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## Defining the cortical visual systems: “What”, “Where”, and “How”

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### Abstract

The visual system historically has been defined as consisting of at least two broad sub-systems subserving object and spatial vision. These visual processing streams have been organized both structurally as two distinct pathways in the brain, and functionally for the types of tasks that they mediate. The classic definition by Ungerleider and Mishkin labeled a ventral “what” stream to process object information and a dorsal “where” stream to process spatial information. More recently, Goodale and Milner redefined the two visual systems with a focus on the different ways in which visual information is transformed for different goals. They relabeled the dorsal stream as a “how” system for transforming visual information using an egocentric frame of reference in preparation for direct action. This paper reviews recent research from psychophysics, neurophysiology, neuropsychology and neuroimaging to define the roles of the ventral and dorsal visual processing streams. We discuss a possible solution that allows for both “where” and “how” systems that are functionally and structurally organized within the posterior parietal lobe. © 2001 Elsevier Science B.V. All rights reserved.

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## 1. Introduction

Despite our conscious experience of a unified perceptual world, our visual system historically has been classified into two subsystems, one for object recognition and the other for spatial localization (Held, 1968; Schneider, 1969; Trevarthen, 1968; Ungerleider & Mishkin, 1982). Well known for their definition of two cortical visual systems are Ungerleider and Mishkin (1982) who classified two distinct anatomical streams projecting from the primary visual cortex (V1). One stream projects ventrally to the inferotemporal cortex whereas the other projects dorsally to the posterior parietal cortex. The two systems were proposed to subservise object discrimination and spatial localization, and thus were labeled “what” and “where”, respectively.

More recently, Milner and Goodale (1995) classified the two streams as “what” and “how”. This distinction focuses less on the differences in the information used by the two systems, and more on differences in the way that information is transformed for output. Goodale and Milner’s “what” system processes object characteristics for long-lasting representations using multiple frames of reference, whereas the “how” system transforms visual information using an egocentric frame of reference in preparation for direct action. Other researchers have taken a similar approach, proposing separate systems for awareness of objects and visually guided action, although with slightly varying views (Bridgeman, Kirsh, & Sperling, 1981; Jeannerod, 1997; Rossetti, 1998). Beyond these two cortical systems, visual processing proceeds along multiple pathways, both cortical and subcortical, incorporating a large portion of brain structures (see Op de Beek, Wagemans, & Vogels, 2001). The focus of this paper, however, is to review the contributions of converging methods in cognitive neuroscience that address the traditional distinction between the two broadly defined cortical visual processing streams.

Whereas there is little debate that the ventral processing stream subserves conscious object identification and recognition, the functions of the dorsal stream (“where” versus “how”) continue to be defined in different ways. Ungerleider and Mishkin’s definition encompasses all spatial processing whereas Goodale and Milner’s approach describes the dorsal stream’s purpose specifically for egocentric visual guidance of action. The latter approach changes the definition of the what stream as well, placing object and spatial processing in both streams, but defining the function of each stream relative to the goal of the observer. The posterior parietal lobe encompasses a large anatomical area, and evidence from animal and human lesion studies shows that parietal lobe lesions result in both visuomotor and some non-motor spatial deficits.

Behavioral deficits resulting from brain lesions in humans can be classified more specifically in terms of a particular parietal area and the characteristics of the spatial impairment. Recently, researchers have proposed a distinction between visual-spatial disorders based on the area of brain lesion within the parietal lobe (Milner, 1997; Perenin, 1997). In humans, it may be that the superior portion mediates visually guided action, whereas the inferior portion, closer to the temporal lobe, mediates other spatial processing using multiple frames of reference. Functionally, one way of

classifying spatial processing is by the frame of reference used to solve the task. Spatial tasks can involve multiple egocentric reference frames (relative to parts of the body) as well as object- or environment-relative reference frames. These different reference frames subserve different roles in spatial perception. Recent monkey neurophysiology research provides evidence for distinct spatial reference frames mediated by distinct areas of the parietal cortex (Anderson, Snyder, Bradley, & Xing, 1997; Colby & Goldberg, 1999).

Although researchers have begun to develop a classification of visual deficits based on the area of parietal lobe lesion, this organization has not been related to normal visual processing. Functional neuroimaging research can be examined to determine whether the areas of activity associated with object and spatial perception tasks are consistent with the patient literature. This review brings together recent research from psychophysical, neurophysiology, neuropsychology, and neuroimaging domains to more clearly define the cortical visual processing streams. Spatial processing itself involves many components, including the goal of the task and the frame of reference used. We evaluate the hypothesis that there are separate “how” (superior) and “where” (inferior) functions within the posterior parietal cortex and suggest future functional neuroimaging studies that might clarify this topic.

## 2. The two visual systems

Evidence for two visual systems comes from a number of different sources within cognitive neuroscience research. This section brings together these sources of evidence to establish the general structure of the two visual systems approach. We begin by reviewing three different theories about the way in which the systems are differentiated and by defining what we mean by an anatomical “dorsal” stream. Next, we consider the behavioral research on dissociations and interactions between the “what” and “how” streams. We then outline specific visual disorders and their relationship to the two visual streams. Lastly, we review the recent functional neuroimaging research relating to ventral and dorsal stream processing.

### 2.1. Recent theories

#### 2.1.1. What and where

The functional distinction between object and spatial perception has been the dominant framework for studying the modularity of higher visual processing. Research from monkey and human lesion studies led Ungerleider and Mishkin (1982) to coin the labels “what?” and “where?” for their ‘Two Cortical Visual Systems.’ To the extent that the visual systems can be separated, this classification appears to a first approximation to be a valid and well-grounded dichotomy. Ungerleider and Mishkin stated that “damage to the temporal cortex produces an impairment in visual recognition [whereas] damage to parietal cortex produces a constellation of visual spatial impairments” (1982, p. 549). However, missing from this explanation was a consideration of the response task itself. In contrast to theories of perception

that have emphasized the necessary coupling of direct action with the perception of the environment (Gibson, 1979) this definition of the cortical visual systems included action within the broad domain of spatial localization.

Evidence for the “what” and “where” cortical distinction came most directly from lesion studies on non-human primates. Ungerleider and Mishkin (1982) defined the ventral stream of processing as projecting from V1 through V2, V3, and V4, and TEO (the posterior portion of inferior temporal area) to IT (inferior temporal cortex). They showed that lesions to the inferior temporal cortex in rhesus monkeys led to severe impairment in visual object discrimination performance. They defined the dorsal stream as projecting from V1 through V2, V3, middle temporal area (MT), medial superior temporal area (MST) to the posterior parietal cortex. Lesions to the posterior parietal cortex led to impaired performance on the classic spatial localization tasks.

