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Marlene Behrmann and Joy J. Geng

Moving one's eyes to view a fly sitting on one's forearm requires that one knows the spatial position of the fly. However, the process of spatial representation is fraught with problems. The tactile stimulation provided by the fly is initially registered in somatosensory cortex but the eye movement is executed to a position defined by the direction and distance from the current retinal position. Of course the sensory inputs, either visual or somatosensory, are subject to the inhomogeneities of their receptor surfaces with greater representation for the fovea in vision and for the fingers, lips, and tongue in touch, making correspondences between the modalities difficult. To complicate matters further, spatial location cannot be defined absolutely and therefore has to be described relatively, with respect to a reference frame with an origin and axes. How spatial position, defined in one modality and one set of coordinates, is represented and then translated to another set of coordinates has been the subject of numerous investigations, but still remains poorly understood.

One way of addressing these issues is to study the behavior of individuals who suffer from hemispatial neglect, a disorder in which the patients fail to orient towards or report information that appears on the contralateral side of space (McGlinchey-Berroth 1997; Driver and Mattingley 1998; Vallar 1998; Bisiach and Vallar 2000; Bartolomeo and Chokron 2001; Driver and Vuilleumier 2001). Neglect occurs most frequently following lesions to the inferior parietal lobule especially on the right (Bisiach and Vallar 1988; Stone et al. 1993; Vallar 1993, 1998; Milner 1997), and so we refer to neglect as 'left-sided' throughout this chapter. Patients with neglect may fail to notice objects on the left of a scene, may ignore words on the left of a page or food on the left of a plate, and typically omit to copy features on the left of a figure while preserving the corresponding features on the right. They may also show neglect of contralesional information in other sensory modalities, such as audition, somatosensation, and olfaction, and the deficit may even impair their ability to plan contralesional saccades or manual movements (Behrmann and Meegan 1998; Behrmann et al. 2001). Importantly, the failure to process contralateral information is not attributable to a primary sensory or motor problem. Rather, neglect is thought to occur because neurons in one hemisphere have predominant, although not exclusive, representation of the contralateral side; therefore, removing neurons impairs spatial representations for contralateral positions to a greater extent than those for ipsilateral positions (Pouget and Driver 2000; Rizzolatti et al. 2000; Cate and Behrmann 2002).

The specific question to be addressed is: When patients ignore information on the contralateral left, what is it left of? Furthermore, is the same form of spatial coding undertaken in different sensory modalities? By examining what coordinates are used to determine the midline such that information to the left of it is neglected, we may obtain an understanding of how spatial position

is coded in parietal cortex and how cross-modal translation may occur. A number of potential reference frames can be used to define positions in space. These can be divided into two broad classes: objects and locations can be defined **egocentrically** (i.e. relative to the vantage point of the viewer) or **allocentrically** (i.e. from an extrinsic vantage point that is independent of the viewer's position). We start by reviewing the relevant neuropsychological findings that provide evidence for different reference frames, in both vision and other modalities, and then briefly review associated evidence from single-unit recording studies and functional imaging.

Neuropsychological evidence

Spatial reference frames

Egocentric reference frames

Many studies have examined spatial representations defined by an origin and axes aligned with the midline of (a) the eyes or vertical meridian of the visual field, (b) the head, (c) the trunk, and (d) the longitudinal axis of the limb that is involved in executing an action, such as the arm. To determine the role of different reference frames in coding spatial position, the experiments typically probe patients' ability to respond to a target that lies on the left or right of one midline which is rotated out of alignment from another. For example, to examine the individual contribution of a reference frame centered on the eyes, we recorded the latency and accuracy of saccades in neglect patients to targets presented individually at 5°, 10°, or 15° to the left or right of the midline of the eye or retinal axis (Behrmann et al. 2002a,b). In the baseline condition, the midline of the eyes was aligned with the midline of the head and trunk as well as the environment (i.e. subjects looked straight ahead) (Fig. 1(a)). In other conditions, the eyes were deviated to the right or left while the head, trunk and midline remained straight ahead (Figs 1(b) and 1(c)). In the baseline, the detection of the targets fell along a gradient with best performance on the right and poorest on the left (of all reference frames). When the midline of the eyes was rotated out of alignment with the other midlines, latency (and also accuracy to some extent) was affected by position defined relative to the eye: detection was good for targets to the right of the retinal axis and poor for targets to its left. Interestingly, there was further modulation of detection with the position of the eye in the orbit; when the eyes were deviated 15° to the right and the targets to the left of the fixation were sampled, neglect was significantly ameliorated compared with the same situation when the eyes were straight ahead. When the eyes were deviated to the left, there was no change in performance, probably because these targets (right of fixation) are already acquired well and there is no room for additional improvement. Support for retinocentric coding is also provided by many other studies (Kooistra and Heilman 1989; Nadeau and Heilman 1991; Duhamel et al. 1992; Vuilleumier et al. 1999) and consistent evidence for an influence of line-of-sight or orbital position has also been obtained in both humans (Bisiach et al. 1985) and animals (Andersen et al. 1985).

