BRAIN REPRESENTATION OF OBJECT-CENTERED SPACE IN MONKEYS AND HUMANS

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■ **Abstract**   Visuospatial cognition requires taking into account where things are relative to each other and not just relative to the viewer. Consequently it would make sense for the brain to form an explicit representation of object-centered and not just of ego-centered space. Evidence bearing on the presence and nature of neural maps of object-centered space has come from two sources: single-neuron recording in behaving monkeys and assessment of the visual abilities of human patients with hemispatial neglect. Studies of the supplementary eye field of the monkey have revealed that it contains neurons with object-centered spatial selectivity. These neurons fire when the monkey has selected, as target for an eye movement or attention, a particular location defined relative to a reference object. Studies of neglect have revealed that in some patients the condition is expressed with respect to an object-centered and object-aligned reference frame. These patients neglect one side of an object, as defined relative to its intrinsic midline, regardless of its location and orientation relative to the viewer. The two sets of observations are complementary in the sense that the loss of neurons, such as observed in the monkey, could explain the spatial distribution of neglect in these patients.

INTRODUCTION

Many everyday behaviors involve the use of spatial information defined relative to an object-centered reference frame. Writing is an example. When I form a lower-case letter *t* by placing a horizontal stroke across a vertical stem, I place the stroke at a location defined relative to a reference object, the stem. The operation is spatial because the point at which the stroke crosses the stem is not marked in any way but instead must be gauged by reference to the stem's top and bottom. It is object centered, not body centered, as indicated by the fact that performance becomes inaccurate if visual guidance is prevented. Moreover, it is also object aligned, in the sense that I can place the stroke appropriately even if the stem is at an off-vertical orientation. Object-centered and object-aligned spatial operations are at the root of nearly all abilities that we think of as spatial, for example, map reading,

construction, and drawing. Spatial skills that depend only on egocentric local-
ization, such as orienting, pointing, and reaching, are few and rudimentary by
comparison, although they have been the subject of much more extensive neuro-
physiological study. In light of our deep reliance on object-centered spatial opera-
tions, it is reasonable to speculate that the brain contains neural systems in which
spatial information is represented explicitly with respect to an object-centered and
object-aligned reference frame. The aim of this review is to summarize current
knowledge bearing on this issue, obtained by means of single-neuron recording in
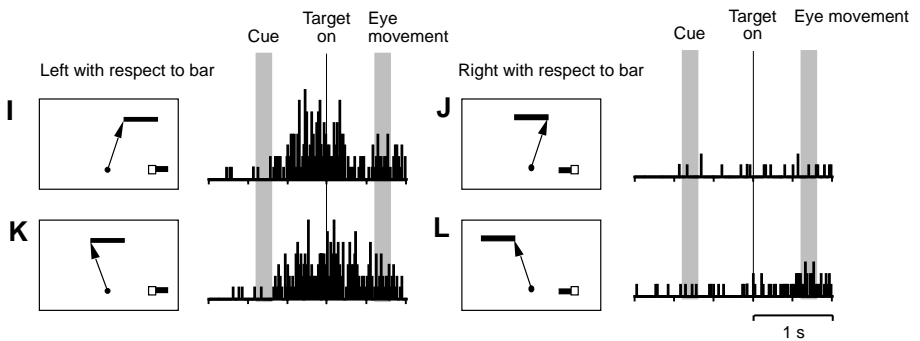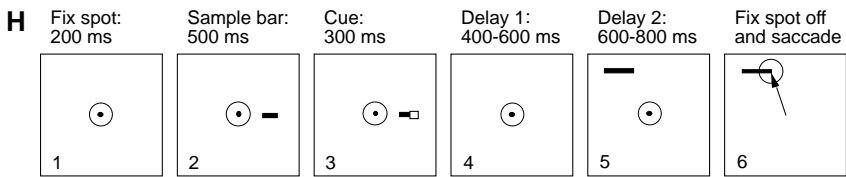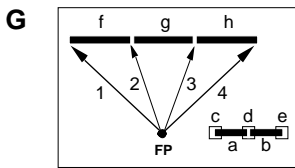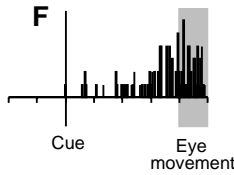monkeys and from studies of hemispatial neglect in patients.
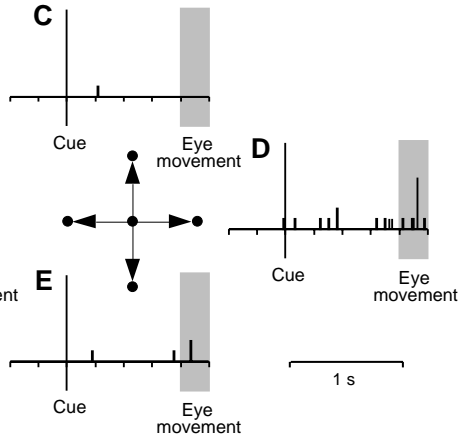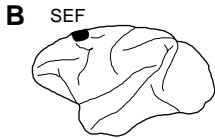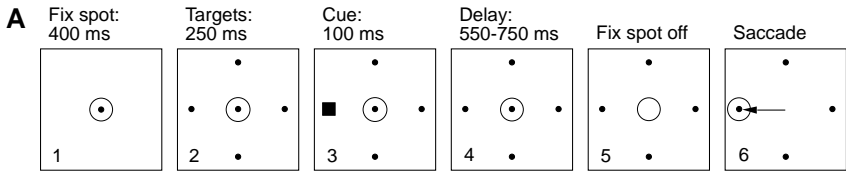
OBJECT-CENTERED SPATIAL SELECTIVITY

Object-Centered Spatial Selectivity in the SEF

BACKGROUND   One approach to understanding the neural mechanisms of object-
centered spatial cognition is to record from single neurons in the cerebral cortex of
monkeys while they perform tasks that require perceiving, remembering, attending
to, and making movements to locations defined with respect to an object-centered
reference frame. This approach has been taken in recent electrophysiological stud-
ies (Olson & Gettner 1995, 1999; Olson & Tremblay 2000; Tremblay et al. 2002).
These studies have focused on the supplementary eye field (SEF) (Figure 1*B*).
Since its discovery by Schlag & Schlag-Rey (1985), the SEF has generally been
viewed as a motor area involved in the control of eye movements because SEF
neurons fire when monkeys are planning saccadic eye movements and are selec-
tive for saccade direction (Schlag & Schlag-Rey 1987, Schall 1991). An example
of saccade-related neuronal activity is shown in Figure 1. In the context of the

