproduced with permission from Milner & Goodale (1995).

## Evidence From Human Neuropsychology

In spite of these concerns about generalizing from monkeys to humans, the two visual systems approach appears to be consistent with the large body of knowledge acquired in human neuropsychology. Lesions of the temporal cortex, particularly on the ventral surface of the temporal lobe, produce disorders of object recognition (Kertesz, 1983; Damasio et al., 1989) that (arguably) are similar to the deficits seen after experimental lesions of inferotemporal cortex in the monkey (Gross, 1973; Dean, 1982; Walsh & Butler, 1996). While the issue of the laterality of lesion necessary to produce such disorders remains contentious (see Farah, 1990), there is a great deal of converging evidence for an occipitotemporal lesion site in prosopagnosia, and in some cases of visual agnosia (Kertesz, 1983; Damasio et al., 1989; Grossman et al., 1996). Similarly, parietal lesions result in disorders that may be broadly characterized as “spatial.” These include visuospatial neglect, the spatial aspects of drawing and constructional tasks, peripersonal spatial disorders such as left–right orientation and ideomotor apraxia, disorders of reaching (optic ataxia), and voluntary gaze (ocular apraxia) (Rondot et al., 1977; De Renzi, 1982; Kertesz, 1983; Perenin & Vighetto, 1988; Newcombe & Ratcliff, 1989). Thus, to a first approximation, the Ungerleider and Mishkin (1982) model seems an accurate account of the gross differences between occipitoparietal and occipitotemporal neuropsychological syndromes.

More recent work has suggested some points of contact between the two cortical visual systems model and work within cognitive psychology. Within the object recognition domain itself, Kosslyn et al. (1990, 1994) have argued that there are two separate mechanisms by which object recognition can be achieved within the ventral stream. The most important of these is a system that is viewpoint-independent, perhaps operating along the lines suggested by Lowe (1985) and Biederman (1987), which involves the development of a viewpoint-invariant structural description of the object. Biederman’s (1987) scheme proposes such a description of an object based on object primitives known as “geons,” which are simple (typically symmetrical) geometric object components such as cylinders and blocks. Kosslyn et al. (1990, 1994) do not commit themselves to the geon concept, which might well be substituted with another viewpoint-independent account, such as that of Marr (1982). Nevertheless, Kosslyn et al.’s (1990, 1994) scheme suggests that the *primary* mechanism by which the ventral stream achieves object recognition is viewpoint-independent. It is notable that Kosslyn et al. (1990, 1994) offer the alternative of feature-based recognition, also carried out within the ventral stream, which may be sufficient for recognition under certain circumstances. Again, such a feature-based system might be presumed to operate by viewpoint-independent means (see review by Biederman & Gerhardstein, 1993, for similar proposals).

Kosslyn et al.’s (1990, 1994) argument clearly offers a great deal more of relevance to the present discussion than

a simple version of the two visual systems theory of Ungerleider and Mishkin (1982), offering a point of contact between cognitive accounts of the recognition process and their neural basis. Another line of research has also reached similar conclusions.

## Milner and Goodale’s Account

In an influential series of papers, Milner and Goodale (1993; 1995; Goodale et al., 1991; Goodale & Milner, 1992; Goodale, 1993; Goodale et al., 1994) have suggested a substantial reinterpretation of the Ungerleider and Mishkin (1982) two visual systems account. Milner and Goodale (1993) agree that there *is* strong evidence for separate dorsal and ventral systems of processing in the monkey and human visual system. However, they suggest that the Ungerleider and Mishkin (1982) description of the properties of the two systems (i.e., between the process of the recognition and the spatial location of the object) does *not* appropriately describe the differences in function between these systems. Specifically, they claim that, although the ventral stream appears to be involved in object recognition, the dorsal stream appears to be more directly tied to visuo-motor processes than to characterizing the spatial location of an object. Milner and Goodale also acknowledge the possibility that *inferior* parietal regions in humans may play a role in many visuospatial cognitive tasks, which could require the use of information from both streams.

