



Representation of Visual Space in Area 7a Neurons Using the Center of Mass Equation

RALPH M. SIEGEL

Center for Molecular and Behavioral Neuroscience, Rutgers University, Newark, NJ 07102

axon@cortex.rutgers.edu

Received July 10, 1997; Revised December 5, 1997; Accepted January 20, 1998

Action Editor: Koch

Abstract. The firing rate of neurons in parietal area 7a of the behaving Rhesus monkey with its head fixed incorporates both visual and eye position information. This neural tuning is not in an ego-centered coordinate space. This physiological result was unexpected as behavioral deficits following parietal damage in human and monkey subjects suggested the existence of egocentric representations. A formulation to extract a world-centered system from area 7a neurons is presented that depends on the linearity of the eye position signal and the similarity of the equation describing the tuning of these neurons to the center of mass equation. This formulation permits the computation of the location of objects in world coordinates using either serial analysis of a single neuron's activity or parallel processing of a collection of neurons. Experimental predictions are made for the relationship between different parameters of angle of gaze neurons.

Keywords: spatial navigation, parietal cortex, angle of gaze, eye movements, vision, parietal cortex, neurons, spatial perception, computational theory, area 7a, frontal eye field, supplemental eye fields

Introduction

The inferior parietal lobule has been shown to be involved in the construction of visual-spatial maps by lesion studies in both monkey (Mishkin et al., 1982; Hyvarinen, 1982) and human subjects (Critchley, 1953). It has been proposed that neurons within this region command eye movements (Mountcastle et al., 1975) or are visual in nature (Robinson et al., 1978). Single unit recording of neurons in this area with the head fixed have shown that the neurons combine both visual input, eye position, and/or eye movement information (Andersen and Mountcastle, 1983; Andersen et al., 1985b; Andersen et al., 1987; Andersen et al., 1990a, 1990b; Read and Siegel, 1997).

Neurons that combine the *eye position in the orbit* and *visual signals* are the most likely candidates for forming maps of extrapersonal space (Andersen et al.,

1985b; Read and Siegel, 1997). These neurons of the inferior parietal lobule have been termed angle-of-gaze cells. One initially surprising aspect of these cells' response was that they did not simply map out visual space (that is, they were not sensitive to a stimulus at a particular location in space regardless of eye position). Instead, these cells showed a modulation of their response to light, as an approximately linear function of eye position.

The response of a typical angle-of-gaze cell taken from area 7a is first described (Fig. 1). The Rhesus monkey was performing a dimming task in which he was required to fixate a 0.1 deg light and pull back on a lever. On dimming the light, the monkey released the lever for a juice reward. Eye position was monitored, and the animal's head was fixed in place. The receptive fields of these cells were measured by the flashing a 5 deg \times 5 deg square of light at different

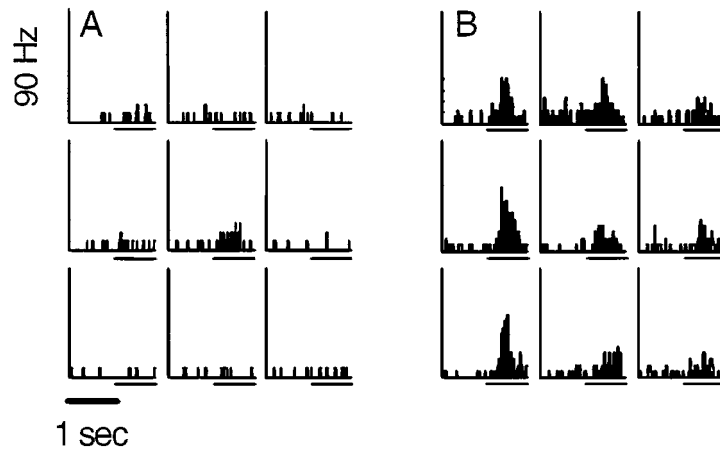


Figure 1. A: Receptive field of a neuron plotted while the animal fixates at the center of a screen. The locations of the peristimulus time histograms indicate the location of the 5 deg square stimulus. The stimuli were placed on a 20 deg \times 20 deg grid. Note that the receptive field is centered on the fovea. B: A recording from the same cell while the animal was fixating at nine different positions in a 10 deg \times 10 deg grid. At each position the 5 deg square was immediately behind the fixation point so that the retinal locus of the stimulus was always at (0 deg, 0 deg). The fixation location had two effects. First, it modified the light evoked response such that the greatest response was seen in the left visual field. Second, there is a weak modulation of the background activity prior to the stimulus onset. The horizontal line under each peristimulus time histogram indicates the light onset in all displays. The vertical axis is firing rate with a maximal value of 90 Hz. (These data were taken from Read and Siegel, 1997, and replotted here as an exemplar of angle-of-gaze neurons. Additional details as to the neurophysiological data may be found therein).

locations relative to the fixation point and measuring the response of the cells. The neurons were light sensitive and had large, bilateral receptive fields, often including the fovea. The neurons' response to the flashed stimulus was tested as a function of the locus of fixation; 66% of the neurons had a linear modulation by the eye position (Andersen et al., 1985b; Read and Siegel, 1997). This *angle-of-gaze effect* is not restricted to visual cells. Cells that combine eye position and saccadic eye movements have also been noted (Gnadt and Andersen, 1988).