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Figure 1   Data from an SEF neuron selective for saccade direction in the standard
ocular delayed response task (*A–F*) and selective for the object-centered location
of the target in the object-centered saccade task (*G–L*). (*A*) Sequence of events in
a representative trial of the ocular delayed response task. Each panel represents the
screen in front of the monkey. Circle: current direction of gaze. Arrow: eye movement.
(*B*) Location of the SEF. (*C–F*) Delay period discharge of an SEF neuron selectively
active when the impending eye movement will be directed to the target on the left (*F*)
as opposed to the targets at the three other locations (*C–E*). (*G*) Factors varying across
trials included location of sample bar (*a–b*) location of cue (*c–e*), location of target
bar (*f–h*), and direction of saccade (*1–4*). (*H*) Sequence of events in a representative
trial of the object-centered saccade task. Each panel represents the screen in front of
the monkey. Circle: current direction of gaze. Arrow: eye movement. The panel to the
left of each histogram indicates the location of the sample bar, cue, and target bar, and
the direction of the eye movement during trials on which the histogram is based. (*I–L*)
Delay-period discharge of an SEF neuron selectively active on bar-left trials regardless
of the saccade's physical direction. Adapted from Olson et al. (1999).

A

Fix spot:
400 ms

Targets:
250 ms

Cue:
100 ms

Delay:
550-750 ms

Fix spot off

Saccade

1

2

3

4

5

6

B SEF

C

Cue

Eye
movement

F

Cue

Eye
movement

D

Cue

Eye
movement

E

Cue

Eye
movement

1 s

G

f   g   h

1   2   3   4

c   d   e

a   b

FP

H

Fix spot:
200 ms

Sample bar:
500 ms

Cue:
300 ms

Delay 1:
400-600 ms

Delay 2:
600-800 ms

Fix spot off
and saccade

1

2

3

4

5

6

Cue   Target
on   Eye
movement

Cue   Target
on   Eye movement

Left with respect to bar

I

K

Right with respect to bar

J

L

1 s

ocular delayed response task (Figure 1*A*) this SEF neuron fired during planning of saccades to the left (Figure 1*F*) and not in other directions (Figure 1*C–E*). It would be natural to interpret this neuron's activity as representing the physical direction of the impending saccade. However, given the results shown in the figure, one cannot reject the alternative interpretation that it represents the location of the target with respect to a frame fixed to some external landmark, for example, the screen.

OBJECT-CENTERED SPATIAL SELECTIVITY   To dissociate neuronal activity related to the physical direction of a planned eye movement from activity related to the target's object-centered location requires the use of specialized tasks. One extensively used task is diagrammed in Figure 1*H*. At the beginning of each trial, a cue spot is presented on the right or left end of a horizontal bar (the sample bar). A delay ensues during which the monkey has to remember the instruction conveyed by the sample-cue display. Then another horizontal bar (the target bar) appears at an unpredictable location. After a further delay, offset of the fixation spot instructs the monkey to make a saccade to the end of the target bar corresponding to the cued end of the sample bar. The crucial feature distinguishing this task from the classic ocular delayed response task (Figure 1*A*) is that the monkey must hold an object-centered location in working memory during the post-cue delay period without knowing the physical direction of the impending eye movement. The direction of the eye movement cannot be known until the target bar appears because the target bar's location varies randomly from trial to trial (Figure 1*G*).

Recording from the SEF while monkeys perform the bar task has revealed that around half of the neurons exhibiting task-related activity fire at different rates during the post-cue delay period on bar-left and bar-right trials (Olson & Gettner 1995). Data from one neuron with object-centered spatial selectivity are shown in Figure 1*I–L*. Each histogram represents the neuron's average firing rate under a condition indicated by the inset to the histogram's left. This neuron fired strongly on trials when the instruction was to move to the target bar's left end (Figure 1*I, K*) and weakly when the instruction was to move to its right end (Figure 1*J, L*). Other factors including the retinal location of the cue and the physical direction of the eye movement had little influence on its firing rate. Subsequent studies have revealed that neurons selective for the bar-right condition predominate in the left hemisphere and vice versa, in conformity with the principle that each hemisphere preferentially represents the opposite half of space (Olson & Gettner 1995, Olson & Tremblay 2000, Tremblay et al. 2002). They have also shown that SEF neurons express object-centered selectivity with respect to off-horizontal axes. Some neurons, for example, fire at different rates on trials requiring movements to the top or bottom of a vertical bar (Gettner & Olson 1997, Olson et al. 1999).

INDEPENDENCE OF VISUAL FEATURES   The object-centered spatial selectivity of SEF neurons is an abstract spatial property largely unaffected by incidental details of the cues and reference objects used in the task. The unimportance of the cues'
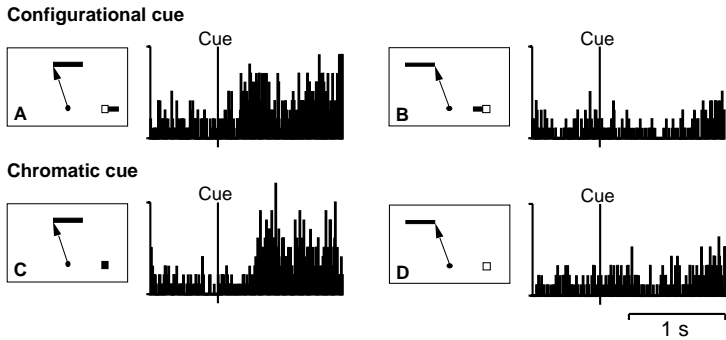
Figure 2 Data from an SEF neuron exhibiting object-centered spatial selectivity regardless of the visual properties of the cue conveying the object-centered instruction. The neuron fired more strongly on bar-left trials when the instruction was conveyed by presenting a spot on the sample bar's left (*A*) or right (*B*) end. It exhibited the same pattern of activity when a blue (*C*) or yellow (*D*) chromatic cue conveyed the instruction. Adapted from Olson & Gettner 1999.

visual properties has been demonstrated by use of a task in which the cues are alternately configurational (a spot presented on the left or right end of a sample bar) and chromatic (blue instructing a bar-left and yellow a bar-right response). SEF neurons exhibit object-centered spatial selectivity regardless of the type of cue conveying the instruction (Olson & Gettner 1999). Furthermore, the preferred object-centered direction remains the same. Data from a neuron firing more strongly on bar-left trials under both kinds of cue regimen are shown in Figure 2. For this neuron, as for the entire studied population, the only notable effect of cue type was on the timing: It takes longer (by ∼200 ms) for a chromatic than for a configurational cue to evoke object-centered activity. These findings indicate that neuronal activity in the SEF reflects the object-centered spatial instruction and not the incidental visual properties of the instructional cue.