Much of their evidence in support of this position comes from a review of the human neuropsychology literature (Goodale & Milner, 1992; Milner & Goodale, 1993; Goodale et al., 1994) and some more recent evidence from patients whom they have investigated. For example, the visual form agnostic D.F. was unable to describe the size, shape, and orientation of visual targets, yet was able to use the same types of visual information to guide her motor responses. The opposite pattern has been demonstrated in a patient with optic ataxia (R.V.), who could describe the shape of objects but could not accurately reach for them (Goodale et al., 1994). This dissociation cannot be easily accommodated within the Ungerleider and Mishkin (1982) account. In the Milner and Goodale (1993; Goodale & Milner, 1992) theory, different forms of *representation* are employed by the visuomotor and object recognition systems, with the ventral (object recognition) stream utilizing “object-centered” (i.e., viewpoint-independent) codes, and the visuomotor systems of the dorsal stream employing viewer-centered codes. Of course, other perceptual constancies such as size and position may also map onto the dorsal–ventral dichotomy (e.g., Cooper et al., 1992; Ito et al., 1995; Wachsmuth, 1995), but will not be considered further in this review.

The argument proposed by Milner and Goodale (1993; Goodale & Milner, 1992) offers some predictions about the types of neuropsychological disorder that might be seen in circumstances where patients have access to only a single form of representation. Milner and Goodale (1993) have suggested that patients with isolated viewer-centered coding

might perform poorly on tasks that required knowledge of an object's three-dimensional structure, or involved manipulation of images in a third (depth) dimension. Alternatively, in the case of isolated access to the object-centered code, object recognition would be intact, but the patient would be particularly challenged on tasks that required the discrimination of attributes that cannot be coded in this type of structural description—namely mirror-images and orientation.

The proposals of Milner and Goodale (1993; Goodale & Milner, 1992), relating to the anatomical basis of viewer- and object-centered representations, links directly to theories of object recognition. As discussed above, viewpoint-independent recognition requires an object-centered code, meaning that the Milner and Goodale (1993; Goodale & Milner, 1992) argument relating object-centered representations to the ventral stream is effectively the same argument proposed by Kosslyn et al. (1990, 1994) that viewpoint-independent object recognition is achieved by the ventral stream.

The claim that object recognition is achieved by viewpoint-independent means within the structures of the occipitotemporal region has a strong bearing on the importance of the various cognitive accounts of the recognition process reviewed earlier. Although neither Kosslyn et al. (1990, 1994) nor Milner and Goodale (1995), explicitly discuss this issue, this position appears to imply a minor, or nonexistent, role for the viewpoint-dependent accounts such as those of Jolicoeur (1985, 1990) and Tarr and Pinker (1989) within the recognition process of the ventral stream. This position is surprising, given extensive evidence that the recognition process, at least under certain circumstances, appears to employ such viewpoint-dependent mechanisms (Tarr & Pinker, 1989; Jolicoeur, 1990; Bulthoff et al., 1995). The situation might be clarified when consensus has been reached regarding specific neural correlates for object recognition using a viewpoint-dependent mechanism (e.g., Logothetis & Pauls, 1996; Perrett et al., in press).

In relation to this point, there is other evidence in human neuropsychology that bears on the issue of the neural correlates of viewer- and object-centered representations that has not previously been directly discussed in relation to the two visual systems account. These data relate to the difficult issue of the role of *parietal* cortex in object recognition (Warrington & James, 1967; Warrington & Taylor, 1973; Jeannerod et al., 1995; Carey et al., 1996).

The only possible role identified by Kosslyn et al. (1990, 1994) for viewpoint-dependent recognition is in circumstances in which the primary routes to recognition (by a viewpoint-independent description or feature-based analysis) fail to strongly implicate a single object. Under these circumstances, Kosslyn et al. (1990, 1994) suggest the orientation information associated with the image (as well as other classes of information, such as scale and position) might be “adjusted” in the dorsal stream until a better match is found between the image and existing memory representations. Kosslyn et al. (1990, 1994) are not clear about the

nature of dorsal stream involvement under such circumstances. They stress the importance of top-down activation, and alteration of the position and resolution of an “attention window” under these circumstances, although they do not directly deal with the issue of mental rotation. However, taken together with the Milner and Goodale (1993) argument that viewer-centered descriptions are coded in the dorsal system, this explanation might offer a role for viewpoint-dependent process in the recognition of objects. The arguments imply that the dorsal stream might be used as an *optional resource* under circumstances where recognition is not immediately successful. This sort of evidence may explain why the effects of picture-plane misorientation on object recognition are greatest under nonoptimal circumstances, such as the initial exposure to a novel exemplar of a known object (Jolicoeur, 1985).