A spatial code defined with respect to the midline of the head is still somewhat controversial. Although Karnath *et al.* (1991) found no modulation of neglect with changes in head orientation in neglect patients, the combined influence of target defined retinally and modulated by orbital position reported above (Behrmann *et al.* 2002*b*) codes position with respect to the head, suggesting some contribution by the midline of the head. There is also support for a head-based reference frame in nonhuman primates (Brotchie *et al.* 1995). Evidence for coding with respect to the trunk midline is more robust. Karnath and colleagues, for example, have argued that the midline of the trunk (body-centered reference frame) plays a fundamental (perhaps exclusive) role, serving as the anchor or midline for dividing space into left and right (Karnath *et al.* 1991, 1993, 1996). In their study, there was significant amelioration of neglect when the patient's trunk was rotated



Figure 1 Schematic depiction of experiment on eye movements and reference frames. The subject is seated in an arc of LEDs with a speaker used to emit auditory signals to help elicit and maintain the subject's fixation. (a) Baseline condition with midline of eyes, head, and trunk aligned with the environmental midline. (b) Eyes right (ER) and (c) Eyes left (EL) with the midline of the eyes rotated 15° right or left but the midline of the head and trunk aligned with the environmental midline. The broken line indicates the position of the eyes and the solid line the position of the head and trunk. (Adapted from Behrmann *et al.* 2002*b*).

to the left compared with the baseline condition, although the neglect was not exacerbated by trunk rotations to the right, a result which they acknowledge is puzzling (see also Karnath (1997) for further discussion and consideration of vestibular and optokinetic variables, and Farnè *et al.* (1998) for a more general evaluation of these findings). Support for the role of the midline of the trunk is also obtained from studies by Chokron and Imbert (1993) and Beschin *et al.* (1997).

Rather less research has been done to evaluate the role of the position of the limb on neglect performance. In one tactile exploration study, Bisiach *et al.* (1985) manipulated the placement of the right limb such that the workspace of the limb either fell along the midline of the trunk or extended into the right side of space (as the board to be explored tactually was placed to the right). Performance did not differ in these conditions, suggesting that the limb coordinates are not crucial in affecting neglect (but for affirmative evidence in monkeys, see Graziano and Gross (1996)).

However, a recent study suggests that there may be some involvement of limb coordinates in neglect, although this may primarily involve the spatial position of the limbs in relation to each other. Aglioti *et al.* (1998) applied bilateral stimulation to the dorsum of the hands when the hands were placed either straight ahead (anatomical position) or one over the other. When the hands were crossed, the crossing could occur across the midline of the body or just in the right or in the left hemispace. Whereas extinction of the stimulus on the left-hand was prevalent in the anatomical position, in the crossed position there was both improved detection of the stimulus delivered to the left hand as well as poorer detection of the right-hand stimulus, and this was the case irrespective of whether the hands were positioned on the left, on the right, or across the midline of the trunk. These findings suggest that the spatial position of a tactile stimulus to one hand is coded with some sensitivity to the location of the other limb and is independent of the midsaggital plane of the trunk.

The studies reviewed thus far clearly point out the modulation of the severity of the neglect as a function of the midline of the trunk, the gaze angle or line-of-sight, and the position of the limb, and perhaps, albeit to a lesser extent, the midline of the head. Whether or not these various egocentric frames are truly separable from each other, and hence independent, or whether they are contingent on each other to varying degrees still remains to be determined.

Allocentric reference frames

Just as a number of different reference frames can be defined egocentrically and can influence performance differentially, so too can different allocentric reference frames. Most research has focussed on a reference frame defined with respect to the midline of a visual scene or environment, or on one defined with respect to the midline of individual objects or perceptual units in the scene.