The unimportance of the visual attributes of the reference object has been demonstrated by recording in a version of the task requiring the monkey to select as target the leftmost or rightmost of two dots instead of the left or right end of a continuous bar (Olson & Tremblay 2000). Most neurons show no effect of this manipulation, firing identically on trials in which the reference object is a bar and those in which it is an array of two dots. Moreover, in the few cases in which neuronal activity depends on the nature of the reference object, the effect takes the form of a change in the strength rather than the quality of the spatial signal. Figure 3 shows data from a neuron that fired more strongly under object-right conditions when the sample and target were an array of two dots. Thus neuronal activity in the SEF represents the location of a target relative to whatever set of elements in the visual display has been selected as a reference and made the object of attention, regardless of whether or not those elements form a continuous shape.
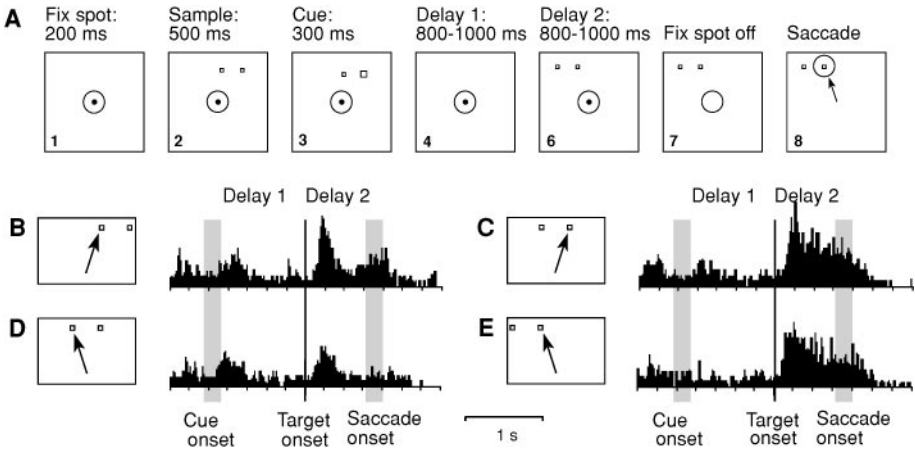
Figure 3   Data from an SEF neuron exhibiting object-centered spatial selectivity on trials in which the sample and target were an array of spots marking the ends of a virtual bar. The neuron fired more strongly on array-right trials (*C, E*) than on array-left trials (*B, D*). Adapted from Olson & Tremblay 2000.

INDEPENDENCE OF OBJECT-CENTERED RULE USE   Object-centered spatial selectivity does not depend on active selection of the target by an object-centered rule. This has been demonstrated by monitoring neuronal activity while monkeys perform a task requiring them to select as saccade target the rightmost or leftmost of two dots but to base their decision on the color of the target and not on its object-centered location (Tremblay et al. 2002). The sequence of events in a representative trial is shown in Figure 4*A*. A sample array first comes on, consisting of two white dots that define the ends of a virtual bar (panel 2); then a colored cue (red or green) appears on the array's left or right end (panel 3); then, after a delay, a target array appears, consisting of one red dot and one green dot (panel 5); finally, upon offset of the fixation spot (panel 6), the monkey must make an eye movement to the target element corresponding in color to the cue (panel 7). The cue can appear on either end of the sample array, and the target dot can appear on either end of the target array. Because there is no correlation across trials between the location of the cue and the location of the target, the monkey cannot follow an object-centered rule and must follow a chromatic match-to-sample rule. The behavior of SEF neurons in this task is very clear cut: They signal the object-centered location of first the cue and then the target. Data from a representative neuron are shown in Figure 4*C–J*. Histograms *C–F* represent neuronal activity under a subset of conditions in which the cue and target were green and the screen-location of each was directly above fixation. On trials in which the cue and target were on the left of their respective arrays (Figure 4*C*), the neuron fired vigorously, whereas on trials in which they were on the right (Figure 4*F*) it fired weakly. On trials in which the cue appeared at one object-centered location and the target at the opposite location (Figure 4*D–E*),
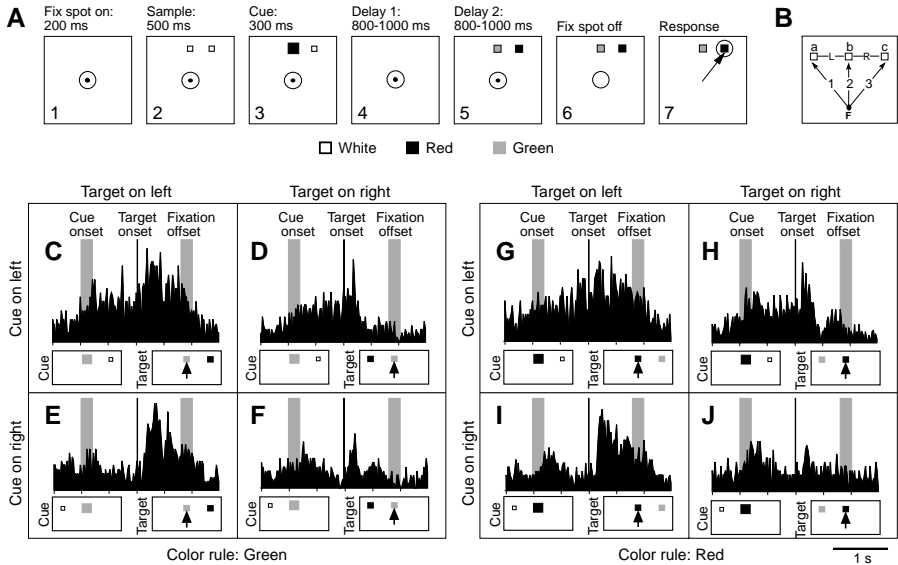
Figure 4 Data from an SEF neuron sensitive to object-centered location and insensitive to color, even on trials in which the monkey had to ignore the object-centered location and use color. (*A*) Sequence of events in a representative trial of the color task. Note that in this case the cue is to the left of the sample array and yet the correct response is to the rightmost element in the target array, which matches the cue in color. (*B*) Factors varying across trials included location of sample array (*L*, *R*), location of the cue (*a*–*c*), location of target array (*L*, *R*), and direction of saccade (*1*–*3*). On trials in which the cue and target were green, the neuron fired most strongly following presentation of the cue on the left of the sample array (*C*, *D*) and following onset of a target array in which the target was on the left (*C*, *E*). The pattern of activity was the same on trials in which the cue and target were red (*G*–*J*). Adapted from Tremblay et al. (2002).

the firing rate shifted, reflecting first the location of the cue and then the location of the target. The same pattern exactly was observed when the cue and target were red (Figure 4*G*–*J*). Like this neuron, most in the sampled population fired at a rate determined by object-centered location, although the monkey was prevented from selecting the target by an object-centered rule, and not at a rate determined by color, although the monkey was required to use a color-based rule. These results indicate that the essential function of neurons with object-centered spatial selectivity is not to represent the rule being used for target selection but rather to represent, relative to an object-centered frame, the location of the element to which the monkey is currently directing attention.