For example, a single parietal neuron responds to a flashed 5 deg square with a vigorous response. It fires strongest when the stimulus is over the fixation point (Fig. 1A). The equation that models this data had quadratic components for both the horizontal and vertical *retinotopic* location of the stimulus. In a recent study that quantified these effects, 40% of the neurons in area 7a showed a significant hump (that is, quadratic term) in the second-order polynomial model using a stepwise procedure (Read and Siegel, 1997). The stepwise procedure adds and removes coefficients until only those that are statistically significant remain.

The same neuron is then tested with the stimulus always over the fixation point—that is, the same retinotopic location (Fig. 1B). In this test, the fixation point is placed in one of nine positions. Although the

monkey views the same visual stimulus (that is, the retinal image is constant), the response of the neuron is modulated such that the strongest responses are found for leftward fixations. Such data were fit with a second-order polynomial via a stepwise procedure (Read and Siegel, 1997). Only linear components were significant for this cell with the quadratic components excluded. In the original study of this phenomenon, Andersen et al. (1985b) found about one-third of the neurons showed a purely linear response similar to that of Fig. 1B. In this study, an additional third had a significant linear component with a significant lack of fit. What this means in practice was that one or two of the nine locations tested deviated from linearity. The linear model did not significantly fit the final third of the neurons.

Read and Siegel (1997) further explored the eye-position tuning for a population of neurons using a stepwise procedure. Again, about one-third had only a linear component. Of the remaining neurons, 45% of the cells were quadratic in the horizontal and/or vertical meridian. Of these, all but one cell were linear along one meridian and quadratic along the other (Read and Siegel, unpublished results). The remaining had complicated angle-of-gaze fields. This study also examined the angle-of-gaze dependency for optic flow fields. Even a larger proportion of the cells showed

linear modulation. These two studies show many neurons with linear modulation of the visual by the eye position in the orbit for area 7a. Also, neurons appear to be nonlinearly modulated by the eye position.

Such data indicate that a peaked model for the retinal location dependence, and a linear model for the eye-position dependence, is reasonable for a subpopulation of the parietal neurons. This article focuses on the linear modulation by eye position, as an earlier study (Pouget and Sejnowski, 1997) has examined the nonlinear tuning in detail. Further data are not forthcoming as to how these area 7a neurons encode the position of the head on the body or in the environment. Because of these lacunae in our knowledge about area 7a neurons, the following theoretical study is restricted to examining how the angle of gaze cells can be used to extract position in a world-centered coordinate system when the head is fixed. A possible extension of the present theoretical approach when the head is free to move is covered in the Discussion.

Methods

The Ideal Area 7a Neuron

From these experimental results about area 7a neurons, we can now write equations for an ideal neuron. It is to be understood that this ideal neuron is an exemplar of the major properties of an area 7a visual neuron.

A symmetrical single-humped function is a good representation of the dependence of neural activity of the retinotopic location of the visual stimulus for a majority of these cells. In the original physiological studies, a Gaussian function was used as a qualitative approximation to the receptive field shape (Andersen et al., 1985b). A later study (Read and Siegel, 1997) used a quadratic to model the data. A Gaussian function (R_1) will mostly be used for the purpose of demonstration. Some of the results will also be derived for a quadratic function (R_2) to illustrate that the essential results are independent of the receptive field shape. The dependence of the light-sensitive signal on eye position can be written as

$$R_1(r_x, r_y) = d^2 \exp \left[- \frac{(r_x - \rho_x)^2 + (r_y - \rho_y)^2}{\lambda_1^2} \right] \quad (1a)$$

$$R_2(r_x, r_y) = d^2 - \frac{(r_x - \rho_x)^2 + (r_y - \rho_y)^2}{\lambda_2}, \quad (1b)$$

where $R_i(r_x, r_y)$ is the activity evoked by the onset of the light, (r_x, r_y) is the retinotopic positions of the object in the horizontal and vertical meridians, respectively, (ρ_x, ρ_y) is the location of the center of the receptive field, λ_i is the space constant, and d^2 is the maximum rate for the retinotopic function. Note that the quadratic function R_2 is defined to only be positive. For values of r_x and r_y for which the quadratic evaluates as less than 0, it is set to 0. Thus, if only considering one dimension, R_2 is 0 outside the interval $(-r_0 - d\lambda_2, -r_0 + d\lambda_2)$.

The space constant of R_1 is defined as the number of degrees for the evoked light response to decrease by e^{-1} . This value can be derived from the data of Read and Siegel by noting the mean amplitude of the quadratic component over all the neurons tested with static squares is a value of approximately 0.011 ± 0.007 Hz/deg² (Read and Siegel, unpublished data). Computing the space constant by fitting a Gaussian function to the quadratic modeled neural data provides an estimate of λ_1 being 15.45 deg. A value of 15 deg will be used for the remainder of this article. The quadratic width parameter λ_2 is approximately 10 deg by inspection.