The derivation of an environment-centered frame requires computations involving gravitational forces on the otolith organ of the vestibular system, visual input to define environmental landmarks with respect to gravity, and proprioceptive and tactile information to provide a sense of the body's posture in relation to gravity. Mennemeier *et al.* (1994) have argued that the environmental frame is perhaps the most important, and is even more salient than a viewer-based frame. Their conclusion is based on a line bisection study in which the environmental and body-centered frames were brought into opposition by rotating the subject's body in left, right, prone, and supine positions. The critical finding was that the patients' bisection errors were predicted better by the environmental than body-centered frames, leading the authors to conclude that environment coordinates dominate in coding spatial position.

In the last few years, considerable evidence has accumulated suggesting that spatial position may also be coded with respect to the midline of an individual object. The evidence comes from several studies showing that patients fail to report information appearing to the left of the object midline even when this information is located to the right of the midline of the viewer and/or the environment (Driver and Halligan 1991; Behrmann and Moscovitch 1994; Behrmann and Tipper 1994; Humphreys and Riddoch 1994*a*; Pavlovskaya *et al.* 1997; Young *et al.* 1990) (but see Farah *et al.* (1990) for contradictory evidence).

One of the earliest documented examples of object-based neglect is from patient NG, who had right-sided neglect and who failed to read the rightmost letters of a word. This was true when the word was presented vertically and in mirror-reversed format, and even when she was required to spell words backward (Caramazza and Hillis 1990*a*,*b*). Arguin and Bub (1993*a*) also showed that their patient's inability to report a target letter in a horizontal array of four elements depended on the object-relative position of the letter not the viewer-relative position. In a series of studies, Humphreys, Riddoch and their colleagues have also documented object-based neglect, showing that patients neglect letters positioned to the left of individual words.

(Humphreys and Riddoch 1994*a*,*b*; Riddoch *et al.* 1995). Interestingly, these same patients show neglect for information on the right in multiple-stimulus displays simultaneous with the object-based effects, providing support for accounts that posit the involvement of multiple spatial frames and coding between as well as within objects (see Haywood and Coltheart (2000) and Subbiah and Caramazza (2000) for a discussion of neglect dyslexia and other object-based neglect findings).

Although all the studies cited above use letters or words as stimuli, object-based neglect has also been reported in studies that use other types of stimuli. For example, Young et al. (1990) reported that their patient performed poorly at identifying the left half of chimeric faces even when the faces were presented upside down and the relative left chimera occupied a position on the right side of space, again suggesting that the left of the object is disadvantaged even when it appears on the right of the viewer. The studies of Pavlovskaya et al. (1997) and Grabowecky et al. (1993) used geometric shapes and showed that information falling to the left of the center of mass of an object was less well detected than information appearing to the right. These data presuppose a computation of a center of mass that is specific to the object, the subsequent determination of the object midline, and the neglect of information to the left of this midline (Driver and Halligan 1991; Driver et al. 2002, 1994; Karnath and Niemeier 1992). The failure to orient towards and process the left half of the chimera is also evident in eye movements. Walker and Findlay (1996) reported that their patient RR restricted his fixations to the right side of an individual object. This object-based pattern could not be attributed to the failure to fixate the left of a display as RR could scan both the left and right of scenes and could also make left saccades when the left half of an object was presented in his left visual field (Walker and Findlay 1996; Walker and Findlay 1997).

The existence of an object-centered representation has not gone without challenge. Driver and colleagues (Driver 1999; Driver and Pouget 2000), for example, have suggested that there is no need to invoke a reference frame that is tied to an individual object. Rather, they have argued that the left and right of an object may be coded solely from one's initial egocentric (and viewpoint dependent) encounter with the object. The claim is that when an object is viewed, left and right are assigned in a purely egocentric manner in accordance with the strength of an underlying attentional gradient (Driver 1999) (for additional evidence of an attentional gradient, see Kinsbourne (1993)). A similar claim is made by Pouget and Sejnowski in their modelling work (Pouget and Sejnowski 1997*a*,*b*; Pouget *et al.* 1999); because the left of the object always appears at the poorer end of the gradient relative to the right of the object, in both absolute and relative egocentric space, the ipsilesional information will always dominate over the contralesional information, which will then be neglected.