The results of the two different ablation studies suggested that the inferior temporal lobe was responsible for object discrimination whereas the posterior parietal lobe was responsible for spatial localization. Ungerleider and Mishkin acknowledged the common finding that lesions to posterior parietal cortex in monkey also led to deficits in reaching as well, but included this deficit under a broader spatial disorder. Their conclusions suggested that the mechanisms underlying visuomotor control and perception of spatial relations are the same. Recently, Ungerleider and Haxby (1994) reviewed their position on the traditional distinction. After reviewing Goodale and Milner’s (1992) case study of an agnostic patient who lacks object recognition but retains accurate visually guided actions, Ungerleider and Haxby argued that visuospatial deficits “may be accompanied by visuomotor deficits, but are not explained by them” (p. 159). Their assertion relies partly on the evidence from Von Cramon and Kerkhoff (1993) who reviewed 67 patients with posterior parietal damage. These patients exemplified impaired performance on visuospatial tasks that did not include visuomotor components.

### 2.1.2. *What and how*

Milner and Goodale’s (1995) theory of “what?” and “how?” diverges from the traditional dichotomy between object and space perception because it focuses on the importance of the goal of the observer. Their theory maintains that a single general-purpose representation of objects or space does not exist. Instead, they define the visual system by the requirements of the output that each stream subserves. Thus, separate systems are defined for conscious visual experience, ‘perception’, and visuomotor transformation, ‘action’. The “what” and “how” theory is based largely on defining systems for the use of different frames of reference. Both streams use the same object and spatial information, but transform it differently for different purposes. They assert that the ventral stream represents the visual world in both egocentric and viewer-invariant frameworks that promote an awareness of the world’s persistent structure. Conscious perceptual awareness uses object-relative or environmental reference systems where attributes and meanings of objects are encoded in relation to themselves or external objects. In contrast, the dorsal stream transforms the information about the location, orientation, and size of objects in mainly

egocentric coordinates for action-tasks such as pointing or grasping. They have shown that information about the object itself is also necessary for accurate grip scaling, but it is in the framework of a direct egocentric response. The functions of the two streams can be differentiated on the basis of time, as well as reference frame. If the goal is to represent an object over time, visually or spatially, then it is a function of the ventral stream. If the goal is to act on the object immediately, then it is a function of the dorsal stream. Extensive research with a visual agnostic patient as well as a number of behavioral studies with normal participants supports this distinction between dissociable systems for perceptual awareness and visually guided action (Goodale, Jakobson, & Keillor, 1994; Goodale, Milner, Jakobson, & Carey, 1991; Haffenden & Goodale, 1998).

### 2.1.3. *Semantic and pragmatic*

Jeannerod's (1997) distinction between "semantic" and "pragmatic" representations is not closely tied to the anatomical dichotomy between a ventral system for 'perception' and a dorsal system for 'action'. A semantic representation involves the integration of elementary features of an object into higher-order properties that ultimately allow a percept to exist as a meaningful entity. The integration occurs on different levels. For example, form must first be extracted from contours and contrast. Further processing allows for the attribution of semantic or contextual properties to the object. Jeannerod states that the mechanisms involved must be distributed over several brain areas. In contrast, a pragmatic representation consists of the rapid sensorimotor transformation involved when treating the object as a goal for an action. Object attributes are only represented to the extent that they elicit specific motor patterns for the body.

Jeannerod also notes that different frames of reference are required to represent objects depending on the goal of the observer. He agrees with a general dichotomy of object-centered descriptions for recognition (Biederman, 1987; Marr, 1982)<sup>1</sup> and egocentric representations for localization tasks such as reaching. However, the question arises as to where object-oriented actions such as grasping fit in. He maintains that the same object is represented in multiple ways. Extrinsic attributes of the object such as its position in space are represented in viewer-centered coordinates. Intrinsic attributes such as size and depth of the object are computed in object-centered coordinates both in the dorsal pathway for grasping the object and in the ventral pathway for object identification. Thus, Jeannerod makes a functional distinction between pragmatic and semantic, which does not necessarily fit into anatomically differentiated dorsal and ventral streams. Both pragmatic and semantic representations can require object-centered coordinate systems.

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<sup>1</sup> However, there is a growing field of evidence supporting the alternate view of object recognition, claiming a viewpoint-dependent representation of objects (Tarr, 1995; Tarr & Pinker, 1990). Viewpoint-dependent and -independent object recognitions were directly compared in a recent neuroimaging study by Vanrie, Béatse, Wagemans, Sunaert, and Van Hecke (1999).

## 2.2. The anatomical “dorsal” stream

It is important to define what is meant by the anatomical dorsal stream. As described above, most of the evidence for the “what” and “where” distinction was first developed with monkeys. However, the monkey and human posterior parietal cortex are very different in their functional organization. The intraparietal sulcus divides the superior and inferior areas of the posterior parietal cortex in both monkey and humans. In monkey, the area described as the endpoint of the dorsal stream is the inferior parietal area (broadly area 7, see Fig. 1). Researchers have argued that the human homologue to this area is the superior parietal cortex (Milner & Goodale, 1995; Milner, 1997; Perenin, 1997) based on similar functional characteristics shown through lesion studies (e.g., Rushworth, Nixon, & Passingham, 1997). The monkey superior temporal sulcus (STS) has been proposed to correspond to the human inferior parietal cortex (Heilman, Valenstein, & Watson, 1994; Perenin, 1997). We will refer to the dorsal stream in humans as one terminating at the superior parietal lobe. We will examine the proposal that inferior regions of the posterior parietal lobe

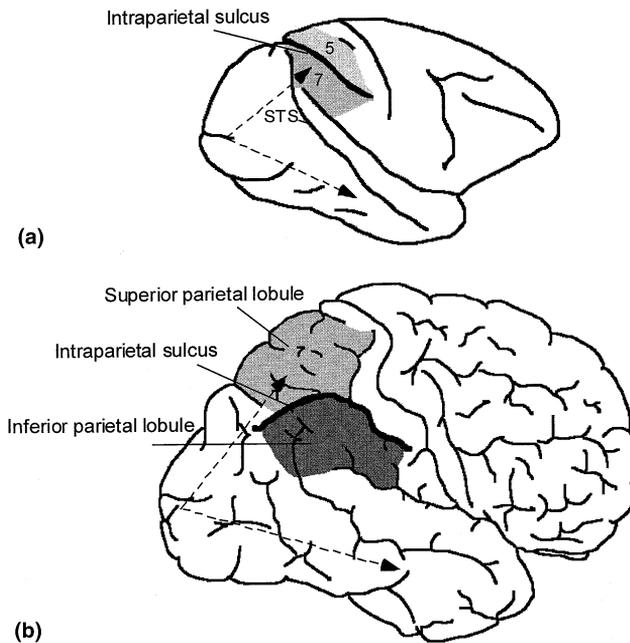


Fig. 1. Representation of the two visual pathways in the macaque monkey (a) and in the human brain (b). Each figure depicts the intraparietal sulcus dividing the posterior parietal cortex into superior and inferior regions. Dotted lines represent the dorsal and ventral processing streams. Milner (1997) has proposed that the human superior parietal lobule may be the homologue to the monkey inferior parietal lobe (area 7), as the endpoint of the dorsal stream. The human inferior parietal lobule may correspond to the monkey superior temporal sulcus (STS). Adapted from Milner (1997). Neglect, extinction, and the cortical streams of visual processing. In P. Their & H. O. Karnath (Eds.). *Parietal lobe contributions to orientation in 3D space*.

subserve visual-spatial functions as well, but serve a more general multi-reference frame spatial processing function that does not correspond to visuomotor control.