The light-sensitive response of these neurons is also modulated by the position of the eye in the orbit (recall Fig. 1A). The angle of gaze effect (gain effect) on the light-sensitive response can be written as follows:

$$G(e_x, e_y) = \alpha_x e_x + \alpha_y e_y + \beta, \quad (2)$$

where $G(e_x, e_y)$ is the gain field dependence of the light response on eye position, α_x and α_y are the scaling factors between eye position and neural activity, and β is the neural response evoked by the light stimulus when the eyes are in the primary position. It is important to note that the center of the receptive field (ρ_x, ρ_y) does not depend on the location of the eye on the orbit—that is, the receptive field remains retinotopic (Andersen et al., 1985b; Read and Siegel, 1997). This model for area 7a neurons is thus the starting point of this study. The question arises as to how such a neuronal representation may be used for spatial representations.

Results

Given these expressions, a model for the light-evoked neural activity A_{I_s} (which is the change in neural firing rate relative to prestimulus conditions) as a function of eye position in the orbit and the light impinging on the

retina is

$$A_{Is}(r_x, r_y, e_x, e_y) = G(e_x, e_y)R(r_x, r_y). \quad (3)$$

This is a description of the dependence of area 7a neurons on visual and eye-position input. The responses of some cells in area 7a do not depend on eye position $\alpha_x = \alpha_y = 0$ while others are independent of the location of the visual input $R(r_x, r_y) = 1$.

A Neural Representation of Space

This representation is interesting, as it is not intuitively obvious how such neurons are used to map out visual space. In daily life, objects are correctly located in space regardless of the eye position in the orbit. Inferior parietal cortex is believed to be necessary for such spatial location based on lesion studies in human and monkey subjects (Lynch, 1980; Critchley, 1953). Furthermore, eye movements are made in a head-centered, not a retinotopic, coordinate system (Sparks and Mays, 1983; Gnadt and Andersen, 1988; Colby et al., 1993). Therefore, one might have expected that the cells in this part of the dorsal pathway would be mapping a world-centered coordinate system. For example, the evoked response of the cell might be thought to depend only on the location of the object in world coordinates and not be sensitive to the position of the eyes in their orbits.

Some unusual examples of nonretinotopic receptive fields have been reported. In the deepest parts of the lateral intraparietal sulcus, neurons have been reported to respond to movements toward particular facial locations with the movement endpoint associated to the face's somatosensory fields (Colby et al., 1993). Similar cells have been reported in ventral premotor cortex with visual receptive fields allied with many different body parts (Graziano et al., 1997). Thus, these parietal and premotor neurons may be representing relationships between visual signals and particular body parts. Recording from frontal eye fields, neurons, which receive a projection from area 7a (Andersen et al., 1985a; Selemon and Goldman-Rakic, 1988; Andersen et al., 1990a) reveal an angle of gaze effect and *not* a world-centered response. Neurons have also been reported in supplemental eye fields that represent responses in object-centered coordinates (Olson and Gettner, 1995). Each of these different regions appears to represent a particular aspect of the animal's immediate surrounding environment. Neurons that closely match the behaviorally based concept of a body-centered coordinate

system only exist in a few cells. In parietal lobe area PO, neurons have been reported that respond to a stimulus at a single spatial location regardless of eye position (Galletti et al., 1993). This study is intriguing; however, these neurons appear to be rare. Only six of over 300 recorded neurons responded to a visual stimulus in only one spatial location.

We next consider how the response of these area 7a neurons might be used to construct a world-centered coordinate response. The first question to ask is how the neural activity in these neurons varies as an object is moved about in space. Second, we ask in what way the activity from several of these neurons to locate an object in space can be combined.

The Response of the Angle-of-Gaze Cells as a Function of Location in Space

In this section we use the geometric relationships between the location of an object in world-centered coordinates, eye position, and retinal image to determine the response of the area 7a neuron as a function of these three variables.

The location of an object in world coordinates relative to the fixed head is given as (w_x, w_y) . If the eyes' gaze is at (e_x, e_y) , a good linear approximation (Fig. 2) to the actual physiological optics (Westheimer, 1957) is

$$r_x = w_x - e_x. \quad (4)$$

Thus, the neural activity as a function of the location of the object in world coordinates and the gaze angle is derived by the substitution of Eq. (4) into Eq. (3):

$$A_{Is}(w_x, w_y, e_x, e_y) = G(e_x, e_y)R(w_x - e_x, w_y - e_y). \quad (5)$$

A similar expression can be derived in terms of location in world coordinates and the retinal locus of the stimulus:

$$A_{Is}(w_x, w_y, r_x, r_y) = G(w_x - e_x, w_y - e_y)R(r_x, r_y). \quad (6)$$

We thus have Eqs. (5) and (6) with four dependent variables for the response of an ideal area 7a neuron. The essential assumptions are that (1) the receptive fields are given by a humped function, (2) the amplitude