This conclusion is subject to one qualification. The experiment was carried out in monkeys trained to select targets by an object-centered rule in other contexts. The neuronal expression of object-centered spatial selectivity could have been a

product of object-centered training, even though it did not depend on the active use of an object-centered rule. To resolve this issue will necessitate recording from SEF neurons in monkeys trained to select targets by color and never to select them by object-centered location. This experiment, still in an early stage, has yielded data indicating that SEF neurons exhibit weak object-centered signals before training on an object-centered task and that the signals become stronger after training (Moorman & Olson 2002).

RELATION OF OBJECT-CENTERED TO OCULOCENTRIC SPATIAL SELECTIVITY   Some neurons exhibiting object-centered spatial selectivity in the bar task (Figure 1*H*) also exhibit selectivity for the physical directions of eye movements in the ocular delayed response task (Figure 1*A*). Among these neurons, there is a significant correlation between the horizontal directions preferred in the two tasks (Olson & Gettner 1995, Olson & Tremblay 2000). Neurons firing more strongly before leftward (or rightward) eye movements in the standard task fire more strongly in conjunction with planning eye movements to the left (or right) end of a bar. An example illustrating this point is presented in Figure 1. Histograms *C–F* and *I–L* represent the activity of the same neuron recorded in the context of the ocular delayed-response task and the bar task. In the ocular delayed-response task, this neuron fired vigorously before leftward eye movements (Figure 1*F*); in the bar task, it fired before eye movements to the left end of the bar (Figure 1*I, K*).

There are two possible interpretations of the yoking of object-centered spatial selectivity in the bar task to selectivity for eye-movement direction in the ocular delayed-response task. First, in any given task, neurons might represent the location of the target relative to the allocentric reference frame currently being used by the monkey (the bar in the bar task and the screen in the ocular delayed-response task). I term this the object-centered response field model to indicate that in both tasks the spatial selectivity of the neuron is defined relative to an object-centered frame. Second, neurons might be sensitive to both the object-centered location of the target and the physical direction of the eye movement. In particular, each neuron might fire before saccades in a restricted range of physical directions, but its rate of discharge might be modulated as a function of the target's object-centered location. I term this the oculocentric gain field model to indicate that neuronal activity associated with making an eye movement into the neuron's oculocentric motor field is subject to modulation by the object-centered location of the target. These models can be tested by assessing how neuronal activity during bar-task performance depends on the object-centered location of the target and the physical direction of the eye movement. The results are distributed between the extremes represented by the two models. On one hand, in harmony with the object-centered response field model, some neurons fire strongly before a saccade to the preferred end of a bar even when the saccade is completely outside the oculocentric response field as mapped out with dot targets. The neuron of Figure 1, for example, fired strongly before saccades to the left end of a bar in the upper visual field (Figure 1*I, K*), although it did not fire at all before saccades to an upper visual

field dot target (Figure 1*C*). On the other hand, in harmony with the oculocentric gain field model, the firing of some neurons is influenced both by the physical direction of the eye movement and by the object-centered location of the target. For example, the neuron of Figure 3 fired especially strongly when a rightward eye movement was directed to an object-right target (Figure 3*C*) and especially weakly when a leftward eye movement was directed to an object-left target (Figure 3*D*). Thus some SEF neurons carry seemingly pure object-centered signals, while others carry a mixture of object-centered and oculocentric signals.

A Model Linking Object-Centered Spatial Selectivity to Behavior

How could SEF neurons, carrying as they do a combination of object-centered and eye-centered spatial signals, contribute to performance of the bar task? A theoretical solution to this problem has been put forward by Deneve & Pouget (1998). They devised a simple network in which a hidden layer embodies the oculocentric gain field principle described in the preceding section. Each hidden unit, when active, triggers a saccade in a fixed oculocentric direction. Each hidden unit is active only if an appropriate control signal is present (for example, if an object-left control line is active) and if an appropriate visual input is present (for example, if the left side of an object occupies the hidden unit's response field). Through the multiplicative interaction of object-centered control signals and visual inputs, the hidden units generate a saccade to the selected location on whatever reference object is currently present in the visual field. The fact that some SEF neurons, like the hidden units in Deneve & Pouget's model, carry a combination of object-centered and oculocentric signals suggests that they are involved in the transformation of object-centered commands into appropriate oculomotor outputs. However, other neurons in which the influence of the physical directions of eye movements is weak or absent are better thought of as representing object-centered locations independently of motor output and thus as corresponding to the command lines in the model.

Relation to Human Performance

The bar task may seem artificial, but it nevertheless embodies a form of landmark-based spatial judgment that almost certainly comes into play under natural circumstances even in humans. This is true not only of manual activities such as writing, drawing, and construction but also of covert attention and eye movements. There is a natural tendency to refer attention to object-centered locations. If a target is presented repeatedly at a certain position in an array, then, by an automatic priming process, subjects begin to allocate attention to that location at a short latency (∼100 ms) following array onset (Maljkovic & Nakayama 1996, Kristjánsson et al. 2001). Moreover, if a location on a moving object is cued, then attention (Umiltà et al. 1995) and, subsequently, inhibition of return (Gibson & Egeth 1994) attach to that location, moving with the object. The same is probably true of eye movements,

although the subject has not been studied as thoroughly. In making eye movements to unmarked remembered locations, humans apparently triangulate automatically from visible objects, as evidenced by the fact that accuracy is enhanced in the presence of a visible background (Gnadt et al. 1991) or landmark (Dassonville et al. 1995, Hayhoe et al. 1992, Karn et al. 1997) as compared to darkness. Moreover, humans are proficient at making eye movements to instructed object-centered locations in the bar task (Edelman et al. 2002). The eye deviates toward the instructed end of the bar even during saccades of very short latency, and the magnitude of the deviation depends on target size, indicating that target selection is based on an object-centered computation and not just on a preprogrammed offset from the target object's center. We conclude that attending to and making eye movements to object-centered locations is a comparatively natural and automatic behavior.