### 2.3. “Perception–action” dissociations and interactions in normal adults

In our everyday experiences, we often perceive the world inaccurately. For example, distances appear shorter and hills appear steeper than they really are. However, these biases in awareness typically do not affect the accuracy of our behaviors. A look at controlled behavioral studies can provide a helpful background to the dissociation seen between phenomenal awareness and visually guided action. This dissociation, clearly apparent in numerous empirical studies, is defined by several components. Much of the work advocating this distinction comprises experimental tasks that tap different frames of reference. The egocentric frame of reference locates the position of an object relative to a reference frame centered on the observer’s body. Object- and environment-relative frames relate the location of things to reference frames that are independent of the observer. “What” functions are defined by the use of multiple reference frames for lasting representations and “how” functions involve egocentric reference frames for transforming visual input immediately for action.

A second important component is time. Dissociations between action and awareness are apparent only when an action is performed without much delay. The action system works on-line within a framework of egocentric coordinates. A system that is dependent on the relationship between the observer and the object must necessarily update the egocentric position of objects often. In contrast, a system for object discrimination relies on unchanging object-relative representations. Thus, as some of the following research shows, when time delays are present, the dissociation disappears and communication results as awareness informs action.

A number of studies support the dissociation between phenomenal awareness and visually guided actions when there is no time delay involved. In a series of studies, Bridgeman and his colleagues asked participants to judge verbally, to point, or to make saccadic eye movements to where a target was displaced (Bridgeman et al., 1981; Bridgeman, Lewis, Heit, & Nagle, 1979). In several experiments, participants were able to make saccades and point accurately to a displaced target, even though they did not verbally report that they detected the displacement.

A similar dissociation between awareness and action has been found in experiments involving pictorial illusions. Several visual illusion studies have found that the phenomenal perception of an illusion is not reflected in an action directed toward the illusory figure. Haffenden and Goodale (1998) presented participants with the Ebbinghaus illusion in which two same-size discs appear to be different sizes depending on the size of the surrounding circles. Participants gave a perceptual estimation through a manual task of matching the distance between their thumb and index finger to the diameter of the target disc. They also responded with a visuomotor task in which they grasped the disk without the view of their hand. Haffenden and Goodale found that maximum grip aperture corresponded to the actual size of the

disk, regardless of the appearance of the disc. In contrast, the manual perceptual estimations of disk size were influenced by the illusion.

A recent study with a large-scale Müller–Lyer illusion further supports the importance of the frame of reference used in encoding for perception-action dissociations (Wraga, Creem, & Proffitt, 2000). A large Müller–Lyer figure was presented on the floor, constructed of a ribbon line with a large hoop at each end. Observers responded with both verbal and walking-while-blindfolded measures of the length of the shaft of the figure. Wraga et al. found a dissociation between walking and verbal responses only when the figure was encoded egocentrically, relative to the observer. The verbal response was influenced by the direction of the hoops, but the walking estimates were not. When observers were slightly displaced from the figure, and thereby, were required to encode the figure using an object-relative frame of reference, an illusion effect was seen in both modes of response.

Despite these and other consistent findings that largely support dissociations (Aglioti, DeSouza, & Goodale, 1995; Brenner & Smeets, 1996; Daprati & Gentilucci, 1997; Gentilucci, Chieffi, Daprati, Saetti, & Toni, 1996; Jackson & Shaw, 2000) other recent studies have questioned whether perception and action measures of illusions can be dissociated (Franz, Gegenfurtner, Bühlhoff, & Fahle, 2000; Pavani, Boscagli, Benvenuti, Rabuffetti, & Farne, 1999; Vishton, Rea, Cutting, & Nunez, 1999). There may be several possible explanations for the discrepant results in the latter studies. For example, Haffenden and Goodale (2000) demonstrated that pictorial displays could have independent effects on perception and grip scaling despite the apparently similar results of the two measures. In all, the majority of research conducted supports a dissociation account, but suggests that careful attention should be placed on designing both the task demands and the physical layout of the stimuli presented.

In a more global task involving slant judgments of hills, Proffitt, Bhalla, Gossweiler, and Midgett (1995) illustrated a clear dissociation between perceptual and motoric estimates. Participants judged the slant of a hill from the top or bottom with verbal, visual, and haptic measures. The verbal measure required participants to report the number of degrees that they perceived the hill to be. The visual measure was an adjustment of a disk to equal the perceived cross-section of the hill. In the haptic measure, the participants gave a motoric judgment by adjusting a tilting board with their unseen hand until they felt the slant was equal to the slant of the hill. Proffitt et al. found that participants greatly overestimated the incline of the hill using the verbal and visual measures, but were much more accurate when using the haptic adjustment. Further studies found that manipulations of physiological state such as fatigue affected observers' conscious judgments, but had no effect on their immediate visuomotor behavior (Bhalla & Proffitt, 1999).

The influence of time on the interaction between the two systems is apparent in Creem and Proffitt's (1998) manipulations of memory for geographical slant. They asked participants to make verbal and motoric judgments of the slant of hills after different time delays and in different locations. They found first, that verbal judgments of the hills always increased in memory compared to perception. Second, the motoric judgments varied depending on the length of delay and location of response. With a short delay of less than two minutes, when the participant was still present at

the hill, motor judgments remained accurate. However, with a longer delay or when the participant was taken to a new location within a short delay, motor judgments increased proportionately with the verbal response. These findings illustrate that motor guidance memory lasts for only a short amount of time and is tied to the location in which it is made. When the motor memory fails, the motor system must rely on a stored representation to inform its action.

Bridgeman, Peery, and Anand (1997) also concluded that conscious perception influences motoric responses after a delay. Using the Roelofs effect, in which people tend to misperceive the position of a target in a rectangular field, they created both an immediate and delay condition. They presented participants with a rectangular frame centered on either their midline or 5° left or right of center, with an 'x' placed inside the frame in one of five positions. Participants responded with both a 'cognitive' response, which involved estimating target position with the keyboard, and a motor response, which was made with a hand-held pointer. Without a delay, all participants showed the Roelofs effect in the cognitive judgment, a bias to judge the target to be farther in the opposite direction of the offset of the frame. However, with the motor response, half of the participants did not show the effect. After a four-second delay, all participants were biased by the frame position in the motoric task. Thus, after a long enough delay before the response, participants used the cognitive information biased by the frame position. Several other recent studies have found similar effects of time delays leading to a necessary interaction between perception and action with normal observers (Gentilucci et al., 1996) and with neuropsychological patients (Goodale et al., 1994; Rossetti, 1998).