Several classes of neuropsychological evidence will be reviewed to support the position that parietal cortex *may* have a role in object recognition. Some of these data relate to the possibility that viewpoint-dependent recognition processes are associated with parietal cortex—in the case of the “unusual views” deficit, and in patients with disorders of mental rotation. These possibilities are of interest because they are associated with (right) parietal lesion sites. This would represent an instance of a lesion of the parietal cortex resulting in a recognition disorder. This would be a challenge to the strong version of the two visual systems account, as it involved a parietal lobe component to object recognition. Finally, some unusual cases (after parietal lobe lesions) of loss of knowledge of object orientation and mirror-image discrimination are reviewed, which may be evidence for isolated access to viewpoint-independent image representations in the ventral stream.

### The Unusual Views Deficit

Patients with the unusual views deficit can successfully identify objects when they are presented from conventional viewpoints, but fail to recognize objects when viewed from perspectives classified as unusual (see Figure 2; Warrington & Taylor, 1973, 1978; Warrington & James, 1986; Landis et al., 1988). Such views of objects may be relatively common (i.e., a bucket viewed from above), but generally do not offer adequate views of many important aspects of object structure, and all such views are noncanonical (Palmer et al., 1981). Several hypotheses have been proposed to explain this deficit. The first is that these patients have a difficulty in establishing the principal axis of an object when it is foreshortened (Marr & Nishihara, 1978; Marr, 1982). A second suggestion is that the deficit is due to a difficulty in identifying the critical features of the object, which become occluded when an object is seen from an unusual perspective (Warrington & James, 1986). A role for both of these accounts has been suggested by the finding that, in a small group of visually agnostic patients, either class of disorder may be the cause of the object recognition deficit (Humphreys & Riddoch, 1984). Four of these 5 patients per-