## Relation to Other Studies in the Monkey

Many years ago, Niki (1974) noted the existence in prefrontal cortex of neurons that fired at different rates when the monkey was preparing to make a right- or left-lever manual response, exhibiting this pattern regardless of the levers' location in the monkey's workspace. The simplest interpretation of this finding is that the neurons were selective for the location of the response lever relative to the two-lever array and so were displaying a form of object-centered spatial selectivity. More recently, single-neuron recording studies incorporating tight controls on eye movements and other potentially confounding factors have provided additional support for the notion that neurons in the brain of the monkey carry object-centered control signals. Horwitz & Newsome (1999), in a study of the superior colliculus, required monkeys to select one of two dots as a saccade target, with the choice determined by the direction of motion of a foveal stimulus. In one version of the task, the dots had the same relative location on every trial but were placed at a location in the visual field that varied from trial to trial (Horwitz 1999). This is an object-centered saccade task with motion as the cue and with a pair of dots as the reference object. During performance of this task, collicular neurons belonging to a particular functionally defined category (those carrying decision-related as opposed to movement-related signals) exhibited object-centered spatial selectivity. Batista & Newsome (2001) have subsequently shown that SEF neurons also carry object-centered signals in this task. We conclude that object-centered spatial selectivity is not a unique attribute of the SEF but instead may be widespread in the primate brain.

Sabes et al. (2002) set out to assess whether neuronal discharges in the lateral intraparietal area (LIP) represent locations on objects invariantly across changes in orientation, thus exhibiting object-aligned spatial selectivity. In their task, the target could be any of five discrete loci on a large irregular object centered on the fovea. With the object at one orientation, the target locus was marked by a cue. After a delay, the object appeared at another unpredictable orientation. After a further delay, the monkey was required to execute a saccade to the previously

marked locus. They found that the activity of nearly all neurons could be accounted for by a combination of two factors: the retina-centered location of the target and the orientation of the object. Few neurons if any carried pure object-aligned spatial signals. It is possible that this finding reflected the strategy adopted by the monkeys: They may have selected targets on the basis of local distinguishing features rather than object-relative location. However, it may also reflect a relative paucity in area LIP of neurons that represent locations relative to objects. It will be of interest in ongoing and future studies to determine whether neurons in the SEF carry object-aligned signals in tasks involving objects that appear at different orientations (Breznen & Andersen 2002, Gettner & Olson 1998) and, conversely, whether neurons in area LIP represent object-centered locations in the bar task.

Relation to Object-Centered Representations in Pattern Recognition

The idea that the brain contains object-centered spatial representations had its origin in the speculation of Marr & Nishihara (1978) that visual recognition might depend on structural descriptions of objects, descriptions in which an object is summarized as a collection of parts at locations defined relative to a coordinate system centered on and aligned to the object. Marr & Nishihara imagined a scheme in which each object had a unique three-dimensional structural description. However, simpler models along the same general lines have been proposed. For example, as shown in Figure 5, a two-dimensional image might be represented for recognition by projecting it through a shift and zoom operation onto an object-centered neural map (Olshausen et al. 1993). Whether images are indeed represented in the ventral
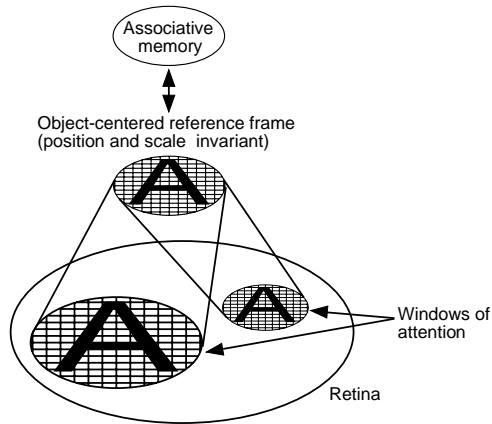
Figure 5   Schema of a system in which the image on which attention currently is focused is projected with appropriate normalizing transformations onto a map of object-centered space. Adapted from Olshausen et al. (1993).

stream as collections of parts at object-centered locations is an interesting question that has recently been addressed in recording studies by Pasupathy & Connor (1999, 2001). They found that neurons in area V4 respond selectively to favored contour elements at favored object-centered locations regardless of the retinal location of the image, so long as it is somewhere in the neuron's receptive field. A collection of such neurons with receptive fields tiling the visual field could provide the foundation for a form of object recognition based on the object-centered locations of the individual parts. It should be clear from the above description that object-centered representations subserving recognition are dissociable from control signals governing motor operations and attention in object-centered space. Nevertheless, it is easy to imagine that control signals such as those carried by neurons in the SEF might act in a top-down fashion on object-centered maps, such as the one proposed by Olshausen and colleagues.

OBJECT-CENTERED AND OBJECT-ALIGNED NEGLECT

If neurons with object-left and object-right selectivity are concentrated in the right and left hemispheres respectively, as suggested by recording studies in the SEF, then lateralized hemispheric damage might be expected to result in impairments specific to the left or right sides of objects. That this is so has been suggested by studies carried out over the last several decades in patients with neglect. Hemispatial neglect is a condition typified by profound unawareness of the contralesional half of space. It is associated most frequently with injury to the right parietal lobe but can occur after injury to the parietal or frontal cortex of either hemisphere. One of the central goals of research in this area has been to identify the spatial reference frames with respect to which neglect is expressed (Behrmann & Geng 2003, Driver 1999, Farah & Buxbaum 1997, Walker 1995). Neglect has been found to depend on the location of a stimulus relative to multiple reference frames both egocentric (centered on the viewer's retina, head, or torso) and allocentric (centered on whatever object is currently within the window of attention). From the vantage point of this review, the observation of greatest interest is that neglect in some patients is object-centered and object-aligned. It is object-centered in the sense that the left (or right) side of an object is neglected regardless of the object's location relative to the viewer. It is object-aligned in the sense that the area to the left (or right) of the object's intrinsic midline is neglected regardless of the object's orientation in the viewing plane.