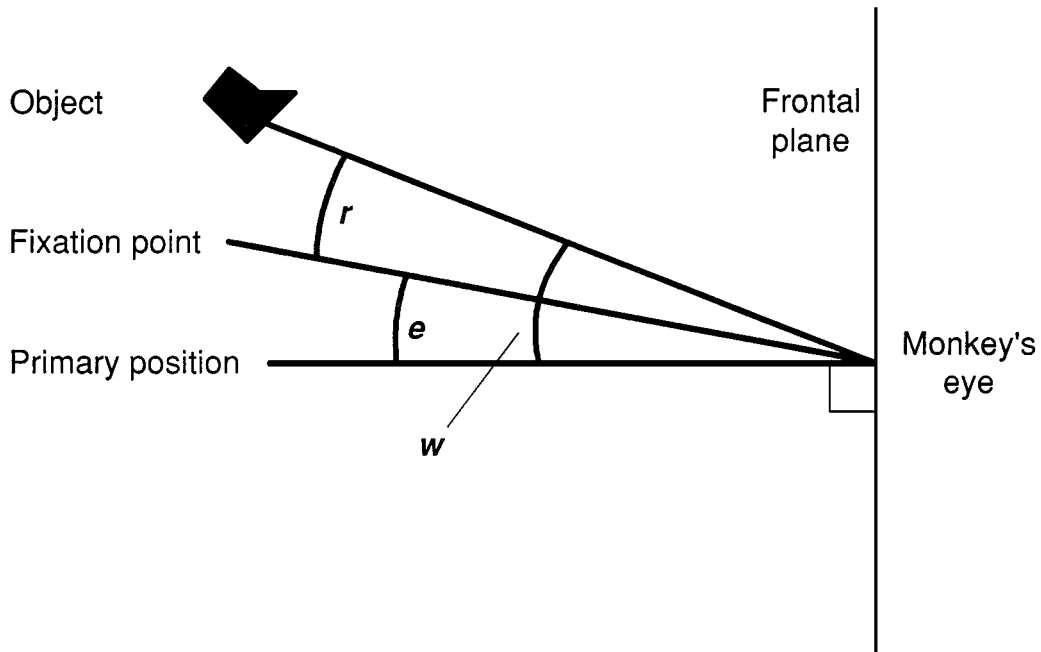


Figure 2. Geometric relationship between world, retinal, and eye coordinates. The monkey's head is fixed. The line perpendicular to the frontal plane is defined as 0 deg. An object is located at an angle in this coordinate system. The animal gaze is centered at e . Therefore, the position of an object on the retina r is $w - e$ —Eq. (4).

of the visual response is linearly modulated by the position of the eye in the orbit, and (3) the receptive field center in retinal coordinates does not change with eye position. The functional expression of these assumptions is encapsulated in Eqs. (5) or (6) and is plotted in Fig. 3. For simplicity, a reduction in the number of independent variables is obtained by only considering the effect of eye movement and retinal position of a stimulus along a single meridian (for example, horizontal). It can be seen that as the object is moved through visual space—say, left to right—the response of the neuron increases and then decreases as a single humped function. As the eye is moved, the firing rate of the cell increases. The location of the peak is seen to shift approximately proportional to the location of the object in world coordinates. (The location of the peak can be explicitly computed by taking the derivative of Eq. (5) with respect to e .)

The problem remains to determine the location of an object in the visual world knowing the functions G and R , the neural activity and the position of the eye in the orbit e or the retinal locus of the image r .

A few points may be made. First, given the neural activity of a single cell at an instant in time, the location of the object in world coordinates is not

uniquely determined. This is because there are more independent variables than equations. The problem is ill-posed, and additional constraints are needed (Poggio and Koch, 1985). One possible solution is to use more cells.

Clearly, as there are four unknown variables in the complete problem, a minimum of four cells (with ideal properties and no noise) would be needed to uniquely determine the location of an object in world coordinates. Even under such improbable conditions, an analytical solution to the problem may not be obtained due to the nonlinearity of the receptive field structure in Eq. (1). Numerical solutions could be obtained. The precision and the convergence of such solutions would be sensitive to the noise in the system; it is also not immediately clear how such a solution could be implemented using known neural circuitry. The actual solution to this problem is in terms of biologically noisy cells that generally compute by the thousands or more, and we are interested in biologically realizable implementations, so this solution of the problem is discarded.

It seems more likely that the cortex uses the activity of a large number of cells to determine where an object is in the world. It is quite simple to imagine neurons in a recipient zone of cortex combining the activity of

