Proc. Natl. Acad. Sci. USA
Vol. 93, pp. 4962–4967, May 1996
Neurobiology

Electrical microstimulation suggests two different forms of representation of head-centered space in the intraparietal sulcus of rhesus monkeys

(parietal cortex/eye movements/saccades)

P. THIER* AND R. A. ANDERSEN†‡

*Neurologische Universitätsklinik, Sektion für Visuelle Sensomotorik, Tübingen, 72076 Tübingen, Germany; and †Massachusetts Institute of Technology, Cambridge, MA 02139

Communicated by John J. Hopfield, California Institute of Technology, Pasadena, CA, January 16, 1996 (received for review April 28, 1995)

ABSTRACT **We examined the effects of eye position on saccades evoked by electrical stimulation of the intraparietal sulcus (IPS) of rhesus monkeys. Microstimulation evoked saccades from sites on the posterior bank, floor, and the medial bank of the IPS. The size and direction of the eye movements varied as a function of initial eye position before microstimulation. At many stimulation sites, eye position affected primarily the amplitude and not the direction of the evoked saccades. These "modified vector saccades" were characteristic of most stimulation-sensitive zones in the IPS, with the exception of a narrow strip located mainly on the floor of the sulcus. Stimulation in this "intercalated zone" evoked saccades that moved the eyes into a particular region in head-centered space, independent of the starting position of the eyes. This latter response is compatible with the stimulation site representing a goal zone in head-centered coordinates. On the other hand, the modified vector saccades observed outside the intercalated zone are indicative of a more distributed representation of head-centered space. A convergent projection from many modified vector sites onto each intercalated site may be a basis for a transition from a distributed to a more explicit representation of space in head-centered coordinates.**

An important issue in motor control concerns the frame of reference used to represent visual objects that are targets for goal-directed movements (see refs. 1–3 for recent reviews). One possibility for computing visually guided saccades is to use a purely retinal coding scheme. According to this scheme, a visually guided saccade is programmed by converting the retinal vector describing the displacement of the target image relative to the fovea into an eye movement vector of equal size in the same direction. This scheme obviously works independently of where the eyes are looking, because the stimulus location and movement are relative to the fovea. However, problems arise with retinal schemes when more complex visually guided behaviors are considered. To determine the location of a target for a reaching movement requires not only its retinal location, but also information about the position of the eyes relative to the head and the head relative to the trunk. Likewise, gaze shifts that are achieved by a combination of eye, head, and body movements would benefit from a representation of space that is more general and abstract than a simple retinotopic map. It therefore comes as no surprise that head-, body-, and even world-centered representations of visual space have been proposed in the context of motor control as well as perception. Such nonretinal representations, if present, could be the basis for goal-directed motor behaviors, including saccades.

As first suggested by Robinson (4), electrical microstimulation offers a conceptually simple method to decide if a saccade-related brain structure relies on retinal rather than nonretinal coding. The rationale is as follows. If a small group of nearby cells represent approximately the same retinal vector, then mimicking their natural activity by microstimulation should evoke a saccade of identical amplitude and direction, independent of gaze direction. On the other hand, if the group represents a location in head-centered space (or any other eye position-invariant space if the head is fixed), we would expect to find that stimulation always drives the eyes to the same location in the head, independent of the initial orbital positions. We have adopted this technique in order to clarify the coding scheme used by saccade-related areas in the intraparietal sulcus (IPS). We report here discrete intraparietal zones that exhibit two different stimulation effects. Microstimulation of one zone produces saccades to locations with respect to the head, suggesting a head-centered representation. Stimulation at other locations produce saccades whose amplitude, but usually not direction, changes with eye position. Local circuits in these regions may have access to information about both eye position and retinal position, but these two parameters do not appear to be combined to unambiguously code locations in head-centered space. Thus these "modified vector saccades" may reflect a representation of head-centered space that is encoded in the activity of neurons that are distributed over larger regions of the intraparietal cortex.