Object-Centered Neglect

The first indications that neglect can be expressed with respect to an object-centered reference frame came from tests requiring patients to copy line drawings of simple scenes (Gainotti et al. 1972, Ogden 1985a, Marshall & Halligan 1993). Some neglect patients exhibit scene-centered or viewer-centered neglect, failing to copy objects on the contralesional side of the scene (Figure 6D–F). However, others exhibit object-centered neglect, copying all or nearly all of the objects in a scene and yet
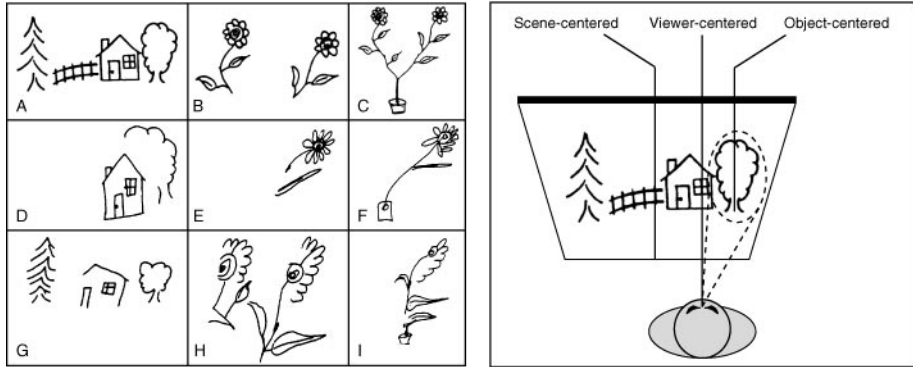
Figure 6 Examples of scene- or viewer-centered omissions (*D–F*) and object-centered omissions (*G–I*) in neglect patients' copies of models (*A–C*). Note object-centered omission of the left side of the house in (*G*), of the left side of each flower in (*H*) and of the left side of the unified plant in (*I*). Adapted from Hillis et al. (1998), patient AS (*A*); Hillis & Caramazza (1990), patient RB (*G*); and Marshall & Halligan (1993), patient 1 (*E* and *F*) and patient 2 (*H* and *I*). As noted in the panel to the *right*, scene-centered and viewer-centered neglect are dissociable in principle. However, in standard copying tests, they cannot be distinguished.

omitting detail from the contralesional sides of individual objects (Figure 6 *G–I*) (Apfeldorf 1962, Doricchi & Galati 2000, Gainotti et al. 1972, Halligan & Marshall 1993, Marshall & Halligan 1993, Walker & Findlay 1997). The distinction is not specific to copying but applies to verbal report as well. Humphreys & Heinke (1998) assessed the performance of five neglect patients on a test requiring them to report on pairs of objects presented side by side. They found that two patients consistently neglected the leftmost object, displaying scene-centered or viewer-centered ("between-object") neglect, whereas three patients consistently neglected the left side of each object, displaying object-centered ("within-object") neglect. Similar performance has been described in another patient by Young et al. (1992). A parallel distinction has been made with respect to reading words in arrays. In such tests, Hillis et al. (1998) and Subbiah & Caramazza (2000) have emphasized that some patients exhibit scene-centered or viewer-centered neglect, omitting words on the contralesional side of the array, whereas others exhibit object-centered ("stimulus-centered") neglect, omitting the contralesional letters of words throughout the visual field. The thrust of these observations is to indicate that neglect can take either a predominantly scene-centered/viewer-centered form or a predominantly object-centered form in different patients. The anatomical basis for the dissociation is not yet known.

These observations raise the question: What is it that confers on a particular collection of elements in a display the status of being an object and thus of being subject to object-centered neglect? The answer is that neglect seems to act on any group of elements selected for processing as a perceptual unit. The elements

must be amenable to unitary processing (because they are physically continuous or stand out as a figure), and they must actually be selected. The importance of physical continuity has been demonstrated by manipulating whether two side-by-side images are connected or not. When separated by even a small gap, both images are detected, but when they are joined the contralesional one falls under the shadow of object-centered neglect (Buxbaum & Coslett 1994, Halligan & Marshall 1993, Marshall & Halligan 1993, Young et al. 1992). For example, both flowers in a side-by-side pair may be copied (Figure 6*H*), but when they are joined by a common stem, the leftmost may be omitted (Figure 6*I*). The importance of figural status has been revealed by studies involving displays consisting of intercalated colored regions. If one of the regions tends to be perceived as figure because it is smaller or more symmetric than the others, then the contour forming this region's left edge tends to be neglected (Driver et al. 1992). The importance of active selection has been demonstrated by instructing the patient to attend to a particular region defined by color. In copying from a display consisting of abutting colored patches, a left-neglect patient may copy a contour when instructed to draw the region of which it is the right edge and yet may omit the same contour when copying the region of which it is the left edge (Halligan & Marshall 1994, Marshall & Halligan 1994).

In tests administered under free viewing, there is room for concern that object-centered neglect might arise as an artifact of how the patient scans the scene. This concern is justified insofar as patients tend not to make eye movements into the neglected field (Behrmann et al. 1997, Karnath et al. 1998, Karnath & Niemeier 2002). Furthermore, in complex tasks such as reading and recognizing line drawings, patterns of gaze parallel patterns of report (Karnath 1994, Karnath & Huber 1992). In particular, patients who exhibit object-centered neglect in copying tend not to look at the contralesional halves of objects when inspecting them (Walker & Findlay 1997, Walker et al. 1996, Walker & Young 1996), whereas other patients display a scene-centered or viewer-centered gaze pattern (Rizzo & Hurtig 1992). It is critical, therefore, to note that object-centered neglect persists under conditions in which scanning is ruled out through requiring patients to maintain steady fixation. The contralesional halves of images, both lexical (Behrmann et al. 1990, De Renzi et al. 1989, Nichelli et al. 1993, Subbiah & Caramazza 2000) and nonlexical (Ládavas et al. 1990, Pavlovskaya et al. 1997, Young et al. 1992), are neglected even when they are confined entirely to the good ipsilesional visual field. Moreover, neglect for a stimulus at a fixed location in the good hemifield can be ameliorated or exacerbated by arranging elements around it so that it forms the right or left end of an array (Arguin & Bub 1993, Subbiah & Caramazza 2000). For example, left-neglect patients are slower (Figure 7*C*) to identify a target letter presented at a given retinal location when it is at the left of a string of distractors (Figure 7*A*) than when it is at the right (Figure 7*B*).