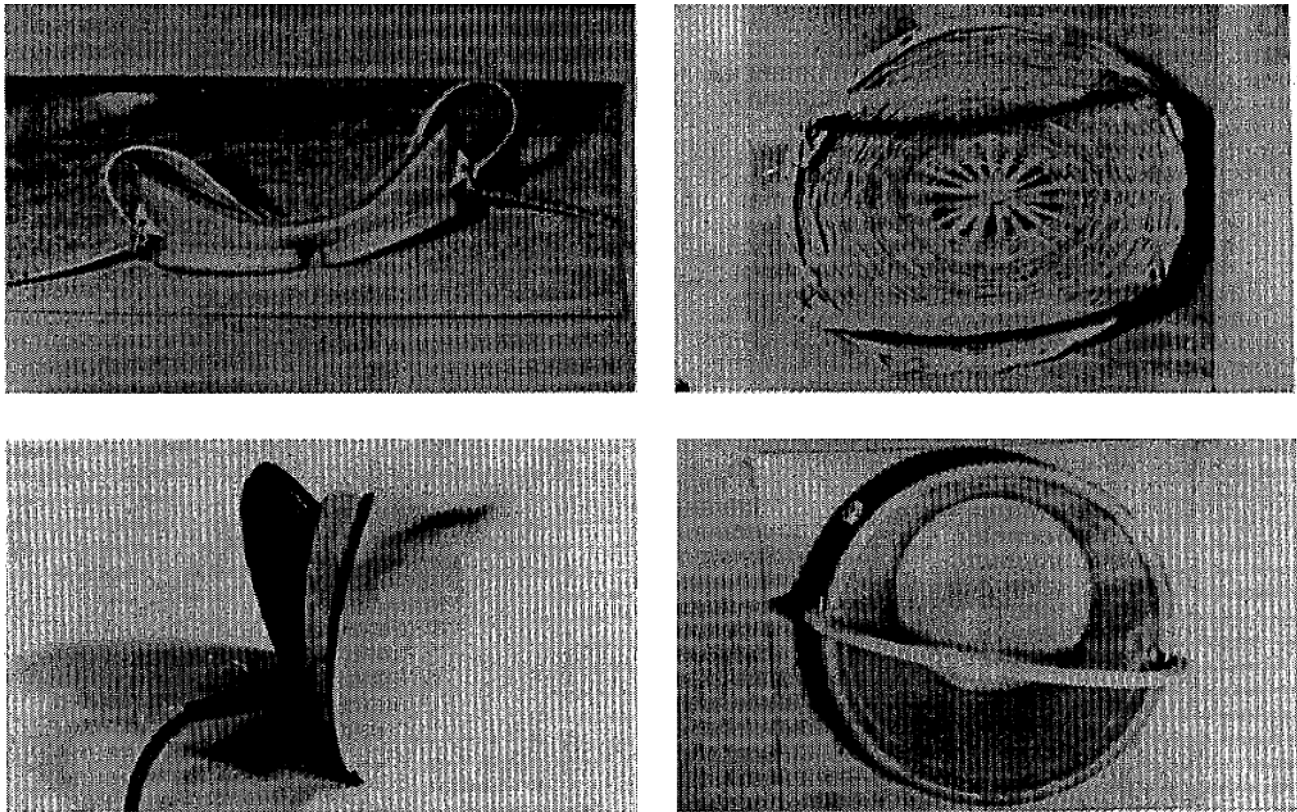


Fig. 2. Examples from the “unusual views” test. Reproduced with permission from McCarthy & Warrington (1990).

formed poorly when the principal axis was foreshortened, although recognition was not affected by the occlusion of features. In a final patient, performance was poor when the critical features could not be seen, but recognition was unaffected by manipulations of the principal axis. Thus, Humphreys and Riddoch (1984) suggest that there are two routes to object constancy: via axes or features.

As discussed above, both the axis-based and feature-based accounts of recognition have been associated with the viewpoint-independent recognition systems of the ventral stream (Kosslyn et al., 1990, 1994; Milner & Goodale, 1993). On such accounts, the ability to derive axis or feature information should be lost after lesions to the occipitotemporal lobes. However, the unusual views deficit appears to follow after an inferior *parietal* lobe lesion (usually on the right; Warrington & Taylor, 1973, 1978; Warrington & James, 1986). Why should a lesion to a brain region that subserves visuospatial abilities have such an effect on object recognition, when viewer-centered spatial information is generally unimportant to recognition? Paradoxically, information about the precise location of object components relative to the observer might be extremely useful under unusual view circumstances, perhaps to *allow* the observer to establish that the principal axis of the object has been foreshortened—and such information is carried in the dorsal system. Notably, however, it has been argued that the *inferior* parietal cortex should not be considered part of the dorsal stream,

on anatomical and neuropsychological grounds (e.g., Milner, 1995). This paradox might be resolved given the suggestion that the inferior parietal lobule (the lesion site in the unusual views deficit) might be involved in *binding* the viewer-centered and viewpoint-independent information derived from the dorsal and ventral systems respectively (Friedman-Hill et al., 1995; Morel & Bullier, 1990; McCarthy, 1993; Milner, 1995; Watson et al., 1994).

Thus, we suggest that the viewpoint-independent (ventral) system might be successful in recognizing objects under optimal viewing circumstances, though it might require further viewer-centered information under nonoptimal conditions. In this account, the inferior parietal lobule, which may have access to both classes of information, would be well placed to provide such data to ventral structures, and a lesion to this region would result in an unusual views deficit. This argument implies that the parietal lobe, in isolation, is not capable of recognizing objects. However, it can play a *role* in object recognition in circumstances where information about the position of the observer in relation to object components is crucial.

This argument does not explain the fact that such patients also have difficulty with stimuli involving overlapping drawings, employing unusual lighting, involving fragmentation of the stimulus, or restricting the stimulus to a silhouette (see Warrington & James, 1986, for a review). The effects of such manipulations on the performance of these neuro-

logical patients suggest some role for the right parietal lobe in a wider variety of image manipulation and reorganization strategies. These might, for example, be used to clean up a degraded image during object recognition (McCarthy, 1993) as part of a process of visual problem-solving (Farah, 1990). This process presumably relies on visuospatial cognitive abilities, which (as noted above) may be more closely associated with the structures of the inferior parietal lobe than the visuomotor systems of the classical dorsal stream (Milner & Goodale, 1995).