METHODS

Recordings were made from two hemispheres of two male rhesus monkeys ("E" and "S") with their heads fixed in most experiments. A total of 626 sites in the posterior parietal regions of these two hemispheres were analyzed, and the present report is based on a subset of 74 stimulation-sensitive sites located in a restricted part of the IPS. Monkeys were rewarded for keeping their line of sight within an eye position window (usually a 5° diameter) in a fixation task. At the beginning of each trial, a small (0.1°) fixation spot was back-projected onto a tangent screen 57 cm from the animal in an otherwise completely dark room. If the monkey kept fixation on the spot for 500 msec, the spot was turned off for 500 msec (gap period) before being turned on again for another 500 msec. Two hundred milliseconds after the beginning of the gap period, electrical microstimulation was applied on half of the trials (the other trials serving as "controls"). Because stimulation often drove the eyes outside the confines of the eye position window, fixation requirements for reward were suspended in stimulation trials from the onset of microstimulation

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "*advertisement*" in accordance with 18 U.S.C. §1734 solely to indicate this fact.

Abbreviation: IPS, intraparietal sulcus.

‡Present address: California Institute of Technology California Institute of Technology, Pasadena, CA 91125.

until the end of the gap period. If the eyes were driven outside the window by stimulation, the monkey was required to make an eye movement back to the original location before the end of the trial. The electrical stimuli were bipolar pulses (0.1-msec duration; current size, typically 200 μA or less) delivered through conventional glass-insulated Pt-Ir electrodes for 100 msec (or occasionally 500 msec for prolonged stimulation; see Fig. 2) at 500 Hz.

Electrodes were introduced through a chamber implanted over a trephine hole lying immediately above the IPS. Eye position was monitored by sampling the voltage induced in a search coil (5) implanted underneath the conjunctiva. The horizontal and vertical eye positions were each sampled at 500 Hz. For a full description of the surgical protocols used, see Andersen *et al.* (6). Whereas in most of our experiments the monkey's head was restrained, the use of a modified head holder permitting head movements about the yaw axis in monkey S allowed us to clarify if electrical stimulation evoked head movements with a horizontal component in addition to eye movements. Head position was recorded by a precision potentiometer mounted on the head holder, and the output of the potentiometer was sampled at 500 Hz.

If stimulation at a given electrode site elicited eye movements, then the effects of microstimulation were tested at nine different eye positions. These positions were 30° off the straight-ahead position on the cardinal axes and 21° off the straight-ahead position on the diagonal axes. Trials for the different eye positions, with and without microstimulation during the gap period, were all presented in a random block design. Stimulation sites were reconstructed using conventional methods relating the coordinates of electrode movement to anatomical landmarks, such as glial scars resulting from electrolytic lesions or small dye deposits made at known locations. Well-established anatomical criteria (7), the response properties of single cells recorded with the stimulation electrode (8, 9), and the characteristic effects of electrical microstimulation were used to define cortical area boundaries.

The size and direction of saccades elicited by stimulation were linearly approximated by vectorially subtracting the eye position at stimulation onset from the eye position 50 msec after the end of stimulation. The choice of this end point was based on a careful analysis that indicated the eyes stopped moving at this time. After a brief pause, the animals made a saccade back to the starting point (see Fig. 3). Means and standard deviations for the stimulation-evoked changes for each initial orbital position were calculated using at least four stimulation trials. To eliminate a contribution of small eye drifts occurring during the gap period unrelated to the electrical stimulation, corresponding measures were derived for the control trials. The difference of the mean changes in eye position for stimulation trials and control trials then served as an estimate of the mean stimulation-induced change in eye position. This estimate will henceforth be denoted as the "mean saccade vector" S. S is a two-dimensional vector with the horizontal component s_x and the vertical component s_y. S is a function of two-dimensional space, defined by the horizontal (e_x) and vertical (e_y) components of the initial orbital position of the eyes; this function is usually referred to as a vector field. The insets in Fig. 1 are graphical representations of such vector fields. The divergence differential operator *div*S $= \delta(s_x)/\delta(e_x) + \delta(s_y)/\delta(e_y)$, when applied to this vector field, derives a scalar that quantifies the amount of divergence or convergence in the field. The divergence differential operator has the following properties. It will be zero in the case of a vector field without any change in direction or length of the individual vectors. It will be positive in the case of a divergent vector field, in which the individual vectors point away from a common central source. Conversely, in the case of a highly convergent vector field, the operator will become negative. We have used the divergence differential operator in an attempt to verify our impression that some of the sites explored yielded vector fields characterized by a high degree of convergence. Toward this end, such vector fields were fitted by a two-dimensional linear regression, resulting in a pair of linear equations ($s_x = f(e_x, e_y)$ and $s_y = f(e_x, e_y)$ from which the divergence differential operator could be derived. We will describe convergence in a vector field as centering or goal directedness. It should be emphasized that *div*S is not invariant to changes in vector length. We also quantified changes in vector length and took this factor into account when interpreting changes in *divS*.