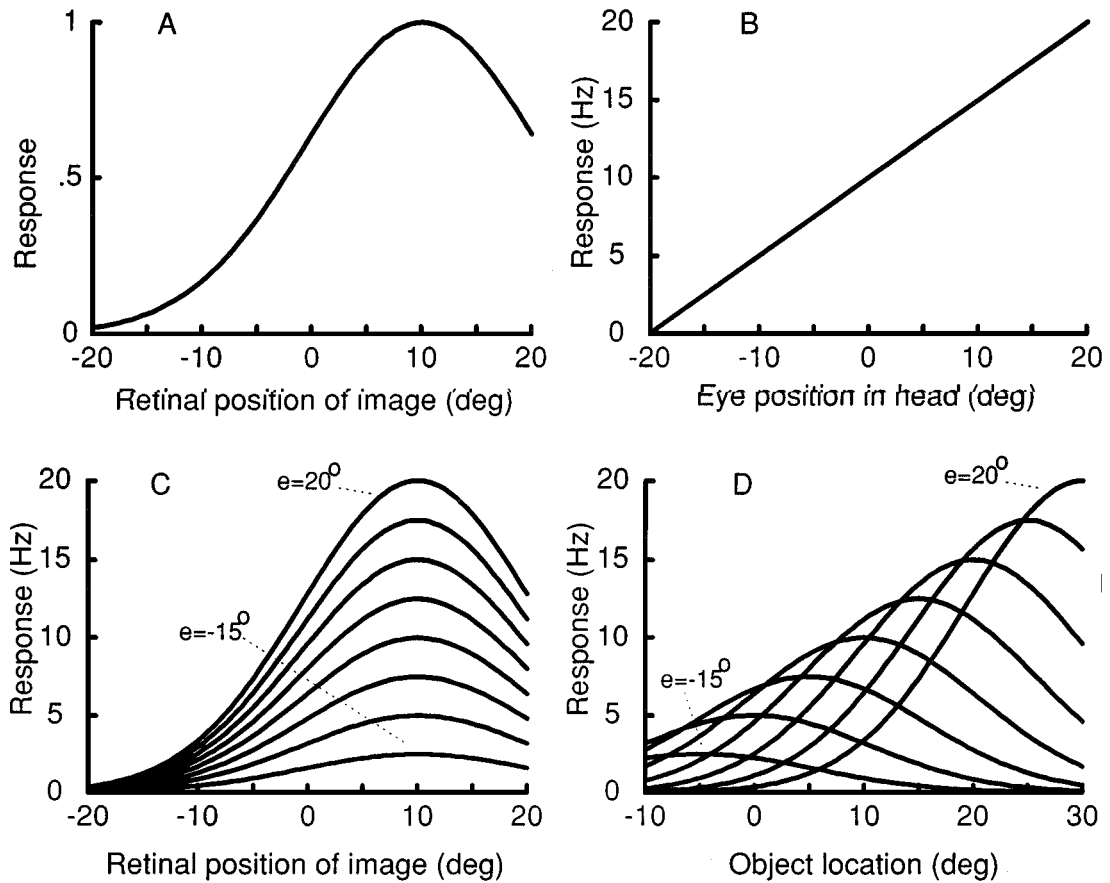


Figure 3. Dependence of neural activity for the idealized angle of gaze cells. A: The response of a cell as retinotopic position of the stimulus is varied with the fixation fixed straight ahead. B: The light-sensitive response of the cell for varied eye positions with the stimulus always at the center of the receptive field. C: The effect of eye position on the retinotopic map of the cell. Note that the receptive field center remains centered in retinotopic coordinates. D: The response of the cell as a function of world position of an object varies for different angles of gaze. For simplicity of presentation, the position of the object and the gaze angle are assumed to lie upon the horizontal meridian. In C and D each of the lines represent a different gaze angle. The abscissa is rate of firing in spikes per second the ordinate is labeled in each plot.

a large number of cells through summation (that is, integration). A demonstration that the activity of area 7a neurons can be used to create a linear representation of world space using integration or summing operation is presented below. The plausibility of the actual implementation of the demonstration under real-world conditions is found in the Discussion.

Integration of the Responses of Neurons Using the Center of Mass Equation

As the dependence of the neural activity on the location of the eye in the orbit and the location of the object in space is known, we can ask how this encoding of visual and eye position information is used to determine the

location of the object in space? The form of Eq. (5) suggests a possible algorithm. This algorithm is interesting in that it lends itself to both serial and parallel processing and may be applicable to other similar problems in the central nervous system.

From classical Newtonian mechanics, one may recall that the equation for the center of mass of an object is

$$\bar{R}_c = c \int_{-\infty}^{\infty} \bar{R} \cdot D(\bar{R}) \cdot d\bar{R}, \quad (7)$$

where

$$c = 1 / \int_{-\infty}^{\infty} D(\bar{R}) \cdot d\bar{R}, \quad (8)$$

\bar{R}_c is the location of the center of mass, and $D(\bar{R})$ is the density of the object as a function of location. (Vector quantities are indicated as \bar{X} .) The reader is referred to Feynman et al. (1963) for background on this physical concept; a number of papers discuss the center-of-mass equation in other contexts (Abbott, 1994; Mussa-Ivaldi and Giszter, 1992; Snippe, 1996). Furthermore, recalling (1) the linear function of G in e_x and e_y and (2) the integrand of Eq. (7), it may be seen that $\bar{R} \cdot D(\bar{R})$ is identical in form to that of the product in Eq. (5). Then it is possible to state a priori that the sum of the response of one parietal neuron, as eye position is varied, is directly proportional to the location of the object in space. This can be stated algebraically as