In addition to the effect of time delays and frame of reference on the interaction between cognitive and visuomotor representations of objects, actions towards objects may be influenced by the semantic representation of what an object is used for. Creem and Proffitt (2001) illustrated that grasping a hand tool appropriately by its handle requires retrieval of semantic information, and therefore, an interaction between cognitive and visuomotor systems. They suggest that an *effective* grasp can be mediated by the visuomotor system alone. However, a grasp that is *appropriate* to the tool's functional identity requires information from a cognitive representational system.

In all, there is a growing literature illustrating dissociable systems for object awareness and visually guided action in normal adults. Recent research also demonstrates interactions between these systems. These interactions, however, do not negate the importance of two independent systems. Rather, they expand on our knowledge of how the systems work together to allow an organism to function adaptively as a whole.

#### 2.4. *Objects, space, and action in neuropsychological patients*

Brain structure–function relationships can be inferred based on deficits seen in neuropsychological patients. If a patient with a localized lesion to one area shows specific behavioral deficits, one might infer that the specific brain area is responsible for the behavior. One convincing way of studying neuropsychological patients is to

find cases of double dissociation in patients with focal lesions. One patient with specific damage may show clear behavioral deficits on certain tasks, but normal behavior on another related but different task. In contrast, a second patient with a different lesion may show normal performance on the former task and impaired performance on the latter task. The following sections review several visual disorders as evidence for at least two separate visual systems.

#### *2.4.1. Deficits in object recognition*

The impairment in the higher visual processes necessary for object recognition with the preservation of basic visual function is known as visual agnosia (Farah, 1990). Traditionally, a distinction has been made between two types of agnosia, apperceptive and associative. Apperceptive agnosia is classified as a failure to see objects normally (although visual sensory systems are intact) which leads to a failure in object recognition. In contrast, associative agnosics seem to perceive objects correctly, although they still cannot recognize them. Disorders that fall under this label include prosopagnosia, or an impairment of face recognition. In this section, the focus will be on the impairments seen in apperceptive agnosia, also termed visual form agnosia. Brain damage associated with visual agnosia is usually situated in the posterior occipital cortex and inferotemporal cortex. In general, visual form agnosics show impairments in the ability to recognize, copy, or match simple shapes and complex objects.<sup>2</sup>

Milner and Goodale (e.g. Goodale et al., 1991; Milner & Goodale, 1995) extensively tested the visual agnosic patient D.F., to examine the dissociation between object recognition and visually guided actions. D.F. has damage in the ventrolateral region of the occipital cortex as a result of carbon monoxide poisoning. She suffers from the inability to discriminate or recognize simple objects. However, Goodale and Milner have found that despite her inability to explicitly perceive the perceptual qualities of objects, her visually guided actions toward these objects are quite accurate. For example, when presented with different size blocks, D.F. could not discriminate between them perceptually, but her reaching and grasping of the objects were normal. The size of her anticipatory grasp was highly correlated to the size of the block, as in normal visually guided behavior. Furthermore, when asked to adjust the width between her fingers to the size of a block, she failed. Thus, it appears that D.F.'s accurate spatial ability depends on an immediate action directed toward an object. Similarly, D.F. could not discriminate the orientation of a slot both verbally or by matching a hand-held card to the slot. However, when asked to insert the card into the slot, she was able to perform accurately. The dissociation seen in D.F. between object discrimination and visuomotor performance suggests a distinction

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<sup>2</sup> Lesions to the primary visual cortex result in a different object-processing disorder. Patients lose conscious visual perception within the corresponding area of the visual field, but often retain the ability to produce motor responses to objects within that space. This disorder, labeled "blindsight," will not be elaborated in the present paper, but is discussed thoroughly by Lamme (2001) in this issue.

between object awareness and visually guided action, rather than one between object and spatial perception.

Other evidence supports a distinction in abilities of D.F. to use certain frames of reference. For example, D.F.'s ability to perceive the orientation-in-depth of a visual field (visual pitch) was tested by Servos, Matin, and Goodale (1995). D.F. was asked to complete two different tasks. The first was a task of visually perceived eye level (VPEL) in which D.F. judged where her eye level was on a pitched surface by telling an experimenter to adjust the height of a laser pointer. The second task involved physically matching a plaque with the pitch of the visual field. She was encouraged to look at the plaque to compare it with the visual field. Her performance was compared with controls in the two tasks. Even though the VPEL task did not involve a direct action, D.F.'s performance was very good, matching that of the controls. In contrast, her performance on the pitch-matching task was severely impaired, whereas performance of the controls was perfect. Here we see a dissociation in D.F.'s abilities based on the frame of reference used to perform the task. The difference in D.F.'s performance between the two tasks involving pitch perception suggests that judgments of egocentric localization, as well as visuomotor acts, may be dissociated from more object-relative perceptual judgments such as shape and orientation.

#### *2.4.2. Deficits in visual guidance of actions*

In contrast to patient D.F., patients with optic ataxia show deficits in reaching and grasping for objects, but have little difficulty recognizing or matching objects (Jakobson, Archibald, Carey, & Goodale, 1991). This disorder results from damage to the posterior parietal cortex. An extensive review of optic ataxic patients was conducted by Perenin and Vighetto (1988). They summarized the brain lesions as well as the abilities of ten patients with optic ataxia. Overall, lesions were mostly localized in the superior parietal cortex, always including the intraparietal sulcus. Some lesions were localized to superior parts of the inferior parietal cortex. Thus, in all, it is thought that optic ataxia results from lesions to the upper portions of the posterior parietal cortex. A review of the patients' abilities led Perenin and Vighetto to conclude that the visuomotor deficits seen in optic ataxia are independent of visual space misperception. Optic ataxia has also been distinguished from unilateral spatial neglect both in area of brain lesion and in deficits in behavior (Perenin, 1997; Perenin & Vighetto, 1988). Evidence suggests that patients with spatial neglect suffer from lesions to inferior rather than superior parietal cortex (Heilman et al., 1994; Karnath, 1997).

Although it has been shown that posterior parietal lesions impair both reaching and grasping, Jeannerod, Decety, and Michel (1994) tested a patient, A.T., who exhibited a dissociation between reaching and grasping. She was able to reach accurately to the location of objects but was impaired in her ability to grasp them. Her abilities to perform a series of tasks requiring grasping actions towards neutral and familiar objects make a distinction between her "semantic" and "pragmatic" systems. First, when asked to grasp neutral cylinders, she failed to adjust her grip size to the size of the objects as normal people do. However, her grasping was improved when familiar cylindrical objects such as lipstick and a spool of thread were used.