RESULTS

Whereas large parts of the parietal cortex, including area 7a, proved to be unresponsive when stimulation currents were 200 μA or less, stimulation of sites on the lateral wall of the IPS and smaller areas on the floor and lower medial bank of the IPS consistently evoked saccade-like eye movements without any indication of desensitization after repeated stimulation. Stimulation-sensitive sites were located in comparable regions of the IPS in both monkeys. These regions were continuous in that they did not contain any nonsensitive sites interspersed with the stimulation-sensitive ones. We refer to eye movements evoked from this region as saccades due to the high velocity of the eye movements. The velocities of the stimulation-evoked eye movements were the same as the velocities of memory-guided saccades made by these monkeys, but they were somewhat lower than the velocity of the visually guided saccades. Occasionally the early component of the eye movement was in the "wrong" direction (see Figs. 1 and 3). It is unlikely that these deviations are due to eye blinks, because they were found in zones of the IPS whose stimulation did not evoke eye blinks as well as in zones that did. Whereas a number of observations, presented below, suggest that the stimulation-sensitive zone in the IPS is not homogeneous for certain eye movement properties, this was not the case for the latency or velocity of the eye movements. The average latency was 31.8 ± 13.8 msec (n = 57) with respect to stimulation onset. Velocity varied with the amplitude of the evoked saccade but, for individual amplitudes, did not vary systematically with stimulation location.

By varying the initial orbital position of the eyes at the time of stimulation onset, two qualitatively different response types could be distinguished. The first response type was a modified vector saccade, characterized by profound changes of saccade amplitude with eye position, but with the direction of the evoked saccade remaining fairly constant (Fig. 1*A*). In most cases, saccade amplitude varied linearly with eye position, becoming smaller when the initial eye position was shifted in the direction of the evoked saccades. However, we also occasionally observed different patterns of amplitude modification, such as larger saccades for central eye positions compared with peripheral eye positions. The mean modification of saccade amplitude was calculated by taking the mean of the ratios of the saccade amplitudes from the two eye positions that gave the largest and smallest saccades. The mean modification was 7.2 (SD, ±8.6; n = 44). The larger part of the intraparietal representation of modified vector saccades was located within a region of the lateral wall of the IPS, corresponding to what has been called the lateral intraparietal area in previous work (6, 8, 9). Saccades evoked from this part of the cortex were always directed into the upper contralateral space. Modified vector saccades directed into the lower contralateral space could only be evoked from a small patch of cortex lying on the floor of the IPS encroaching on the medial wall (Fig. 2). The two patches in which stimulation produced upward and downward modified vector saccades were separated from each other by a small strip of cortex, which we will refer to operationally as the "intercalated zone" (Fig. 2). Stimulation of sites within