$$\int_{-\infty}^{\infty} A_{Is}(\bar{w}, \bar{e}) \cdot d\bar{e} = \int_{-\infty}^{\infty} G(\bar{e}) \cdot R(\bar{w} - \bar{e}) d\bar{e} = \bar{C}_1 + \bar{C}_2 \cdot \bar{w} \quad (9a)$$

$$\int_{-\infty}^{\infty} A_{Is}(\bar{w}, \bar{e}) \cdot d\bar{e} = (C_{1x} + C_{2x}w_x, C_{1y} + C_{2y}w_y), \quad (9b)$$

where the constants \bar{C}_1 and \bar{C}_2 depend on α_x , α_y , β and the precise form of the function R . The second line of Eq. (9) shows this explicitly. Thus, it can be seen that the integrated activity of the neuron will be linearly proportional to the position. It is possible in theory to determine the location of an object by a simple integration (which could be approximated in neural tissue by *addition* implemented in a dendritic tree).

Serial Computation of the Activity of a Single Cell.

We would like to restate the above result in physiological terms. If one were able to monitor the light-sensitive activity of one neuron in area 7a and sum it up while the eye scanned many positions in space, one would have a vector proportional to the object's location in world space. This would be a serial (as opposed to parallel) computation and would allow a cell at a second cortical area to use input from one cell in the parietal lobe to compute the location of an object. To be somewhat more realistic, a similar result could be constructed from a population of neurons with identical properties as the eye was moved in the orbit (note that this result does not change if the integral is performed over r for Eq. (6) instead of (5) and substituting into Eq. (7)).

Algebraically this is simple to compute for the two forms of the receptive field in Eq. (1). If we consider only a single meridian and assume a Gaussian-shaped

receptive field of Eq. (1a), Eq. (9a) becomes

$$A_{Is} = \int_{-\infty}^{\infty} (ae + b)d^2 \exp\left[-\frac{(w - e - \rho)^2}{\lambda^2}\right] de \quad (10a)$$

$$A_{Is} = d^2\lambda\sqrt{\pi}(aw - a\rho + b). \quad (10b)$$

Recall that ρ is the receptive field center, a and b are the linear parameters of the gain field, λ is the space constant, and d^2 is the amplitude of the visual response.

The result of assuming a Gaussian-shaped receptive field and an integration over all eye positions therefore leads to the result that the integrating neuron will fire as a linear function of the position of the object in world coordinates.

This result can be further illustrated by assuming a single meridian, with a quadratic receptive field (Eq. (1b)). The integral becomes

$$A_{Is} = \int_{h-\rho-d\lambda}^{h-\rho+d\lambda} (ae + b) \left[\frac{d^2 - (w - e - \rho)^2}{\lambda^2} \right] de \quad (11a)$$

$$A_{Is} = -\frac{4}{3} d^3\lambda(b - a\rho + aw). \quad (11b)$$

Note that in both Eqs. (10b) and (11b), the integral is linear in the position of the object in world coordinates w .

This temporally serial computation could take place in any one of a number of cortical areas that receive projections from area 7a (for example, frontal eye fields, parahippocampal gyrus, and supplemental eye fields). Such a serial analysis would suggest that there were point-to-point projections between such a two cortical regions as there would be no reason to integrate across regions of cortex. Furthermore, this solution would indicate that some amount of time would need to pass for the percept to be constructed.

However, this serial computation is at odds with what is known about the projections of neurons in the parietal lobe to the prefrontal cortex and psychophysics of spatial analysis. Small injections (presumably taken up by a localized population of axonal terminals) of retrogradely transported tracer into the frontal eye fields result in a patchy and banded collection of cells in the parietal lobe 7a (Andersen et al., 1985a; Selemon and Goldman-Rakic, 1988; Andersen et al., 1990a). Elsewhere such banded patterns are indicative of orderly projections between neural tissue (e.g., Hubel

and Wiesel, 1977; Law and Constantine-Paton, 1981). This suggests that a local region receive projections from a collection of different cells in the parietal lobe that are arranged with some topography.

Furthermore, the speed by which we are able to form an internal representation of visual space (Matin et al., 1966; Matin, 1982) suggests that we are doing this computation in parallel and that we do not need to scan the visual environment to form a working map of visual space. Furthermore, one would expect based on physiological studies (Andersen et al., 1985b; Read and Siegel, 1997) that a map of surrounding visual space exists in area 7a.

Parallel Processing of a Set of Area 7a Neurons. Are there other ways to use the center of mass equation for neural activity in area 7a to form a map of visual space? Is it possible to predict relationships between some of the parameters of the tuning fields that would allow us to extract the location of an object in space from a population of cells? This section addresses these problems with two different parallel processing computations that use area 7a neurons to constantly compute the location of an object in world-centered coordinates.

To simplify the graphical and analytical discussion of this problem, we return to the simplified representation of the problem with the assumption that both the location of the object in world space and the position of the eye in its orbit lie on a single meridian. The variables are thus e (eye position) and r (retinal position); the dependent variable is neural activity A_{I_s} . ρ is the receptive field center. Thus, Eq. (1) substituted into Eq. (5) in one dimension becomes

$$A_{I_s} = (\alpha e + \beta)R(w - e - \rho). \quad (12)$$

This is illustrated in Fig. 3D. An object moved in world coordinates causes the response of the neuron to increase until the object's image is over the center of the receptive field. Then it decreases.