This view suggests that object-centered coding is not necessary and that the same pattern of data may be obtained by simply assuming an egocentric gradient. Indeed, Mozer (2002) has conducted simulations of so-called object-centered neglect in the context of a computational model MORSEL, which assigns spatial position purely egocentrically (by virtue of a retinotopic attentional gradient) and does not have any object-centered representation. He shows that this implementation can account for a host of object-centered neglect effects (Driver and Halligan 1991; Arguin and Bub 1993*a*; Driver *et al.* 1994; Pavlovskaya *et al.* 1997). In all these cases, the left of the object always appears further left than the object right, both absolutely and relatively, and so is less activated.

An experimental paradigm in which the left of the object does not always appear further left than the right of the object can also reveal neglect (Behrmann and Tipper 1994, 1999; Tipper and Behrmann 1996). In one such paradigm (Fig. 2), a barbell appears on a screen with the left and right circles colored blue or red (the color remains constant for a single subject but is counterbalanced across subjects). In the first (static) condition, a position on the right or left is probed and this position is both right and left in both viewer and object coordinates and serves as



Figure 2 (a) Depiction of the static and rotating conditions in the barbell paradigm with identical final displays. One circle of the barbell was colored red and the other was colored blue. (b) Mean reaction time for four patients with neglect to detect the target on the left and right in the static and moving conditions. Note that, because a fifth subject made so many errors, his data are not included here in the RT analysis, but they reveal the same pattern with accuracy as the dependent measure. (Adapted from Behrmann and Tipper 1994.)

a baseline against which to compare performance in the second condition. In the critical rotating condition, the barbell is previewed and then undergoes a rotation of 180° so that the left, defined by the barbell, appears on the right of the viewer, and the right of the barbell appears on the left of the viewer. When a spatial position on the viewer-defined right or left is probed, both accuracy and speed of detection are influenced by whether this position occupies a right or left position, defined by the object. Thus, when the probe appears on the viewer's right but is on the left of the barbell (which rotated into that side), detection is poorer than when the position is both viewer-and object-right. Similarly, when the probe appears on the viewer's left, detection is better when the position occupies the right of the barbell (which rotated in) compared with when it is both viewer- and object-left.

In this experiment, because the left of the barbell does not fall further left than the right, a simple egocentric gradient cannot obviously account for the data. Instead, Mozer (2002) simulated the findings in the following way. When the barbell appears initially, the activation of the left and right is set by the strength of the egocentric gradient. As the barbell turns, because of the hysteresis of the system, the initial activation is pulled along with it and, through covert attention, is carried to the new location. Probing the new location then yields poor performance even when the probe appears on the right as the activation associated with that location has been carried there by the covert tracking of the moving barbell. According to Mozer, these simulations demonstrate that the results of the barbell studies do not necessarily implicate object-based representations (see Chapter 3.2 for further discussion of these issues and an approach to dealing with the egocentric versus object-centered issue).

An outstanding question is what mechanism would allow for the representation of the object and its parts under conditions of misorientation. When objects are translated in the picture plane, the left of the object always remains to the relative left of the right of the object, but this is not true when objects are rotated. Two potential processes have been suggested to deal with rotated objects. As described above, Mozer (2002) suggests that covert attentional tracking represents the left and right of a stimulus, initially defined egocentrically, as the objects rotate. The second suggested process is mental rotation; Buxbaum *et al.* (1996) have suggested that, in the case of misoriented stimuli, the stimulus is first normalized to its upright orientation through mental rotation and then the relative left is neglected. This implies that an egocentric gradient can still explain the empirical results; in the case of the barbell, the patients transform the rotated barbell to its canonical upright position and then neglect the left of the 'upright' barbell (i.e. now defined gravitationally or egocentrically). They base their claim on the fact that they only obtained object-centered results when they specifically instructed a neglect patient to perform the mental transformation on the barbell paradigm.

However, both proposed mechanisms appear to encounter problems. With regard to covert tracking explanations, it is now well established that patients with neglect have problems directing covert (and overt) attention contralesionally (Arguin and Bub 1993b; Posner *et al.* 1984). Functional imaging studies have also shown that the right parietal region plays a critical role in directing attention to the left (Corbetta *et al.* 1993; Nobre *et al.* 1997); after damage to this region, as in the case of neglect, attentional monitoring, either covert or overt, would be compromised. There is also the problem of how such a tracking system might operate when stimuli are static and do not need to be tracked, for example when a stimulus is displayed inverted as in the faces study by Young *et al.* (1990) or the words study by Caramazza and Hillis (1990a). In these cases, there is no opportunity for covert attention to carry the activation of the egocentric gradient along with it. It is precisely under such conditions that one might invoke a process of normalization via mental rotation.