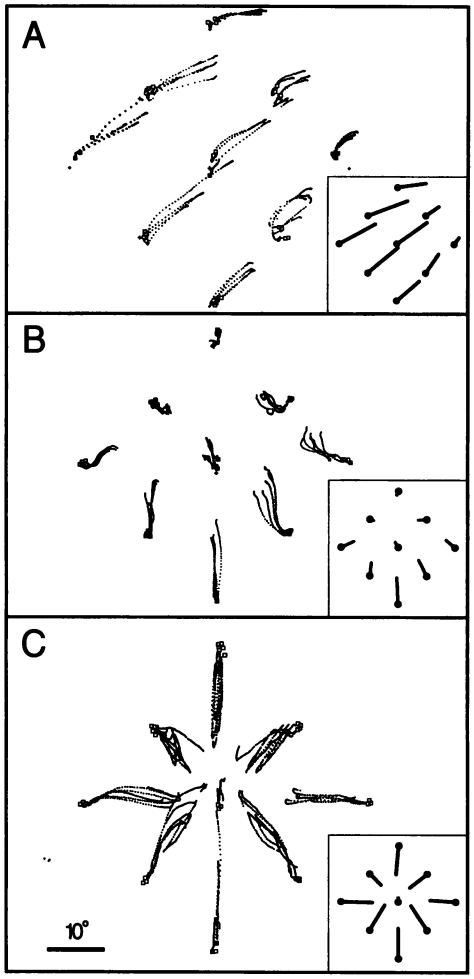

FIG. 1. (*A*) Modified vector saccades evoked from the lateral intraparietal area. Small squares indicate initial eye position on each trial before electrical stimulation. Note that varying the initial orbital position affected saccade amplitude, whereas the effect on direction was minor. (*B*) Saccades evoked from the intercalated zone separating the representations of modified vector saccades with an upward and downward component, respectively. Stimulation drives the eyes into a head-centered location (goal zone) independent of their orbital position at the time of stimulation onset. (*C*) Goal-directed saccade evoked from a site in white matter underneath the intercalated zone.

the intercalated zone evoked eye movements that depended on eye position in a qualitatively different way from neighboring stimulation-sensitive cortex. Varying the initial orbital position of the eyes not only modified the amplitude but also the direction of saccades evoked, with complete reversal of saccade direction in many instances (Fig. 1*B*). The modification of the saccade vector in the intercalated zone always drove the eyes to a particular zone (the "goal zone") relative to the head. This goal zone could lie either in the contralateral or the ipsilateral head-centered space and was usually not congruent with straight-ahead. Patterns of evoked saccades showing centering of the eyes closer to straight-ahead (Fig. 1*C*) were the hallmark of stimulation sites in white matter underneath the intercalated zone.

The discrimination of sites in the intercalated zone yielding centering saccades from those located in neighboring cortex yielding modified vector saccades was first based on purely subjective inspection of x, y plots of evoked saccades like the ones presented in Fig. 1. This discrimination was tested quantitatively by comparing the divergence differential operators from the two regions (see *Methods*). The divergence differential operators from the intercalated zone were on average much larger than the divergence operator for stimulation-sensitive sites outside the intercalated zone (means, -0.435 versus -0.171; t test, $P < 0.000001$). Because the amount of amplitude modification was the same for the intercalated zone and simulation-sensitive cortex outside (t test, $P > 0.05$), this result indicates a significantly larger degree of centering in the intercalated zone.

Our experiments revealed two additional differences distinguishing stimulation responses in the intercalated zone from those in the neighboring modified vector zones. One was the occurrence of non-eye movements, which accompanied saccades evoked from the intercalated zone, and the other was the effect of prolonged electrical stimulation, which was different in the two regions. The non-eye movements evoked from the intercalated zone included movements of the shoulders, arms, parts of the face (which sometimes involved eye blinks), and movements of the pinnae and the head. Whereas the occurrence of non-eye movements other than those of the head was noted only qualitatively, head movements were analyzed quantitatively in monkey S, whose head restraint was relaxed to permit head movements about the yaw axis. Whereas we were unable to evoke head movements from sites outside the intercalated zone, stimulation of sites within the intercalated zone consistently evoked short latency (≈50-msec) head movements, accompanying the saccades. A detailed analysis of responses obtained from four sites in the intercalated zone of monkey S showed that the horizontal component of the head movements and eye movements did not add up to constant horizontal displacements. The second difference relates to the effect of longer duration pulse trains. Twenty sites in the stimulation-sensitive zone of both monkeys were tested with 500-msec pulse trains in addition to the standard 100-msec train. Whereas prolonged stimulation of sites in the modified vector saccade regions of the IPS typically evoked a sequence of saccades of increasingly smaller amplitude (Fig. 3*A*), prolonged stimulation of sites in the intercalated zone in most cases elicited slow, drifting eye movements once the eyes had arrived inside the goal zone (Fig. 3*B*).