Another explanation of the unusual views deficit is that of Layman and Greene (1988), who suggested that these patients had lost their ability to mentally rotate images. This argument was based on the gross anatomical association between loss of mental rotation and the unusual views deficit—as both tend to follow from right posterior brain lesions (Layman and Greene, 1988). This suggestion is somewhat at variance with a single-case dissociation found by Farah and Hammond (1988), whose patient was able to perform orientation-invariant object recognition, but failed a number of tasks of mental rotation. We have investigated a patient (A.S.) who shows the reverse dissociation—impaired performance in the recognition of misoriented objects, with good performance on mental rotation tasks (Turnbull & McCarthy, 1996b).

While the patient of Farah and Hammond (1988) appears to show that mental rotation is not the *only* means by which a misoriented object is recognized, this does not imply that mental rotation has *no* role in the recognition process. Mental rotation may be another optional resource, to be used when more direct viewpoint-independent mechanisms fail. As discussed above, the cognitive psychology literature on mental rotation (Jolicoeur, 1985, 1990; Tarr & Pinker, 1989), suggests that viewpoint-dependent recognition would be based on a viewer-centered representation. Thus, in the account of Milner and Goodale (1993) it might be expected that such a system would operate in the parietal lobe. This possibility is investigated in the following section.

### Loss of Mental Rotation After Brain Injury

The vast majority of neuropsychological studies on mental rotation have been in the comparison of the performance of groups of brain-damaged patients. These studies have generally involved comparing the deficits of patients with lesions in large anatomical regions, in particular the left–right or anterior–posterior dimensions (De Renzi & Faglioni, 1967; Butters et al., 1970; Butters & Barton, 1970; Ratcliff, 1979; Kim et al., 1984; Mehta et al., 1987; Ditunno & Mann, 1990). Unfortunately, such group studies have not compared mental rotation abilities after lesions to parietal or temporal lobe structures.

Some more pertinent anatomical data come from case studies. L.H., the patient of Farah et al. (1988) had bilateral occipitotemporal lesions, leaving the parietal lobes intact. Consistent with this lesion site the patient had a profound visual recognition deficit for both faces and common objects.

L.H.'s deficit extended into the domain of visual imagery (Farah et al., 1988), where he was impaired at providing information about object properties such as color, shape, and relative size. However, he had above average mental rotation abilities, as assessed on letter and Shepard and Metzler (1971) type figure-rotation tasks (Farah et al., 1988).

A second patient (R.T.; Farah & Hammond, 1988) had extensive frontoparietal lesions in the right hemisphere, partly extending into the lateral surface of the right temporal lobe. Consistent with a more parietal site of pathology, R.T. had poor constructional abilities, and had recovered from a severe hemispatial neglect. He performed below control levels on three tasks of mental rotation, including the Ratcliff (1979) manikin task (although not including the Shepard and Metzler (1971) tasks administered to L.H.). In contrast, R.T. showed no disturbances in reading, nor in recognizing people or real objects (although he was mildly impaired at recognizing line drawings). He also showed no decrement in performance when he was required to recognize inverted objects or read inverted words. Thus, R.T. had the obverse pattern of dissociation to that seen in L.H. (Farah et al., 1988), showing normal visual imagery for object properties, but having a profound impairment on several tasks of mental rotation (Farah & Hammond, 1988). More recently, Morton & Morris (1995) described a patient (M.G.) with poor mental rotation ability (as assessed by Shepard & Metzler's task, Ratcliff's manikin task, and the Flags Test) with intact object recognition (including unusual views). M.G. had an occipitoparietal lesion after a cerebrovascular accident in her left hemisphere.