Possible Mechanisms of Object-Centered Neglect

The view that object-centered neglect arises from lateralized damage to an object-centered neural map of space is appealing but is not universally held. It has been
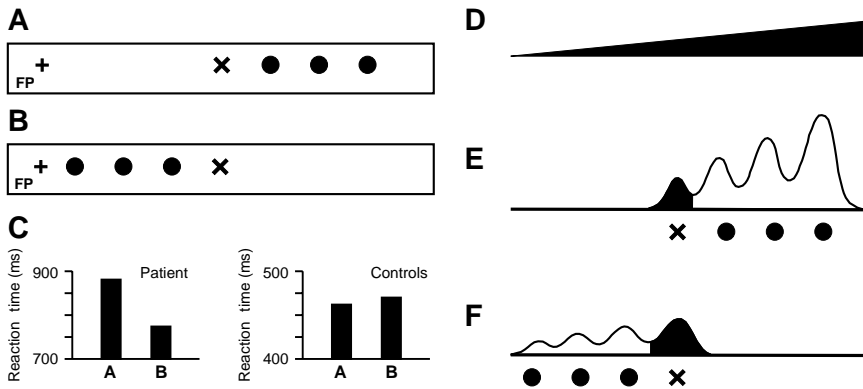
Figure 7 Patients with left neglect are slower (*C*) to report the identity of a letter occupying the leftmost location in a string of distractors (*A*) than to report the identity of a letter occupying the rightmost location (*B*), even when the retinal location of the letter is the same. This result might arise from damage to neurons occupying the left half of an object-centered map. However, it might also arise from a relative egocentric mechanism involving competitive lateral interactions among neurons arranged in a retinotopic map. If neglect took the form of a gradual decrease in the stimulus salience from right to left across the retina (*D*), then neurons representing the target letter would be more suppressed by salient distractors to the right than by weak distractors to the left. Consequently, their net activation (black area under curve) would be relatively low with distractors to the right (*E*) and relatively high with distractors to the left (*f*). Curves in (*E–F*) represent strength of neural activation as a function of location on the retinotopic map. FP: Fixation point. X: Target letter. Filled circles: Distractors. (*A–C*) Adapted from Arguin & Bub (1993). (*D–F*) Adapted from Pouget & Sejnowski (2001).

argued that lateralized damage to a strictly egocentric (retina-centered or body-centered) spatial map could give rise to object-centered neglect under certain conditions. The necessary conditions are (*a*) that stimuli at neighboring locations compete for neural representation and (*b*) that the brain injury creates a graded impairment of salience such that stimuli displaced progressively farther into the contralesional field are progressively less salient. Under these conditions, an element at the same location on the retina would be neglected if it occupied the contralesional end of an array (because its neighbors, having greater salience, possess a competitive advantage) but would be detected if it occupied the ipsilesional end (because its neighbors, having less-intense salience, are at a competitive disadvantage). Neglect arising from such a mechanism has been termed relative egocentric neglect (Driver & Pouget 2000, Pouget & Sejnowski 2001). It has long been appreciated that models implementing the relative egocentric principle can account for phenomena associated with neglect (Mozer & Behrmann 1992). Recently, a strong case has been made for the view that they can reproduce nearly all object-centered phenomena. For example, results described by Arguin & Bub (1993) have been mimicked by relatively egocentric models (Mozer 1999, 2002;

Pouget & Sejnowski 1997, 2001), as illustrated in Figure 7. In the presence of a lesion-induced gradient of salience (Figure 7*D*), units representing the target letter are less active (the black area under the curve is smaller) when distractors are located to its right (Figure 7*E*) than when they are located to its left (Figure 7*F*).

The relative egocentric account of object-centered neglect is not, however, without problems. In the first place, it has difficulty accounting for the fact that neglect seems to take a scene-centered or viewer-centered form in some patients and an object-centered form in others. In the second place, demonstrations that it is feasible are not equivalent to demonstrations that it is factual. In the third place, a recent effort to test it has produced results seemingly incompatible with it (Niemeier & Karnath 2002, 2003). In this study, torso-restrained left-neglect patients searched with eye and head movements for a target embedded in an array of letters covering the wall of a spherical cabin (Figure 8*A*). First, the patients were instructed to scan the entire cabin. Under this condition, the peak of the distribution of fixations was displaced around 40° to the right (Figure 8*B*). From 40° to 80° right (Figure 8*B*: gray backdrop), fixations fell off, reflecting a decline in the ability of letters on the wall to capture attention and thus a decline in their salience. Next, the patients were instructed to search only within a chromatically defined strip on the wall of the cabin extending from 40° to 80° right. Under this condition, neglect assumed an object-centered pattern, with fixations falling off in a steep gradient from the strip's right edge to its left edge (Figure 8*C*). A relative egocentric model would have predicted a gradient of opposite sign because, by the measure shown in Figure 8*B*, letters to the strip's left were more salient than letters to its right. To fit these data required a model containing parameters for both egocentric and object-centered location (Niemeier & Karnath 2002, 2003).

Object-Aligned Neglect

Neglect arising from lateralized damage to a fully object-centered spatial representation would affect the intrinsic left or right side of even a tilted image. Several studies have sought to determine whether neglect is indeed object-aligned in this sense. Driver and his colleagues approached this problem by using shapes that, owing to their inherent geometric properties or the context in which they were placed, possessed an unambiguous intrinsic midline. They found that left-neglect patients were impaired at discriminating features to the left of the intrinsic midline even when the shape was tilted 45° or 60° away from perceived upright by a rotation in the viewing plane (Driver & Halligan 1991, Driver et al. 1994). Behrmann & Tipper used the object's history rather than its geometry to mark its intrinsic left and right sides. Left-neglect patients in their study viewed a screen on which appeared, first, a barbell-shaped frame consisting of two circles joined by a horizontal stem and then, after a delay, inside one of the circles, a target (Behrmann & Tipper 1994, 1999; Tipper & Behrmann 1996). Patients manifested neglect through their slowness to detect the target if it appeared in the circle on the left side of the screen. Remarkably, if the barbell, after its appearance and before presentation
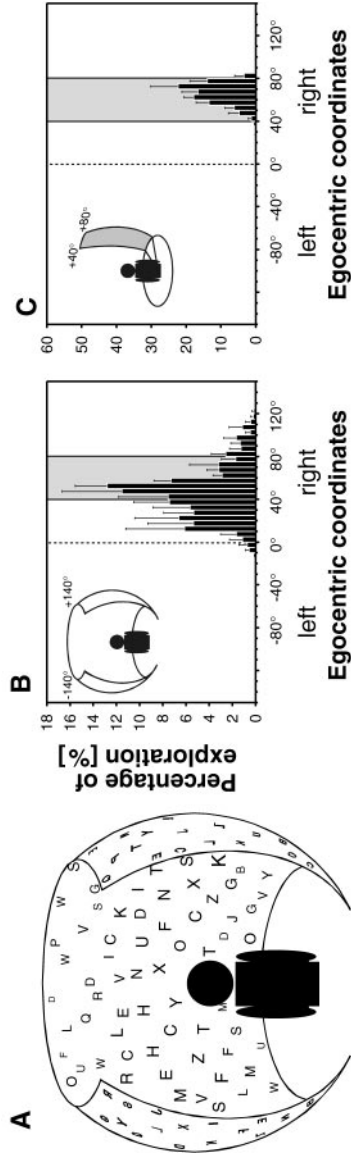
Figure 8   Left-neglect patients scanning a letter array on the wall of a spherical cabin (*A*) distribute their fixations in a bell curve displaced 40° to the right of the body's straight-ahead axis (*B*). However, required to confine their search to a chromatically defined strip of the cabin's wall extending from 40° to 80° right, they distribute their fixations in a steep gradient declining from right to left. These results are difficult to reconcile with models of neglect based on a relative egocentric mechanism. Adapted from Niemeier & Karnath (2002, 2003).

of the target, underwent a visible 180° rotation in the viewing plane, this pattern was reversed. Responses were slowest to targets presented on the right side of the screen, as if neglect had attached to the barbell's left end and traveled with it as it rotated into the right visual field.