Although we did not carry out a detailed study of current thresholds in the IPS, the data available clearly suggests that the size of the stimulation current needed to evoke a saccade was comparable for sites in the intercalated zone and those located in neighboring stimulation-sensitive cortex, typically varying between 50 and 150 μA and occasionally being as low as 25 μA. These numbers are crude approximations because, at least for the zone of modified vector saccades, it became clear quite early in our experiments that current threshold depended on eye position. Typically, current thresholds were lower for orbital positions yielding larger amplitude saccades (9 out of 10 sites analyzed in detail). We did not have sufficient data to determine if a comparable interaction of eye position and current threshold held for sites in the intercalated zone.

DISCUSSION

Electrical microstimulation of the posterior parietal cortex has allowed us to define zones in the IPS from which saccades can be evoked. These two zones differed in the way eye position modified the size and the direction of evoked saccades. Modified vector saccades showing modulation mostly for amplitude but not direction were characteristic for most of the stimulation-sensitive zones in the IPS. However, stimulation of a narrow strip on the floor of the IPS produced goal-directed eye movements. We referred to this area as the intercalated zone. It separates areas of cortex representing upward and downward saccades, respectively. This intercalated zone appears to be a small subdivision of the ventral intraparietal area as defined by Maunsell and Van Essen (10), but may be more posterior than the ventral intraparietal area as defined by Colby *et al.* (11).

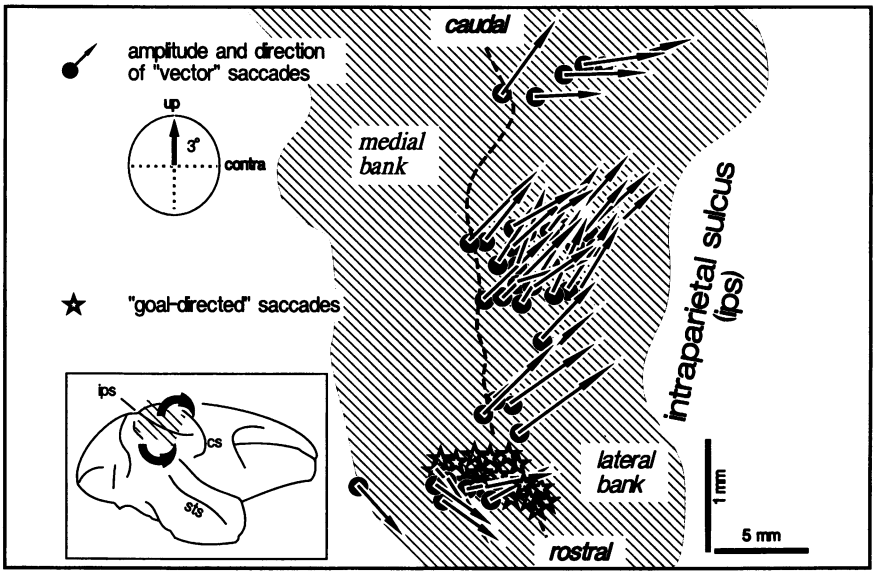

FIG. 2. Flattened reconstruction of the IPS and its neighboring structures of one of the monkey hemispheres used in the present study. The arrows indicate the amplitude and the direction of the saccades evoked at a particular site using straight-ahead as starting position. Asterisks indicate sites where goal-directed eye movements were evoked. Stimulation at sites (data not shown) on the medial bank of the IPS and in area 7a proved to be ineffective. The inset in the lower left shows a lateral view of the hemisphere. The hatched region indicates the part of cortex shown in a flattened view.