Furthermore, her ability to match the size of virtual cylinders with her thumb and index finger was normal, as was her performance when asked to imagine the familiar objects and adjust her fingers to the size of the objects previously seen. These behaviors are in stark contrast to what was seen in the agnosic patient, D.F. Whereas D.F. can grasp, but not match her fingers, A.T. can match her fingers, but not grasp. Again, the subtle difference seen between adjusting fingers to the size of an object, and actually reaching for that object shows a distinction between purely object-relative action, and object-relative coordinates transformed for egocentric action toward that object. A.T.'s performance, thus, reveals an intact semantic system but an impaired pragmatic system. The fact that the knowledge of the identity of an object can help her in grasping that object also shows that the systems interact.

#### 2.4.3. *Visuospatial deficits*

In general, visuospatial deficits with and without motor components have been attributed to the posterior parietal lobe. Von Cramon and Kerkhoff's (1993) review of 67 parietal patients showed impaired performance on non-motor, visuospatial tasks. The tasks involved matching orientations of lines, estimating line length, estimating and matching distance, and discriminating position. Performance on specific tasks varied with area of lesion, but it is difficult to conclude consistencies between patients. Overall, the authors concluded that visuospatial deficits were a result of lesions to the dorsal stream.

Another set of case studies was conducted by Newcombe, Ratcliff, and Damasio (1987) who found a dissociation between ventral and dorsal areas of lesion for face recognition and visuospatial performance. Case 1 suffered right parietal lobe damage as a result of a shell fragment, determined postmortem to extend into the supramarginal gyrus and the superior parietal lobule. He had difficulty performing spatial tasks such as judging distances, and was extremely impaired on a maze-learning task. In contrast, Case 2 suffered right temporal lobe damage also from a shell fragment. He had a striking inability to perceive faces, but performed well on a number of spatial tasks. Although case studies such as those described above are present in the literature, many of the extensive reviews of visuospatial disorders fail to classify brain localization. For example, Newcombe and Ratcliff's (1989) "Disorders of Visuospatial Analysis" outlines many cases of visuospatial impairments, but often only classifies them structurally by hemisphere. Their review suggests that most visuospatial disorders result from right hemisphere lesions.

Although there is a good amount of evidence for parietal involvement in spatial tasks, a number of cases involve patients with spatial topographical disorders who suffer from ventral stream damage. Maguire, Burke, Phillips, and Staunton (1996) conducted an environmental study with right temporal- and left temporal-removed patients and controls. Overall, tasks of proximity and distance judgments, route knowledge, map sketching, and locational accuracy were all impaired in both left and right temporal patients compared to control participants. Another patient described by Humphreys and Riddoch (1987), suffered from topographical agnosia as a result of temporal lobe damage. He was unable to judge distances and speeds of objects, such as passing cars. He was also severely impaired in finding his way

through surroundings previously familiar to him. Thus, these cases of impaired environmental knowledge suggest that environment-relative spatial encoding may be mediated by the ventral stream.

#### 2.4.4. *Unilateral neglect*

Unilateral spatial neglect is defined as the failure to report, respond, or orient to stimuli presented on the opposite side of the brain lesion, that cannot be attributed to sensory or motor deficits (Heilman et al., 1994). Most often, the deficit results from right hemisphere lesions to the inferior parietal lobe (Heilman et al., 1994; Karnath, 1997; Perenin, 1997). There are different accounts of the underlying mechanisms of neglect. However, these accounts are not mutually exclusive. Neglect has been attributed to a deficit in spatial attention (e.g. Kinsbourne, 1993) as well as an impairment in representing space (e.g. Bisiach, 1996; Karnath, 1997). The attentional account proposes that the contralesional side of space is ignored because of an attentional bias with excessive orienting to the ipsilesional side of space. There is a gradient of attention across both hemispaces so that if attention is biased toward the ipsilateral direction, it will be inhibited from the contralateral direction.

The spatial representation theory of neglect proposes a disrupted conscious representation of the left side of space (as a result of right hemisphere lesion). This account defines neglect as a representational disorder, differentiating it from other contralesional deficits such as extinction and optic ataxia that involve egocentric orienting in space. Bisiach's representational model originally came from his study of Milanese patients who neglected to describe the right side the Piazza de Duomo when asked to visualize it (Bisiach, Capitani, Luzzatti, & Perani, 1981). Their descriptions changed when they were given a new vantage point, so that they always neglected their egocentrically defined right. Karnath's (1997) spatial account proposes that neglect is caused by a disturbance of mechanisms of coordinate transformations that leads to a deviation of egocentric space to the side of the lesion. This ipsilesional deviation causes patients to neglect the contralesional side of space.

Although much research points to neglect as a deficit in the representation of egocentric space, there is evidence that neglect may be object- or environment-relative as well (Behrmann, 2000). Some patients with neglect are impaired in processing the left sides of single objects as well as the more general left side of space. When asked to copy pictures of objects, neglect patients tend to leave out the left side of objects. A convincing study involving the object-based account asked a neglect patient to detect a target within a barbell-shaped stimulus (Behrmann & Tipper, 1994). In the static condition, the left side of space was yoked to the left circle of the barbell. In the dynamic condition, the patient watched as the barbell rotated 180° so that its left circle was on the right side of egocentric space. In this case, detection of the target was inhibited on the right side of space because it held the left side of the object. In all, there is evidence that neglect includes deficits in the use of multiple reference frames, not only egocentric representations of space.

Evidence from neuropsychological research provides considerable support for separable ventral and dorsal stream processing defined by frames of reference. Deficits in object-based tasks such as recognition are associated with ventral stream

damage. Within the posterior parietal lobe, action-oriented spatial processing can be classified to the dorsal stream as seen in optic ataxia, whereas global spatial deficits as seen in neglect are associated with inferior parietal lobe damage. Environment-relative spatial tasks are associated with even more inferior regions of the brain in the temporal lobe. There are some inconsistencies with the superior/inferior distinction (e.g. Von Cramon & Kerkhoff, 1993) as well as unanswered localization questions (e.g. Newcombe & Ratcliff, 1989) that are apparent in neurological reviews. Future goals of cognitive neuroscience research should aim to combine neuropsychological research with functional imaging techniques to address specific cognitive function-brain localization questions (see Humphreys & Price, 2001; Parsons, 2001).

## 2.5. *Functional neuroimaging methods*

Functional brain imaging is a technique that allows the study of brain function–structure relationship in normal humans, neuropsychological patients, and non-human animals. The sections below describe some relevant positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) studies in humans relevant to defining the object and spatial visual systems, focusing on the differences between visually guided action and other “non-motor” spatial tasks.