These investigations into the neuropsychology of mental rotation suggest that a profound loss of object recognition after temporal lobe lesions *can* coexist with intact mental rotation abilities. Further, a parietal lobe lesion can severely disrupt the ability to perform mental rotation while sparing the ability to recognize objects, even when they are inverted (a simplified case of recognition across multiple viewpoints). This is consistent with the claim that the viewer-centered representations required for the performance of mental rotation are not coded in the ventral stream (Goodale & Milner, 1992; Milner & Goodale, 1993) and that such a strategy is used in the recognition process only when viewer-centered information is required because the more "direct" route of viewpoint-independent recognition has insufficient information for its usual processes (Kosslyn et al., 1990, 1994). Thus, mental rotation would be employed as an optional resource, which would occur under circumstances where recognition was not immediately successful—perhaps on the first exposure to a new exemplar (Jolicoeur, 1985), or under unusual views conditions. Given the available lesion evidence and recent theories regarding inferior parietal cortex, it seems plausible that this region plays a major role in visuospatial cognitive operations including mental rotation.

However, a recent report by Cohen et al. (1996) is at odds with this suggestion: They found evidence for *superior* parietal activation in subjects performing mental rotation. Bonda et al. (1995) and Parsons et al. (1995) report supe-

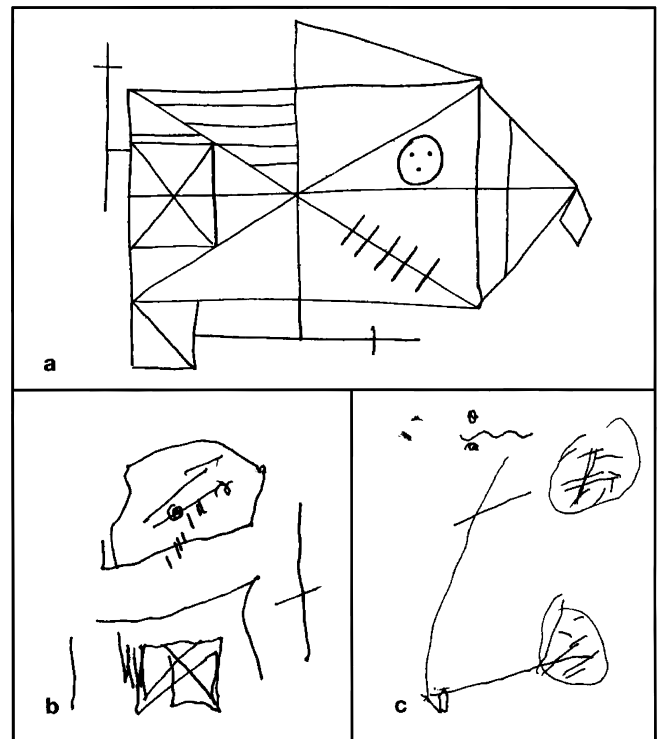
rior and inferior parietal activation using tasks that included a mental rotation component (see also Alivisatos & Petrides, 1997; Tagaris et al., 1996). Clearly additional experiments may be required to disentangle some of these discrepancies. As noted by Milner and Goodale (1995), it is fairly crucial to ensure that differential eye movement patterns do not occur in experimental and control conditions in imaging studies, if it is claimed that superior parietal activation is a consequence of visuospatial or visuo-cognitive processing *per se*.

### Spontaneous Rotation and Mirror-Image Discrimination

There are other neuropsychological disorders that are not generally cited in the debate on viewpoint-independent object recognition. The first relates to a neuropsychological sign previously referred to as spontaneous rotation (see Royer & Holland, 1975 for review). An example was reported by Solms et al. (1988) whose patient, W.B., made substantial errors of orientation on a number of tasks. He frequently copied drawings accurately but rotated them relative to the original (the Rey Complex Figure was usually rotated through 90°, onto its base, or through 180°). He also failed orientation-dependent letter identification tasks (e.g., discriminating “p” from “d”), and made structurally correct, but orthogonally rotated, responses on a number of other tests.