However, the involvement of mental rotation to account for the results is itself problematic. Unlike Buxbaum *et al.* (1996), Behrmann and Tipper (1994, 1999) did not explicitly instruct the patients to perform mental rotation and yet they still obtained the critical pattern of results. Moreover, nothing in the demands of the task (simple light detection) would have prompted patients to engage in what is generally considered to be an effortful time-consuming process. Furthermore, it has been repeatedly demonstrated that the right parietal lobe plays a critical role in mental rotation (Alivasatos and Petrides 1997; Tagaris *et al.* 1997) and that, when it is damaged, mental rotation is significantly impaired (Farah and Hammond 1988). Because the neglect patients typically have extensive damage to parietal cortex, it is unlikely that they are capable of exploiting mental rotation processes. Therefore it is unlikely that object-centered effects emerge from covert attentional tracking or from normalizing via mental rotation; instead, an object-centered reference frame may exist, potentially in tandem with a reference frame that is defined by the viewer (Behrmann and Plaut 2002) (see also Chapter 3.2).

Support for a representation of spatial position, defined with respect to the midline of an individual object, has also been obtained from studies with animals. Olson and colleagues obtained recordings of single neurons in monkeys who were required to move their eyes to the left or right of objects (Olson and Gettner 1995; Olson *et al.* 1999; Olson 2001). Interestingly, the results showed that neurons in the supplementary eye field, a premotor area in frontal cortex, as well as in parietal cortex participate selectively when the monkey is planning to make an eye movement to the left of an object. This object-based directional selectivity occurs regardless of the direction of the eye movement required and the retinal position of the object, regardless of the exact visual features of the object, and regardless of whether the monkey was specifically following an object-centered instruction. These results point directly to a neural mechanism which might be responsible for locating positions in an object-based reference frame. Damage to neurons with object-left spatial selectivity would then give rise to the object-based neglect that is revealed by the patients (see Chapter 2.2 for a review of spatial representation studies in monkeys).

Cross-modal neglect

The question of which reference frames are compromised in hemispatial neglect has largely been investigated within single modalities, and in fact has been addressed almost exclusively in

the visual modality. However, evidence for cross-modal representations has been documented in behavioral psychophysics as well as in monkey physiology. Driver and Spence (1998), for example, have shown in a number of studies that attending to a stimulus in one modality can attract attention to stimuli from other modalities in that location. Similarly, bimodal neurons sensitive to visual and somatosensory information have been found in association areas such as premotor and parietal cortex (Graziano *et al.* 1994; Colby and Goldberg 1999). Furthermore, these neurons have receptive fields tied to shared arm centered reference frames (Làdavas *et al.* 1998) (see also Chapter 3.4).

In an early study of cross-modal extinction, Mattingley *et al.* (1997*a,b*) found cross-modal extinction both when a contralesional tactile stimulus was coupled with an ipsilesional visual stimulus and in the reverse condition. In this study, the patient's hands were occluded from view, but the visual stimulus was presented near the hand, just above the occluder. Extinction was more severe in the cross-modal condition than in the unimodal visual condition, but less severe than in the unimodal tactile condition. This asymmetry suggests that there are overlapping as well as discrete areas of representation for different modalities within an interactive network.

A host of recent studies have elucidated the cross-modal effects well. For example, the extent of the extinction appears to depend on the exact location of the visual stimulus, with greater extinction when the visual stimulus is presented near the body (di Pellegrino *et al.* 1997; Làdavas *et al.* 2000; Maravita *et al.* 2000). The extinction is reduced when the visual stimulus appears near the contralesional hand. However, the mere presence of a visual stimulus in the vicinity of a passive hand, without vision of the hand, does not seem to be sufficient (Rorden *et al.* 1999; di Pellegrino and Frassinetti 2000; Làdavas *et al.* 2000), although proprioceptive information via movement of the arm does contribute significantly when vision is dissociated (Làdavas *et al.* 1997; Vaishnavi *et al.* 2001). These results reinforce the notion that cross-modal effects are produced by an interaction between converging visual and tactile stimuli and used to build multidimensional representations of a single action, object, or sensation.