Equation (12) illustrates the response of a given neuron to an object in a particular position in world coordinates when the eyes are at a certain angle of gaze. Let us suppose that the tuning properties (that is, receptive field center and angle-of-gaze effect) for each cell in the cortex depends on the position p of the cell on the surface of the cortex. For the current discussion, p is taken as a one-dimensional vector. This is denoted by using the notation $\alpha(p)$, $\beta(p)$, $\rho(p)$.

One could imagine that these parameters are mapped among the neurons of area 7a. Evidence for some order to the topography of area 7a was cited earlier with respect to anatomical and behavioral studies. It is suggested here that there might be relationships between the parameters $\alpha(p)$, $\beta(p)$, $\rho(p)$. for some subpopulations of area 7a neurons.

Inspection of Eq. (12) and comparison with the center of mass equation (Eq. (7)) suggests two different relationships of the parameters that would allow a simple mapping of space in area 7a. These relationships are between the receptive field center (ρ) and either one of the parameters of the gain field (α and β).

For the first relationship, it is assumed that for all positions p in cortex the receptive field center $\rho(p)$ is proportional to intercept of the gain function $\beta(p)$. Then in order to extract the location of an object in world coordinates, the responses of cells with different receptive field centers are integrated (that is, summed).

If $\rho(p)$ is proportional to $\beta(p)$ —that is, $\rho(p) = \zeta \cdot \beta(p)$ —for all locations in the cortex, Eq. (10) becomes

$$A_{I_s}(p) = [\alpha e + \beta(p)] \exp \left[- \frac{(w - e - \zeta \beta(p))^2}{\lambda^2} \right]. \quad (13)$$

We can analytically compute the activity of a cell that integrates the output of a large population of cells with different values for β . The output of such a cell would be

$$\begin{aligned} \int_{-\infty}^{\infty} A_{I_s}(\beta(p)) \cdot d\beta(p) \\ = \sqrt{\pi} \lambda \cdot \text{sign}(\zeta) \frac{(\alpha \zeta - 1)e + w}{\zeta^2} \end{aligned} \quad (14a)$$

$$\int_{-\infty}^{\infty} A_{I_s}(\beta(p)) \cdot d\beta(p) = k_1 e + k_2 w. \quad (14b)$$

This integrating neuron's response, given by Eq. (14), varies linearly with both position of the eye in the orbit and the position of the object in space (Fig. (4B)). Thus, if the intercept of the eye-position signal (β) varies in proportion with the center of the receptive field (ρ), we have been able to describe an algorithm that yields a linear signal in both eye and world coordinates. We call the parameter ζ the *eye-retina proportion* to indicate the relationship between those two parameters. One could construct this algorithm with