Other studies have assessed the ability of neglect patients to discriminate detail within recognizable objects oriented 90° from their canonical upright orientation. A patient studied by Young et al. (1992) showed neglect for the contralesional halves of chimeric faces oriented 90° from upright so that the top of the head pointed to the left or right. Farah et al. (1990) failed to obtain object-aligned neglect in a group of patients required to search for target letters scattered across drawings of familiar objects oriented 90° from upright. However, Hillis & Rapp (1998), upon reanalyzing data from the study, found that the heterogeneous pool of subjects included some who did show significant object-aligned effects. Behrmann & Moscovitch (1994), in a test requiring patients to detect patches of color around the perimeter of an object, elicited object-aligned neglect when using some kinds of objects but not others. These heterogeneous findings may be reconcilable within a framework proposed by Buxbaum et al. (1996). They required a patient with neglect, but with intact ability for mental rotation, to describe colored patches on the perimeters of 90°-rotated objects, reporting the locations either relative to the object itself (which required mental rotation) or relative to screen coordinates (which did not require mental rotation). Only under the condition requiring mental rotation did they find that neglect was object-aligned in the sense that there was impaired detection of patches located to the left of the object's intrinsic midline. Thus, in studies of other patients, neglect may have been object-aligned or not according to whether the conditions of the test did or did not favor imagining the reference object as if upright.

Possible Mechanisms of Object-Aligned Neglect

It is intuitive to suppose that object-aligned neglect must arise from lateralized damage to a neural map of object-centered space. However, models embodying the relative egocentric principle are able to reproduce at least some of the phenomena of object-aligned neglect. In the case of shapes oriented 45° or 60° from upright (Driver & Halligan 1991, Driver et al. 1994), the representation of elements to the left of the intrinsic midline is degraded because they fall predominantly to the left of neighboring elements in the egocentric map (Mozer 2002). However, to account for object-aligned neglect of shapes rotated 90° or more from upright, additional features must be added to the model. In the case of a rotating barbell, the representation of the barbell's left side remains degraded even when rotation carries it to the right side of the visual field if local excitatory interactions among neighboring units and hysteresis are allowed (Mozer 1999, 2002). Alternatively, object-aligned phenomena have been explained by assuming that the left and right hemispheres are specialized for processing objects rotated counterclockwise and clockwise respectively (Pouget et al. 1999). These additions detract from one of the major virtues of the relative egocentric model, namely its freedom from arbitrary assumptions about brain operation and organization.

Buxbaum et al. (1996) have taken a much more radical approach to explaining object-aligned effects in terms of egocentric representations. Their argument hinges on two assumptions: (*a*) that object-aligned neglect depends on mental rotation (picturing the object as if upright) and (*b*) that mental rotation involves forming a representation of the object in upright orientation on a purely egocentric spatial map somewhere in the brain. Damage to one side of this egocentric map, they argue, would lead to neglect for one side of the mentally rotated upright image. The neglect would appear to be object-aligned because it would be specific to one side of the object as defined relative to its intrinsic midline. This logic applies with equal force to object-centered neglect. If attending to an upright object in the peripheral visual field involved imagining it as if centered straight ahead, and if this were accompanied by forming an image of it at the center of a map of egocentric space, then lateralized damage to the egocentric map would give rise to a neglect that appeared to be object-centered. This argument is concordant with several demonstrations that neglect can occur for mental representations in the absence of corresponding retinal images. Representational neglect has been demonstrated for scenes imagined from memory (Bisiach & Luzzatti 1978), shapes reconstituted from successive views as they pass behind a slit (Ogden 1985b), and spoken words or words spelled out by upright letters in a vertical array (Caramazza & Hillis 1990).

The flaw in the argument arises from taking the view that any neural map can be used both as a scratch pad for representing images distinct from those on the retina and at the same time as a purely egocentric map. The incompatibility of these two things is clear if one considers the case of the SEF. Given that neurons in the SEF exhibit selectivity for the physical directions of eye movements in traditional oculomotor tasks, we might assume that the area contains a map of egocentric space. Given that the same neurons fire according to whether the monkey is imagining the left or right end of a bar, we might assume that the image of the bar has been projected onto the egocentric map through a mental transformation. Given (and this has not been shown) that a lesion of the right SEF produces a left object-centered neglect, we might assert that the neglect has arisen from damage to a purely egocentric map. This conclusion would be false except in some narrow academic sense because neurons in the SEF, unlike neurons in the retina, do possess the distinctive trait of being selective for object-centered locations. The representation of space in the SEF may be egocentric by default and perhaps by evolutionary origin, but, insofar as the area is available for representing locations decoupled from the body's coordinate system, its map of space is object centered and not purely egocentric.

CONCLUSION

We have reviewed evidence indicating that neurons in the SEF of the monkey represent the object-centered locations of targets selected for eye movements and attention and that hemispatial neglect in humans can take an object-centered and object-aligned form. It is natural to regard these findings as complementary

reflections of the existence in the brain of neural systems specialized for the representation of object-centered space. However, some fundamental outstanding issues need to be resolved before we can fully understand their significance. In monkeys, it will be necessary to demarcate the cortical network in which object-centered spatial signals are present by carrying out single-neuron recording in multiple areas outside the SEF. It will also be necessary to assess the importance of these signals for behavior by measuring the impact of cortical lesions on object-centered performance. In humans, it will be necessary to devise and carry out experiments that allow choosing between the competing models of object-centered and object-aligned neglect, based on damage to object-centered and egocentric spatial maps. What we know at present is that primates rely deeply on object-centered spatial skills and that there are strong indications, both from physiology and from neuropsychology, that these skills depend on neural systems specialized for the representation of object-centered space.

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