### 2.5.1. *Object-oriented action*

According to a “what” and “how” account, differences in brain activity should be found in an object discrimination task compared to an object-oriented action task. Although both tasks involve perception of object characteristics, the goals of each task differ substantially. The former task requires object-centered comparisons whereas the latter requires the perception of the object with the aim of generating an action toward it. A number of recent studies have explored brain mechanisms involved in actions directed at an object. Faillenot, Toni, Decety, Gregoire, and Jeannerod (1997), using PET, conducted one of the few studies that directly compared a grasping task and a discrimination task involving the same nonsense objects. In addition, they included a third pointing task to control for the difference in the motor component of the grasping and the object discrimination task. Participants followed explicit instructions for each task. For the pointing task, they were told to point with the right index finger towards the center of the object and then return to the starting position. In the grasping task, participants were told to grasp the object between their right fingertips and place it on the table. In the matching task, the participants were told to observe the presented objects and press a mouse button each time the shapes of two consecutive objects were identical.

The resulting patterns of activation were somewhat surprising in light of the Goodale and Milner model. As expected, the inferior temporal cortex (BA 37) was activated in the right hemisphere during the matching task. However, several other areas in the dorsal pathway were also activated by the matching task, namely the right posterior parietal cortex (BA 7/19) and the right intraparietal sulcus (BA 7/40). For the grasping task, areas of activation were seen in left hemisphere motor areas,

as well as the right intraparietal sulcus, the same area seen activated in the matching task.

These results suggest that object-oriented action and object recognition activate a common posterior parietal area. Thus, some aspect of object perception appears to be involved in the analysis of object properties regardless of the task required. These findings differ from the general assumption that object discrimination is performed solely by a ventral stream network. Faillenot et al. suggest that one possibility may be that the intraparietal sulcus is responsible for integrating three-dimensional properties of objects such as orientation and volume. It may be that the infero-temporal cortex covers more purely semantic functions related to object discrimination (Jeannerod, 1997). In any case, these results do identify a shared posterior parietal area for object-oriented action and shape comparison. This type of object analysis appears to be distinct from an analysis performed by the temporal cortex. These findings are more in line with theories that there is some object-based analyses in the dorsal stream (Jeannerod, 1997; Milner & Goodale, 1995).

A number of other studies have looked specifically at the brain areas involved in visually directed actions, without including a task of object identification. For example, Grafton, Fagg, Woods, and Arbib (1996) designed a PET study to examine visually guided reaching and grasping. They asked participants to either grasp, point, or look at cylindrical targets. These studies were designed to identify mechanisms involved in prehension by comparing the localized activation for reaching with grasp to reaching with pointing movements. The objects were specifically not meaningful objects so that Jeannerod's "pragmatic" type of prehension could be examined. The analysis of activation for the movement conditions revealed a distributed set of areas involving cortex, thalamus, and cerebellum including premotor, sensorimotor, and superior parietal cortex. Another PET study examined visually guided movements of the finger and other body parts in a tracking task relative to visual tracking alone and found a similar network of sensory and motor areas as well as bilateral superior parietal lobule (BA 7) activation (Grafton, Mazziotta, Woods, & Phelps, 1992). This parietal activity is consistent with the most common lesion area in patients with optic ataxia (Perenin & Vighetto, 1988). These results support the notion of functionally distinct portions of the posterior parietal lobe. Grafton et al. suggest that the superior parietal lobule and the precuneate cortex are necessary for integrating visual cues into movement selection. In contrast, the inferior parietal lobule may be more responsible for directed visual attention and may be more involved in "where" functions such as recognizing movement and velocity.

### 2.5.2. *Perceiving actions*

Given the wealth of research examining the separability of systems for perception *and* action, it is an intriguing question to investigate the brain mechanisms involved in perception *of* action. Monkey and human research suggests that there is a strong connection between the execution of actions and the perception of actions. In monkeys, specific "mirror" neurons in the premotor cortex have been found to be responsive when a monkey grasps an object *and* when the monkey observes an experimenter grasping an object (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). A

number of functional neuroimaging studies have examined the perception of actions in humans. Decety and Grezes (1999) reviewed the recent literature, concluding that an explicit goal may determine whether the observation of an action corresponds to dorsal or ventral stream activation. However, if no goal is given, then perception of action seems to lead to activity in both dorsal and ventral stream areas.

For example, Decety et al. (1997) manipulated the strategy given to participants as they observed meaningful and meaningless actions in a PET experiment. A striking finding was that the brain activity for the same visual stimuli differed as a result of the cognitive strategy performed. When the task was to observe the actions to imitate later, a network of areas involved in action planning, from dorsal stream superior parietal areas to prefrontal motor areas, were involved. In contrast, when the goal was to recognize the actions at a later time, the right parahippocampal gyrus, involved in object memory and representation, was activated. A number of other studies have shown that observation of grasping or of pantomimes without explicit goal instructions lead to activation in both ventral and dorsal areas (Decety & Grezes, 1999; Rizzolatti et al., 1996). Thus, the recent literature supports similar areas of representation for perception and execution of actions, but this is qualified by the goal and strategy of the observer.

### 2.5.3. *Object recognition versus spatial localization*

Whereas the studies described above focus on object recognition and action, other studies have examined the “what” versus “where” distinction, comparing brain activation in object recognition to that in spatial localization tasks (Haxby et al., 1993; Haxby et al., 1991). Haxby et al. (1993) used PET to compare face matching and location matching. Participants were instructed to compare two targets with a sample stimulus and to press a right or left button corresponding to the target they chose as the same as the sample. In the face-matching task, they chose the face that was the same as the sample. In the location-matching task, they chose the stimulus that had the same relationship of a square and a double line as the sample. A control task consisted of simply looking at the same stimuli with nonsense patterns and alternated pressing the left or right response buttons.

The analysis revealed that face matching was associated with increased activation in bilateral occipito-temporal cortex whereas location matching selectively activated bilateral occipito-parietal cortex (superior parietal, BA 7). In addition, activation was seen in the posterior part of the fusiform gyrus (BA 18) in the face task, and dorsal occipital cortex (BA 19) in the location task. These findings of superior parietal activation for a task that lacks an egocentric response contradict the distinction between superior and inferior parietal areas that several researchers have asserted (Milner, 1997; Perenin, 1997). Milner (1997) suggests that the superior parietal activation seen in this study might be a consequence of additional eye movements needed in the location-matching task. Although it is difficult to assess whether this explanation is correct, the issue of eye movements is definitely one of which to be aware. It is known that neurons in parietal areas are active during directed saccades in humans (Pierrot-Deseilligny & Muri, 1997) and in monkeys (Anderson, 1989).

Aguirre and D'Esposito (1997) conducted an fMRI study to test “what” and “where” differences in environmental knowledge. After learning a virtual environment, participants were asked either appearance or position questions relating to the environment. In appearance questions, participants answered whether or not the word presented with a picture of a part of the environment correctly named the place. In position questions, participants were given a picture and its name, followed by another name of a new location. They indicated the direction of the specified new location. In all, the pattern of activation for each task was segregated into ventral and dorsal streams for appearance and position questions, respectively. For appearance questions, activation was seen in the fusiform gyrus (BA 37), parahippocampus, lingual gyrus (BA 19), and occipital gyrus (BA 19). In contrast, for position questions, activation was selective to inferior parietal (BA 7/40), precuneus (BA 7), superior parietal (BA 7), superior frontal (BA 6), and premotor cortex (BA 6).