We have recently described similar patients, L.G. (Turnbull et al., 1995), and N.L. and S.C. (Turnbull et al., 1997), who also appeared to lack knowledge of the upright canonical orientation of objects (see Figure 3). For example, in a series of experiments it was possible to show that L.G.’s deficit also involved loss of the knowledge of the orientation of known objects, such as a chair and a bicycle (Turnbull et al., 1995)—a disorder that might be described as an agnosia for object orientation. Critically, L.G. was able to name objects for which she could not provide the correct upright canonical orientation, suggesting that she had some form of viewpoint-independent object recognition. It is also notable that W.B. was also reported to have had clinically intact object recognition, though Solms et al. (1988) did not assess his recognition abilities for the objects that he rotated. This apparent dissociation between the ability to recognize objects and knowledge of their upright canonical orientation would be consistent with an argument in which such patients had lost the viewer-centered descriptions necessary to accurately judge object orientation (as a result of parietal lobe lesions), though they retained access to viewpoint-independent descriptions of the object necessary for recognition (see Turnbull et al., 1995; Turnbull et al., 1997, for more discussion of this point).

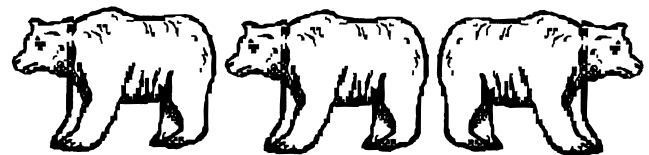
Another neuropsychological deficit that may well be related to the issue of viewpoint-independent object recognition is the inability of some patients to discriminate between mirror-image objects (Riddoch & Humphreys, 1988; Gold et al., 1995; Turnbull & McCarthy, 1996a; for a review of



**Fig. 3.** L.G.’s copy (b) of the Rey Figure (a). Note that her copy appears to be rotated by 90°, as does her spontaneous drawing of a bicycle (c). Reproduced with permission from Turnbull et al. (1995).

the relevant animal lesion literature, see Walsh & Butler, 1996). These patients failed on a number of tasks that required the discrimination of objects that differ in the left–right dimension, though R.J., the patient reported by Turnbull & McCarthy (1996a), could perform mirror-image *word* discriminations, while failing to distinguish between mirror-image drawings of objects (see Figure 4). However, the patients could perform tasks on which the stimuli differed on the up–down dimension.

Based on the argument presented above, patients showing spontaneous rotation and mirror-image discrimination deficits should have occipitoparietal lesion sites, leaving the occipitotemporal structures (subserving viewpoint-independent recognition) intact. Some of the cases have clear-cut parietal lesions (e.g., Turnbull & McCarthy, 1996a). How-



**Fig. 4.** Patient R.J. could not select the odd-one-out from this and similar stimuli. Reproduced with permission from Turnbull & McCarthy (1996).

ever, the lesion sites in these cases are not always so easy to interpret in terms of the two visual systems account (Milner & Goodale, 1995). For example, several cases (Riddoch & Humphreys, 1988; Turnbull et al., 1995) had largely parietal lesions that also involved the temporal lobe, and some (Turnbull et al., 1997) involved large middle cerebral artery lesions with similar problems of localization. In such instances, involvement of the ventral stream cannot be excluded (though the structures of the inferior temporal lobe were clearly quite distant from the main focus of the lesion, and the patients invariably showed a number of visuospatial deficits, rather than disorders of object recognition). Finally, W.B.'s lesion (Solms et al., 1988) was restricted to the *frontal* lobes, rather than involving the posterior brain regions, which have been the focus of interest in the two visual systems account. Note, however, that the dorsolateral aspect of the frontal lobes have been considered an extension of the dorsal system into the frontal lobe for the purposes of action (Milner & Goodale, 1995).

In conclusion, there is extensive evidence from human neuropsychology to support the argument that the object recognition systems of the temporal lobe operate along viewpoint-independent lines. Further, viewpoint-dependent recognition, which may well be mediated by the structures of the inferior parietal lobe, might be employed under some circumstances to perform a variety of visuospatial manipulations that might assist the operation of the ventral system. A further source of evidence is derived from work in animals.

### Evidence From the Animal Literature

The original Ungerleider and Mishkin (1982) finding offers support for the broad claim, discussed above in regard to human neuropsychology, that object recognition involves structures in the occipitotemporal region. However, of far greater interest for the present discussion is the more specific claim that the achievement of object recognition in the ventral stream occurs using some form of viewpoint-independent mechanism. In this regard, single-cell recording has produced a great deal of relevant data (see Desimone & Ungerleider, 1989, for review; Perrett et al., 1985, 1989, 1991, 1992; Logothetis & Pauls, 1995).