One question that follows from these studies in extinction patients is why cross modal effects occur if the areas containing cross-modal neurons are damaged. Intriguing suggestions come from functional magnetic resonance imaging (fMRI) studies by Macaluso *et al.* (2000*a,b*; 2002). They presented flashing light-emitting diode (LED) stimuli near the left or right hand while maintaining central fixation. LED stimulation occurred either alone or with a tactile vibration delivered to the right hand. Although the lingual gyrus is generally considered to be a unimodal sensory area, the authors found stronger activation in the left lingual gyrus in response to right visual stimulation when simultaneous tactile stimulation occurred. Conversely, there was a nonsignificant reduction in right lingual gyrus when left LEDs were accompanied by right tactile stimulation. These findings suggest that feedback from multimodal association areas to primary sensory areas may act to support processing of a single spatial location when multiple modalities present converging information.

Therefore the studies with extinction patients can be thought of as reflecting a competitive interaction between both primary sensory and association areas representing disparate locations in space. Although only visuotactile studies have been discussed so far, other cross-modal effects have also been found (Làdavas and Pavani 1998; Bertelson *et al.* 2000). Information from multiple sensory sources that converge can increase the likelihood of attention being distributed to that location. Thus the competitive strength of a particular stimulus is increased when multiple sources of information support its presence. When the right parietal network is damaged, cross-modal sensory information on the ipsilesional side can cause extinction via the distributed network of activation in primary sensory and association areas. Similarly, cross-modal contralesional information can help support weak representations in another modality.

Functional imaging and spatial reference frames

Insight into the neural mechanisms involved in the computation of spatial reference frames has also been gained from recent studies using positron emission tomography and fMRI. The studies that have compared the neural bases of egocentric and allocentric reference frames most directly use the same visual stimuli but require different judgments in the two conditions (Fink *et al.* 2000*a*). For example, Galati *et al.* (2000) asked participants to determine whether a vertical bar, which intersected a horizontal line, was located to the left or right of their subjective midline (egocentric) or the midpoint of the horizontal line (object). As a nonspatial control, subjects were asked to determine whether the color of the vertical bar was lighter or darker than that of the horizontal bar. Their results showed that both spatial tasks activated a common network of frontoparietal areas, including the right posterior parietal and right frontal premotor cortex (Brodmann areas 7 and 6 respectively), but that the activation in the object judgment task was much less extensive (only 12 per cent of that in the egocentric condition).

Similar findings from other studies have found additional areas such as left inferior parietal, dorsolateral prefrontal cortex, cerebellar vermis, bilateral precuneus, and bilateral superior parietal cortex to be activated by both egocentric and allocentric tasks (Faillenot *et al.* 1997; Fink *et al.* 1997; Creem *et al.* 2001). Similar areas of activation have been found in PET studies comparing reaching or grasping with perceptual matching (Faillenot *et al.* 1997; Honda *et al.* 1998) and line bisection in near compared with far space (Weiss *et al.* 2000). These results suggest that this network is involved in action-oriented processing.

Areas of activation when object conditions are subtracted from egocentric conditions include right inferior temporal gyrus, bilateral cuneus, and extensive frontal areas, as well as those described above (Fink *et al.* 1997; Creem *et al.* 2001). Areas unique to object conditions include extrastriate, bilateral occipital, lingual gyrus, right hippocampal, inferior occipitotemporal, and inferior parietal cortex (Fink *et al.* 1997; Honda *et al.* 1998; Creem *et al.* 2001). Fink *et al.* (2000*b*) investigated object-based spatial representations further by contrasting one- and two-dimensional objects. Participants were asked to determine whether a line was correctly bisected (Landmark task) or if a dot was located in the center of a square (Squaremark task). The interesting finding was expressed in an interaction implicating the right intraparietal sulcus in the Landmark task and the lingual gyrus bilaterally in the Squaremark task. The authors suggest that both areas are preferentially activated in response to object-based spatial processing, but that more ventral stream areas are recruited when an object forms a better *gestalt*. Both egocentric and object-based tasks have resulted in greater right-hemisphere activation (Vallar *et al.* 1999; Fink *et al.* 2000*a*).