Previous stimulation studies of the posterior parietal cortex have failed to delineate these well-defined zones in the IPS (12–15). The reports by Shibutani *et al.* (14) and by Kurylo and Skavenski (15) describe observations of goal-directed saccades, suggesting that some of their electrode tracks may have tapped the intercalated zone in the IPS. Neither of the two reports mention the conspicuous modulation of saccade amplitude by eye position characteristic of IPS cortex outside the intercalated zone. Goal-directed saccades have also been demonstrated outside the posterior parietal cortex in a number of brain structures, including the caudal superior colliculus of the cat (16–18), the dorsomedial frontal cortex (refs. 19–24;

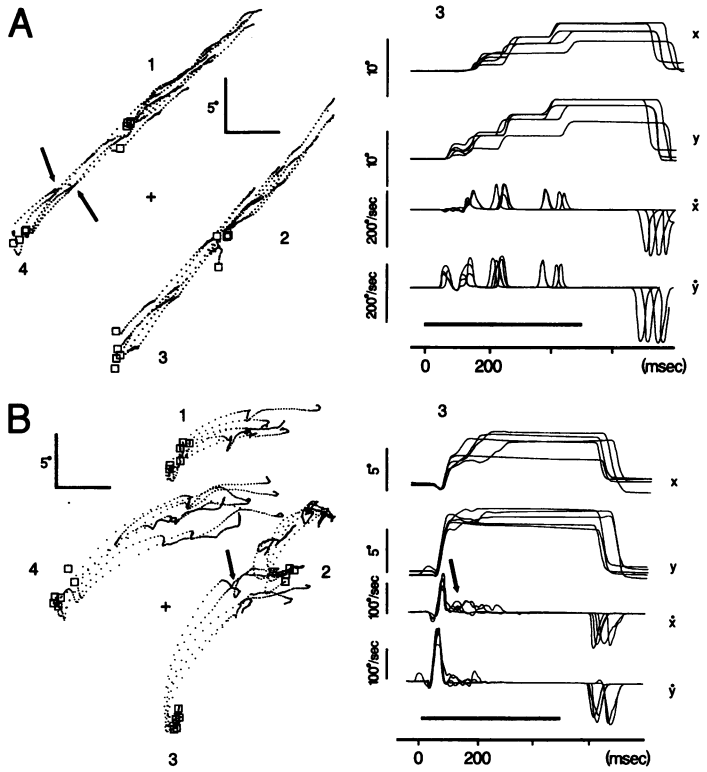

FIG. 3. Different effects of electrical microstimulation with pulse-trains of prolonged duration (500-msec train duration; other parameters as described. (*A*) Staircase saccades elicited from site in the lateral intraparietal area. The left part of *A* is an *x*, *y* plot of eye positions of saccades evoked from 4 different initial orbital positions (positions 1–4). The cross indicates the straight-ahead position. The two arrows mark the end points of the first saccade in two selected staircases. The plots on the right are representations of the *x*, *y* components of eye position and velocity as a function of time for one of the four orbital positions (position 3) tested. (*B*) Absence of staircase saccades after stimulation of a site in the intercalated zone. After having arrived within the confines of the goal zone, continuing stimulation is largely ineffective. Format of presentation similar to *A*.

see ref. 25 for an opposing view) of the monkey, and the cat cerebellum (26). The studies dealing with the superior colliculus are particularly important, because they have prompted an interpretation of goal directedness completely different from the one we have considered so far. Stimulation at sites that generate goal directed eye movements when the head is fixed results in vector gaze shifts when the head is free to move. Vector gaze shifts, much like conventional vector saccades, could be programmed by directly converting a vector of retinal error into a gaze shift vector. In other words, these studies emphasize the important point that eye position-dependent modulation of evoked saccades can only be interpreted conclusively if head movements are taken into account. We therefore studied the effects of electrical microstimulation of the IPS in a monkey whose head was not restrained around the yaw axis. Our observations suggest that this particular interpretation of goal directedness for the caudal superior colliculus does not pertain to the intercalated zone.

The modification of vector saccades evoked from cortex surrounding the intercalated zone could be due to a downstream mechanism, such as constraints imposed by orbital mechanics, having the effect that centripetal saccades require less muscular effort than corresponding centrifugal saccades (27–29). Alternatively, the modification of the vector saccades could result from neural signals related to eye position, having a direct effect at the site of stimulation. Two observations suggest the latter. (*i*) Although for most sites the amplitude decreased when the eyes were shifted in the direction of the evoked saccade, there were clear exceptions to this rule. Such exceptions, even if atypical, are not compatible with the notion that amplitude modification results from orbital mechanics, which of course should have the same effect, independent of the site being stimulated. (*ii*) The current thresholds for evoking saccades depended on orbital position. Again this finding is more compatible with a neural source for the eye position since one would normally assume that mechanical effects would operate after the trigger to make an eye movement.