Cells in the temporal cortex of monkeys have long been known to respond preferentially to "biologically important" objects, such as faces and hands (Gross et al., 1972; Bruce et al., 1981). Much of the more recent research has focused on the properties of the cells sensitive to faces (human or monkey), and there has been interest in the fact that the responses of some of these cells appeared to be insensitive to the viewpoint from which the face was observed (i.e., from the front, the back, or either profile; Perrett et al., 1985, 1991, 1992). These findings appear to offer support for viewpoint-independent accounts of the recognition process such as those of Marr (1982) and Biederman (1987). It is notable that the cells in this brain region (the superior temporal sulcus) also respond to other classes of information such as complex body movements (Oram et al., 1993).

Nevertheless, there are problems with the simple interpretation that viewpoint-insensitive cells in the monkey temporal cortex are evidence of the employment of viewpoint independent recognition by the ventral stream. For example, it may be that such cells are responding to a simple feature of a face common to all views, such as the presence of hair (Perrett et al., 1985). Secondly, the *majority* of such face-selective cells *were* found to be highly sensitive to the viewpoint from which the face was observed, that is, they were not viewpoint-independent (Perrett et al., 1985). Recently, these data have been interpreted (Perrett et al., 1992) as supporting accounts that suggest that viewpoint-independent object recognition is achieved by the interpolation across multiple two-dimensional views of an object (e.g., Poggio & Edelman, 1990; Edelman & Weinshall, 1991; Edelman & Bulthoff, 1992; but see Perrett et al., in press, for an alternative viewpoint). These data support *some* role for viewpoint-independent object recognition, and suggest that some form of viewpoint-dependent representation (perhaps only two-dimensional in nature) may participate in the development of viewpoint-independent recognition.

Further support for viewpoint-independent representations in the ventral stream comes from evidence on mirror-image discrimination. Even neurologically normal monkeys have some difficulty with tasks that require mirror-image discrimination. However, if bilateral lesions to the temporal lobes of the monkey result in a *loss* of the ability to generalize identity across viewpoint one might expect that, unlike normal monkeys, such monkeys should treat mirror-image objects as different, and perform well on tasks of mirror-image discrimination. This paradoxical finding, which implies that performance on this task *improves* after brain lesion, has been confirmed on several occasions (Gaffan et al., 1986; Weiskrantz & Saunders, 1984; see Milner & Goodale, 1993; Walsh & Butler, 1996 for reviews). The information necessary to discriminate between an object and its mirror-image is not available in a viewpoint-independent representation (Biederman & Cooper, 1991; Hummel & Biederman, 1992). Thus, the fact that such discriminations are unaffected by temporal lobe lesions offers further support for the claim that viewpoint-independent representations are coded in the ventral stream.

### CONCLUSIONS

In summary, the evidence from various fields of neurobiology offers some clear points of contact with the issues of visual representation that have been of interest in the cognitive literature on object recognition. There appears to be support for the claim that a viewpoint-independent mechanism is the primary means by which object recognition is achieved, although some recent psychophysical and physiological evidence still supports viewpoint-dependent processing, at least in learning to recognize novel objects (Bulthoff et al., 1995; Logothetis & Pauls, 1995). There is some debate about precisely which account of the recognition process (Marr, 1982; Biederman, 1987; Poggio &



Edelman, 1990) produces such viewpoint-independent recognition. However, regardless of the debate, such a system (or systems) may be found in the structures of the occipitotemporal region (i.e., the ventral stream). There appears to be further support for a second mechanism by which the recognition process may be assisted, which operates along viewpoint-dependent lines, and involves the structures of the occipitoparietal region (i.e., the dorsal stream, or perhaps a “third” stream; cf. Milner, 1995). It would appear that this is not the primary route to recognition, but operates in nonoptimal circumstances, serving perhaps to reorganize and normalize an otherwise “noisy” visual image in order for another attempt to be made at object recognition (presumably by the ventral system). Thus, the two streams model offers a neurobiological basis for both viewpoint-dependent and independent accounts of the recognition process, and suggests the participation of diverse areas of visual cortex in the complex process of object recognition.

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