While a frontoparietal network appears to be involved in egocentric and object-based reference frames, it is still unclear what role the parietal lobe plays in creating a coherent perceptual representation of spatial information. Lumer and colleagues (Lumer *et al.* 1998; Lumer and Rees 1999) have proposed that perception is dependent on the covariation of activation between multiple areas. Using binocular rivalry to dissociate subjective perception and sensory input, Lumer and colleagues found that extrastriate (Brodmann area 18/19) activation reflected changes in subjective perception of rivalrous stimuli, whereas activation in striate cortex did not. Consistent with this, activation in fusiform and temporal gyri was correlated with extrastriate activation when face and motion stimuli were used. Additionally, bilateral superior and inferior parietal cortex, right superior frontal cortex, and middle and inferior frontal gyrus activation were correlated with extrastriate activation, but only inferior parietal and inferior frontal regions were significantly more correlated during rivalry than during stable viewing.

These data suggest that a network of areas, operating in synchrony, is responsible for the experience of perceiving one stimulus to the exclusion of others. In particular, the frontoparietal network (predominantly in the right hemisphere) may mediate switching between perceptual

experiences (Rees 2001). Lumer and colleagues suggest that although switches in binocular rivalry are not spatial, they do involve the selection of a subset of available information over other subsets. It may be that frontoparietal areas are involved in both object-centered and egocentric spatial processing because this network is integral for the selection of spatial reference frames. This selection naturally interacts with the competitive strength of stimuli represented within each frame. The winner of the competition is then further processed by functionally specialized areas, which give rise to the emergent perception of a stimulus within a particular reference frame.

Further evidence supporting the notion of an integrative network including frontal and parietal areas being involved in selective perception comes from imaging and ERP data with extinction patients. The critical comparisons in these studies are (a) between bilateral stimulus trials in which the left stimulus is extinguished and those in which only one right visual field stimulus is present, and (b) between bilateral stimulus trials in which the left stimulus is extinguished and those in which both stimuli are detected. In the first case, perceptual report is the same but sensory information differs; in the second, sensory information is identical, but perceptual report differs. The interesting finding is that while some activation is preserved in the first comparison, a more extensive network of activation occurs when the left stimulus is reported (Marzi et al. 2000; Rees et al. 2000; Vuilleumier et al. 2001). For example, Vuilleumier et al. (2001) found preserved fMRI activation in right V1 and bilateral postero-inferior temporal areas when faces in the leftvisual field (LVF) were extinguished, but right V1, bilateral cuneus and fusiform gyrus, and left superior parietal cortex activation when the LVF face was reported as seen. Similarly, in their event-related potential (ERP) data, extinguished faces elicited normal early N1 and face-specific N170 activity, but only seen faces elicited P1 and P190 activity (although P190 may have been associated with eye movements specific to that condition). Thus, less competitive stimuli may become extinguished when neural information representing that stimulus is not synchronized in multiple areas at once.

Imaging studies offer fertile ground for understanding how networks within the brain may interact to produce the experience of a coherent spatial visual world (Bottini *et al.* 2001). Understanding how different regions of human parietal cortex map onto better understood monkey models of parietal areas promises to bring greater understanding to the contribution of this area to visuomotor function and representations of objects in space (Culham and Kanwisher 2001).

Concluding comments

The focus of this chapter has been on brain–behavior correspondences in the domain of spatial representation. The data from neuropsychological studies, fMRI studies, and neurophysiological investigations with nonhuman primates have been presented. While there is general convergence and agreement between these studies, the questions posed at the outset are far from being answered. Although we know that multiple spatial reference frames are used for coding spatial position, we do not know how these are coordinated to subserve integrated behavior. And, although we know that there is some cross-modal coding which might facilitate translation among different sensory modalities, much work remains to be done to understand exactly how this is achieved. There are also many issues which have not been addressed here. This chapter has focused exclusively on reference frames coding left and right, but similar questions apply with regard to other spatial dimensions such as up–down (vertical) and near–far (radial). It is known, for example, that some patients show 'altitudinal neglect' in which they omit more information from the upper than the lower portion of the array (Shelton *et al.* 1990) or vice versa (Butter *et al.* 1989; Halligan and Marshall 1989; Nichelli *et al.* 1993; Mennemeier *et al.* 1994; Pitzalis *et al.* 1997). Performance may also differ along the radial dimension, with some patients showing personal neglect (Guariglia

and Antonucci 1992; Beschin and Robertson 1997; Peru and Pinna 1997) and others showing neglect for peripersonal space (Halligan and Marshall 1991; Mennemeier *et al.* 1992) or extrapersonal space (Bisiach *et al.* 1986; Cowey *et al.* 1994). What spatial reference frames are used for coding space in the altitudinal and radial direction remain to be determined. Finally, how these different representations mediate outputs and action requires further investigation and exploration.

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