Is there a relationship between the two representations of space within the IPS? A possible answer is suggested by the location of the intercalated zone at the border between the representations of upward and downward saccades. As illustrated in Fig. 4, eye movements directed to a goal zone in head-centered coordinates would be expected to occur if a site being stimulated integrated inputs from sites representing modified vector saccades with several directions more or less equally distributed between 0° and 360°. Centering would be the necessary consequence of the eye position-dependent modification, enhancing the contribution of modified vector sites representing centripetally directed saccades while conversely reducing the contribution of centrifugally directed saccades. Goal zones other than straight-ahead can be realized by adjusting the strength of the contributions of the different directions converging on the same cells. This mechanism may explain why the best examples of centering patterns were seen when stimulation was applied to the white matter underneath the intercalated zone. If sites in the intercalated zone integrated only inputs from the adjoining representations of upward-contralateral and downward-contralateral modified vector saccades, we would expect to see eye movements always converging in zones located in contralateral head-centered space. Goal zones congruent with the straight-ahead location or goal zones in ipsilateral head-centered space would require input reflecting modified vector saccades with an ipsilateral component. Because saccade vectors with this directionality are found in the opposite hemisphere, a specific and testable prediction derived from these considerations is that the intercalated zone should integrate callosal inputs in addition to inputs from the adjoining parietal cortex of the same side. In summary, our observations, based on electrical microstimulation, show a way in which a localized representation of head-centered space may be derived from an earlier distributed representation of head-centered space. A distributed code would be fully sufficient to encode locations in head-centered space and, moreover, would have several advantages over a more localized representation. For instance, only gradual decline of function would result following lesions; this representation is simpler to implement, and retinal position and eye position information are not lost in forming the head-centered representation. In fact, since retinal position information is not lost, such a distributed representation could represent both the retinocentric and head-centric location of a stimulus. Why, then, does the brain take the trouble to implement a second, localized representation of head-centered space which, in principal, could be less powerful? One possible answer is suggested by our observation that eye movements evoked by stimulation of the intercalated zone are usually accompanied by varying combinations of other movements such as movements of the head, shoulders, arms, parts of the face, or the pinnae. This area could be involved in the early stages of complex, coordinated movements involving many body parts. Integration of a signal derived from a localized head-centered representation, rather than independent inputs of eye position and retinal position, might help to reduce the size and complexity of such a network.

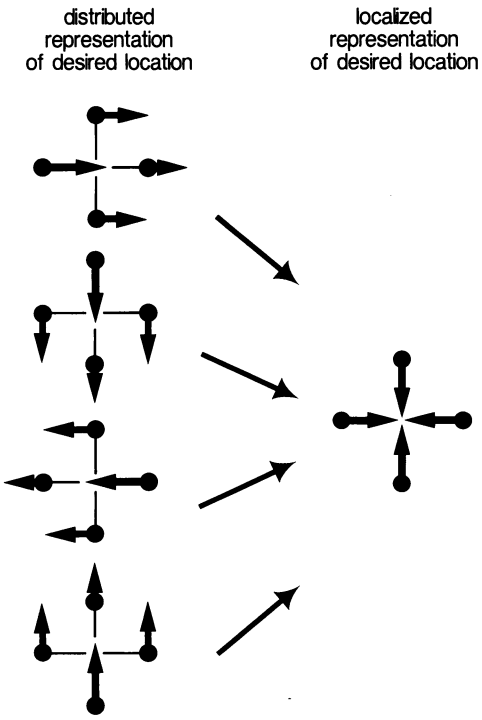

FIG. 4. Scheme of how a desired location in head-centered space might be derived from an earlier, distributed representation. A site assumed to represent a localized representation of head-centered space is assumed to integrate input from four sites containing a representation of saccade vectors with sufficiently dissimilar directionalities, each modified by eye position. See text for discussion.