The network of parietal and frontal structures found in the position task were most likely associated with both spatial as well as motor strategies to solve the task. Similarly, spatial imagery tasks such as mental rotation have been associated with both inferior and superior parietal areas (Alivisatos & Petrides, 1997; Cohen et al., 1996; Kosslyn, Digirolamo, Thompson, & Alpert, 1998; Parsons et al., 1995; Vanrie et al., 1999). Although mental rotation tasks do not involve direct egocentric action, motor strategies may be used that lead to similar dorsal stream and frontal motor areas of activity as seen in visually guided action tasks (see also Parsons, 2001).

Together, the neuroimaging research supports a dorsal stream for “how/where” tasks and a ventral stream for “what” tasks. However, it is not as clear whether “where” tasks can be localized to more inferior regions of the parietal lobe. One reason for this uncertainty is that tasks involving spatial localization often recruit attentional mechanisms and motor strategies as well, (e.g. eye movements or imagined movement) which would be associated with superior parietal and premotor areas. More research is needed to directly compare egocentric motor tasks, egocentric spatial non-motor tasks, and allocentric spatial tasks within single neuroimaging studies.

### **3. The posterior parietal cortex**

The above review of behavioral, neuropsychological, and functional brain imaging research suggests that although object and spatial vision can be broadly classified into two visual streams, this dichotomy only serves as a rough first approximation. The inferior temporal cortex is generally agreed upon as the mediator of object recognition. The posterior parietal cortex is implicated in many different kinds of spatial transformations. The classic definition of a “where” stream for space perception is evident in some patient and neuroimaging findings. Patients with unilateral neglect as well as those who have general deficits in spatial perception most often have suffered posterior parietal lesions. Functional neuroimaging research shows activation in the dorsal stream for judgments of spatial location. However, there is also evidence in support of a “how” stream. Behavioral research with normal

participants shows many examples of dissociations between systems for phenomenal awareness and visually guided actions, although this research cannot make claims about the anatomical locus of the effects. Patient research shows double dissociations between those who can identify but not direct actions towards objects, and those who can use vision to guide their actions, but not to identify objects. In addition, other patients with spatial disorders of environmental disorientation suffer from ventral rather than dorsal stream lesions. Furthermore, tasks of visually guided actions in PET consistently show activation of the superior parietal lobe.

The task at hand, then, is to try to classify the different functions of the posterior parietal lobe. Is visually guided action simply a subset of larger visuospatial functioning as Ungerleider and Mishkin (1982) originally proposed? Alternatively, is it more appropriate to divide the systems by the functions they subservise rather than the type of visual information entering the system? As we will discuss in more detail in this section, instead of choosing between “where” and “how”, another way to approach the problem is to categorize the posterior parietal lobe structurally and functionally into somewhat distinct subsystems of spatial processing. Evidence from both monkey and human work suggests that distinct portions in the posterior parietal lobe subservise functionally different spatial tasks. In humans, the traditional dorsal stream may process egocentric “how” information in preparation for action, whereas inferior areas of the parietal cortex may play a role in more global spatial “where” processing involving multiple frames of reference.

### *3.1. Multiple representations of space in the posterior parietal cortex*

In primates, neurophysiological data involving distinct areas of the inferior parietal lobe support the claim that different parietal areas transform spatial information differently for different actions (Colby & Goldberg, 1999; Rizzolatti, Fogassi, & Gallese, 1997; Snyder, Grieve, Brotchie, & Andersen, 1998). A number of studies have investigated the different egocentric reference frames involved in the spatial representations of areas lateral intraparietal (LIP), ventral intraparietal (VIP), medial intraparietal area (MIP) and anterior intraparietal (AIP) in the inferior temporal lobule of the monkey. These areas can be differentiated by their representations of egocentric visual space. The neurons in LIP have receptive fields that are defined relative to the retina, and combine visual and eye-movement information to form an eye-centered representation of space (Colby, 1998). VIP neurons can be purely visual neurons or visual and tactile neurons. Some of the bimodal neurons link gaze-independent visual receptive fields with tactile receptive fields on the face. Thus, these neurons code space in a head-centered rather than a retinocentric coordinate system and may specify goals for movements of the head and mouth (Colby & Goldberg, 1999). MIP neurons are selective for stimuli within reaching distance and are thought to provide spatial information for visually guided reaching movements. Neurons in AIP show different responses from those in MIP because they represent the shape of a grasping hand rather than the object’s egocentric position.

Sakata et al. (1997) questioned whether the signals concerning 3D features are processed in the inferotemporal cortex and sent to AIP or whether the signals are

processed in the parietal cortex itself. They found evidence that these parietal neurons code 3D shape and orientation of objects in space. One task required the monkey to grasp one of six different objects in three different sizes. They found highly selective visual-dominant neurons for each of the six objects. Their results suggest that the visually responsive neurons in area AIP may represent different simple geometric shapes. Further studies reported by Sakata et al. suggest that some of the parietal visual neurons may discriminate surface orientation. Using a stereoscopic display, they found that axis-orientation and surface-orientation selective neurons responded much more strongly to the stereoscopic stimulus than to one presented monocularly. Although studies have found that neurons in the inferotemporal cortex respond to 2D images of objects just as strongly as they respond to real 3D objects (e.g. Tanaka, 1993), Janssen and colleagues (Janssen, Vogels, & Orban, 1999, 2000) recently found inferotemporal neurons that are specifically sensitive to 3D shape as defined by stereopsis. The work by Sakata et al. suggests that the posterior parietal cortex may be at least equally as important for the perception of 3D structure and orientation mediated by stereopsis as the inferotemporal cortex.

These results support the findings of several studies in humans that suggest binocular information is important for accurate visuomotor control (Marotta, Behrmann, & Goodale, 1997; Servos, 2000; Servos & Goodale, 1994). For example, Marotta et al. (1997) tested grasping behavior in visual agnostic patients when binocular cues were reduced. Although normal participants can rely on pictorial information processed by the ventral stream to inform grasping when binocular cues are taken away, visual form agnostics cannot. Thus, their grasping of objects becomes impaired without binocular information. The findings of Sakata et al. strongly suggest that posterior parietal function is not limited to movement and position perception, but also includes the perception of 3D shape and orientation mediated by stereopsis. A main purpose of this 3D representation of objects may be to visually guide actions such as grasping objects as suggested by Milner and Goodale (1995), rather than to identify objects. However, this evidence also supports the findings of spatial disorders of orientation after parietal lesions (e.g. Von Cramon & Kerkhoff, 1993) that do not directly involve the visual guidance of action.