1. Andersen, R. A., Snyder, L. H., Li, C.-S. & Stricanne, B. (1993) *Curr. Opin. Neurobiol.* **3,** 966–972.
2. Jeannerod, M. (1988) *The Neural and Behavioral Organization of Goal-Directed Movements* (Clarendon, Oxford).
3. Hepp, K., Haslwanter, T., Straumann, D., Hepp-Reymond, M.-C. & Henn, V. (1992) *Exp. Brain Res. Suppl.* **22,** 307–319.
4. Robinson, D. A. (1972) *Vision Res.* **12,** 1795–1808.
5. Robinson, D. A. (1963) *IEEE Trans. Biomed. Eng.* **10,** 137–145.

6. Andersen, R. A., Bracewell, R. M., Barash, S., Gnadt, J. W. & Fogassi, L. J. (1990) *J. Neurosci.* **10,** 1176–1196.
7. Blatt, G., Andersen, R. A. & Stones, G. (1990) *J. Comp. Neurol.* **299,** 421–445.
8. Barash, S., Bracewell, R. M., Fogassi, L., Gnadt, L., Gnadt, J. W. & Andersen, R. A. (1991) *J. Neurophysiol.* **66,** 1095–1108.
9. Barash, S., Bracewell, R. M., Fogassi, L., Gnadt, L., Gnadt, J. W. & Andersen, R. A. (1991) *J. Neurophysiol.* **66,** 1109–1124.
10. Maunsell, J. H. R. & Van Essen, D. C. (1983) *J. Neurosci.* **3,** 2653–2586.
11. Colby, C. L., Duhamel, J.-R. & Goldberg, M. (1993) *J. Neurophysiol.* **69,** 902–914.
12. Fleming, J. F. R. & Crosby, E. C. (1955) *J. Comp. Neurol.* **20,** 230–244.
13. Wagman, I. H., Werman, R., Feldman, D. S., Sugarman, L. & Krieger, H. P. (1957) *J. Neuropathol. Exp. Neurol.* **16,** 269–277.
14. Shibutani, H., Sakata, H. & Hyvärinen, J. (1984) *Exp. Brain Res.* **55,** 1–8.
15. Kurylo, D. D. & Skavenski, A. A. (1991) *J. Neurophysiol.* **65,** 1243–1253.
16. Roucoux, A., Guitton, D. & Crommelinck, M. (1980) *Exp. Brain Res.* **39,** 75–85.
17. Guitton, D., Crommelinck, M. & Roucoux, A. (1980) *Exp. Brain Res.* **39,** 63–73.
18. McIlwain, J. T. (1986) *J. Neurophysiol.* **55,** 97–112.
19. Tehovnik, E. J. & Lee, K. (1993) *Exp. Brain Res.* **96,** 430–442.
20. Schlag, J. & Schlag-Rey, M. (1987) *J. Neurophysiol.* **57,** 179–200.
21. Bon, L. & Lucchetti (1992) *Exp. Brain Res.* **89,** 571–580.
22. Mann, S. E. M, Thau, R. & Schiller, P. H. (1988) *Exp. Brain Res.* **69,** 460–468.
23. Mitz, R. A. & Wise, S. P. (1987) *J. Neurosci.* **7,** 1010–1021.
24. Schall, J. D. (1991) *J. Neurophysiol.* **66,** 559–579.
25. Russo, G. S. & Bruce, J. (1993) *Neurophysiology* **69,** 800-1993.
26. Ohtsuka, K., Edamura, M., Kawahara, K. & Aoki, M. (1987) *Neurosci. Lett.* **76,** 173–178.
27. Robinson, D. A. (1964) *J. Physiol.* **174,** 245–264.
28. Hepp, K. & Henn, V. (1986) *Prog. Brain Res.* **64,** 31–38.
29. Bruce, C. (1990) in *Signal and Sense, Local and Gobal Order in Perceptual Maps*, eds. Edelman, G. M., Gall, W. E. & Cowan, W. M. (Wiley–Liss, New York), pp. 261–313.