It is clear that the posterior parietal cortex is part of the network involved in the visual control of action. A history of human lesion studies involving Balint's syndrome and optic ataxia clearly suggest the posterior parietal lobe as the endpoint of a dorsal visual stream responsible for directing egocentric actions on the world. There is also evidence for processing of allocentric spatial functions in the posterior parietal cortex. Deficits in spatial tasks of orientation and localization after posterior parietal lesion were seen in Von Cramon and Kerkhoff (1993) review. Furthermore, the condition of unilateral neglect, regardless of whether it is attentionally based, illustrates an example of global spatial deficits as a result of posterior parietal damage. Neurophysiological studies have also found separate world-centered representations of space in the parietal cortex in monkeys (Snyder et al., 1998). Snyder et al. (1998) cleverly distinguished between body- and world-centered visual signals by presenting targets at identical retinal locations and rotating the body without rotating the head

(body-centered) or rotating the body with the head (world-centered). They found that cells with body- and world referenced gain fields were segregated anatomically. Cells in LIP were predominately body centered, whereas neurons in area 7a were predominantly world centered. Area 7a projects heavily to the parahippocampal gyrus in primates, an area thought to be involved in topographical memory and navigation.

### 3.2. *Dissociable structures and dissociable functions*

This paper has examined a solution to defining the posterior parietal lobe by structurally and functionally organizing “where” and “how” within the large structure. We asked whether it is possible to define two systems within the dorsal stream both involved in spatial perception, but involving qualitatively distinct types of processing. One hypothesis is that in humans, the inferior parietal lobule is responsible for more enduring, conscious representations underlying spatial cognition and complex spatial behavior (Milner, 1997; Perenin, 1997). In contrast, the superior parietal area may be responsible for short-lived spatial representations and on-line transformations of space for action. Functionally, the posterior parietal lobe may be defined by the frame of reference used in the spatial task. A spatial discrimination task such as spatial localization or mental rotation may involve frames of reference external to the viewer, using either environmental or object-relative frames. In contrast, visually guided actions as well as judgment tasks requiring viewer-relative decisions, involve an egocentric frame of reference, in which the target object must be processed relative to the observer’s momentary position.

Within the realm of visuospatial disorders in neuropsychological patients, specific deficits have been associated with distinct areas. Perenin and Vighetto’s (1988) review of optic ataxic patients led them to conclude that lesions were focused in superior areas of the posterior parietal lobe in either the right or left hemisphere. In contrast, unilateral neglect is most often classified as a result of damage to the inferior parietal lobule, specifically in the right hemisphere (Heilman et al., 1994). Although both types of visual deficits were historically classified under a broad spatial disorder like Balint’s, it is clear that there are distinct differences between the disorders. Perenin (1997) illustrated a dissociation between optic ataxia and unilateral neglect using a pointing task and a task involving subjective localization of body orientation. In the pointing task, optic ataxic patients showed systematic pointing error to the side of the lesion with their contralesional hand. Neglect patients showed no evidence of this systematic pointing bias toward the side of the lesion. In contrast, the neglect patients showed a marked shift of their subjective straight ahead that they did not show with pointing performance.

Whereas the distinction between inferior and superior regions holds true when looking at specific dissociations in neuropsychological patients, most results from brain imaging studies on normal participants have not been explicitly evaluated in this way. From the studies reviewed earlier, there are some consistencies that support this organization of the posterior parietal lobe, but there are some discrepant findings as well. Consistent with this proposal, tasks involving visually guided actions

involve superior parietal activation, including the intraparietal sulcus (e.g. Grafton et al., 1992, 1996; see Petit, Orssaud, Tzourio, Mazoyer, & Berthoz, 1997 for a PET review). Tasks that have examined non-motor spatial localization and judgment tasks, however, have found both inferior and superior parietal activity (Aguirre & D'Esposito, 1997; Haxby et al., 1993; Kosslyn et al., 1998). In addition to the parietal activities, these tasks were associated with premotor activity. This premotor activity suggests that participants may have been using motor processes to solve the given task. It is difficult to distinguish whether activation in parietal and motor areas is a result of spatial representation or motor strategies (see also Parsons, 2001). More finely controlled within-subject neuroimaging experiments are necessary to examine separate processes for spatial representation and action.

In addition to a distinction between conscious global spatial processing and visually guided action, dissociable parietal systems may be defined based on the frame of reference used in the task. The differential use of reference frames could help to clarify the inconsistencies seen in posterior parietal lobe function. The goal of the task is related to the reference frame used. A visually guided action requires an egocentric transformation of space. Alternatively, long-lasting representations of space are better suited to environmental or object reference frames that do not change over time with respect to the observer. Future human studies should compare spatial localization tasks involving object, environmental, egocentric frames of reference to determine whether differential mechanisms and brain areas are involved in the tasks. Holding the stimuli and response constant, but changing the decision task, would control for uncertainties in the present literature that result from comparing across studies.

Stein (1991) organized the posterior parietal lobe based on the idea that space can be defined by how it relates to ourselves. He defined 'personal space' as knowledge of position of body orientation, mediated by the superior parietal lobe; 'peripersonal space' as the space in which we can reach out and touch objects, mediated by area 39, a portion of the inferior parietal lobe; and 'extra-personal space' as space beyond which we have egocentric information about the location of object, mediated by area 40 of the inferior parietal lobe. Similar distinctions of egocentric space are apparent in the monkey neurophysiology literature. As described earlier, neurons in the intraparietal sulcus of the macaque can be differentiated by their egocentric representation of space (e.g. eye, head, arm, grasp). More evidence is needed to determine whether the human parietal systems can be differentiated on the basis of frame of reference alone. Functional neuroimaging studies that require decisions relative to the egocentric frame, without visually guided action, could help to clarify this question.

#### **4. Conclusions**

There is an abundance of literature involving the cortical visual systems in cognitive, neuropsychological, neurophysiological, and neuroimaging domains. This review brought together the different domains of research in an attempt to review the

concept of “two visual systems”. The solution proposed in this paper does not choose between “where” and “how”, but rather distinguishes between them structurally and functionally within the posterior parietal lobe. In effect, the proposal involves separate systems for spatial perception and visually guided action within the parietal lobe itself. Furthermore, this review suggests that it may be possible to generalize this distinction even further by the frames of reference used to perform spatial tasks.

Within this review, we aimed to clarify the posterior parietal lobe’s role in spatial representation. Neuropsychological evidence supports the distinction between superior and inferior parietal areas. A close look at the functional imaging research mostly supports this distinction with evidence from visually guided action studies, but findings from spatial non-motoric tasks are less clear. We suggest that motor strategies used to solve the tasks may make the differentiation between areas more difficult to see in neuroimaging studies than in neuropsychological research.

Examining frames of reference can help to differentiate between spatial processing mechanisms. The differentiation between visually guided action and spatial representation involves a distinction between frames of reference used in spatial tasks. Visually guided actions require egocentric transformations of the visual information whereas other spatial representations may be based in multiple frames of reference. Future studies using converging cognitive neuroscience methods are needed to determine whether spatial processing in humans can be dissociated structurally and functionally on the basis of frame of reference alone.

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