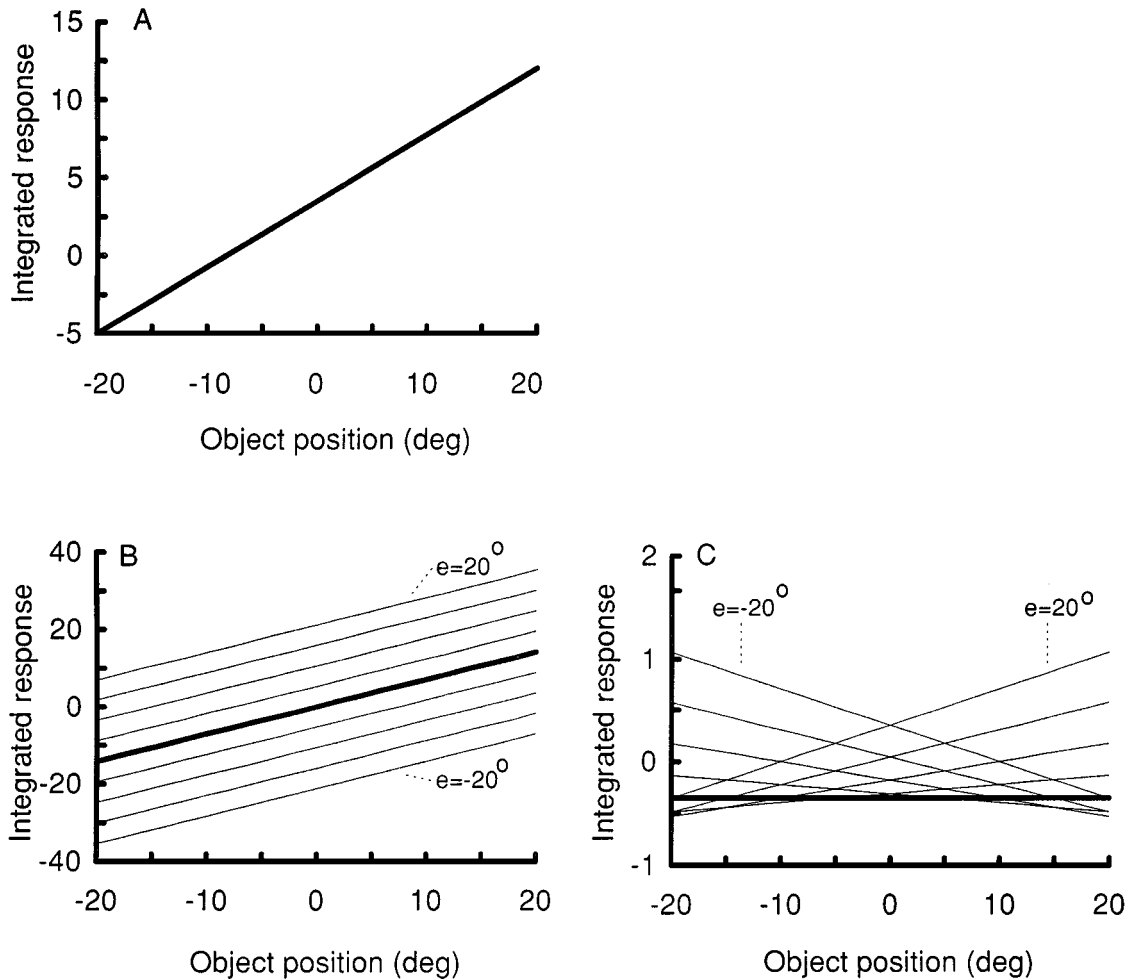


Figure 4. The response of a neuron that would integrate the activity of area 7a cells using a number of hypothetical schemes. A: Serial integration. The final response of a cell that sums the activity of an angle of gaze cell as the eye is moved to many different fixation locations is plotted against the location of the object. There is a linear dependence of the activity of this integrating neuron on the position of the object in world coordinates. B, C: The result of two different parallel computations that use the center of mass equation and the angle of gaze neurons. B: Under the assumption that the receptive field center is proportional to the intercept β , the response of the integrating neuron is directly proportional to eye and world position. C: Under the assumption that the receptive field center is proportional to the slope of the gain function, the response of the integrating cell is still proportional to its position in world coordinates. However, the slope varies with eye position.

simple neural circuitry by proposing axons from area 7a converge on neurons that simply sum the total synaptic input in the dendritic tree. The result of the summed activity of this recipient cell would vary in proportion to the location in world coordinates and with eye position.

A variation in either the location, or an object of eye position, would result in a change in the neural activity directly proportional to the distance between the eye and the object in world coordinates. This change in neural activity with change in object position is the same regardless of where the eye is in the orbit. It should be emphasized that the linear response of such

an integrating neuron is dependent on both eye position and world coordinate of the object. This cell, or group of cells, does not unambiguously indicate where something is in space. The signal is not in absolute coordinates; it remains in a relative coordinate space. However, this linear signal could be used to indicate to the eye-movement system the amplitude and direction of an eye movement that is needed to reach the target.

Another possible relationship between the receptive field and eye-position signal is that the slope of the gain function $\alpha(p)$ varies in direct proportion to the center of the receptive field $\rho(p)$. This formulation begins by

assuming $\rho(p) = \zeta \cdot \alpha(p)$. Substitution into Eq. (12)

$$A_{Is}(p) = [\alpha(p)e + \beta] \exp \left[-\frac{(w - e - \zeta\beta(p))^2}{\lambda^2} \right] \quad (15)$$

and integrating over $\alpha(p)$ yields

$$\int_{-\infty}^{\infty} A_{Is}(\alpha(p)) \cdot d\alpha(p) = \sqrt{\pi}\lambda \cdot \zeta \cdot \text{sign}(\zeta) \cdot \frac{(\beta\zeta - 1) + e(w - e)}{\zeta^2} \quad (16a)$$

$$\int_{-\infty}^{\infty} A_{Is}(\alpha(p)) \cdot d\alpha(p) = k_1 + k_2(e w - e^2) \quad (16b)$$

Equation (16b) is illustrated in Fig. 4C. Note that when the eye is in the primary position $e = 0$, the neural activity ceases to depend on the location of the object in space. Teleologically, this would be a poor way to organize the analysis of space in that it would indicate that there would be eye positions where it would not be possible to determine the location of an object in space. No such psychophysical phenomena are known to occur in the primate visual system. This hypothesis of linearity between the neuron's center of receptive field and the slope of the gain field can be discarded. The prediction from the analysis of two possible means for parallel processing is that there is dependence between the center of the receptive field and the activity of the neuron when the eyes are in the primary position.

Both of these parallel computation schemes assume that there is a linear relationship between the different parameters defining the response of the area 7a neurons. Evidence for such relationships between defining parameters of a cell have been found in (1) striate cortex and a number of other cortical areas where receptive field size is proportional to eccentricity (Hubel and Wiesel, 1977), (2) the middle temporal region (MT) of macaque where the optimal velocity and field size is proportional to retinotopic position (Van Essen et al., 1981; Albright et al., 1984). Thus, it is possible that such relationships will exist in area 7a between the parameters. It is suggested here that such relationships may be the basis for the mapping of surrounding visual space in area 7a.

Guidance of Eye Movements

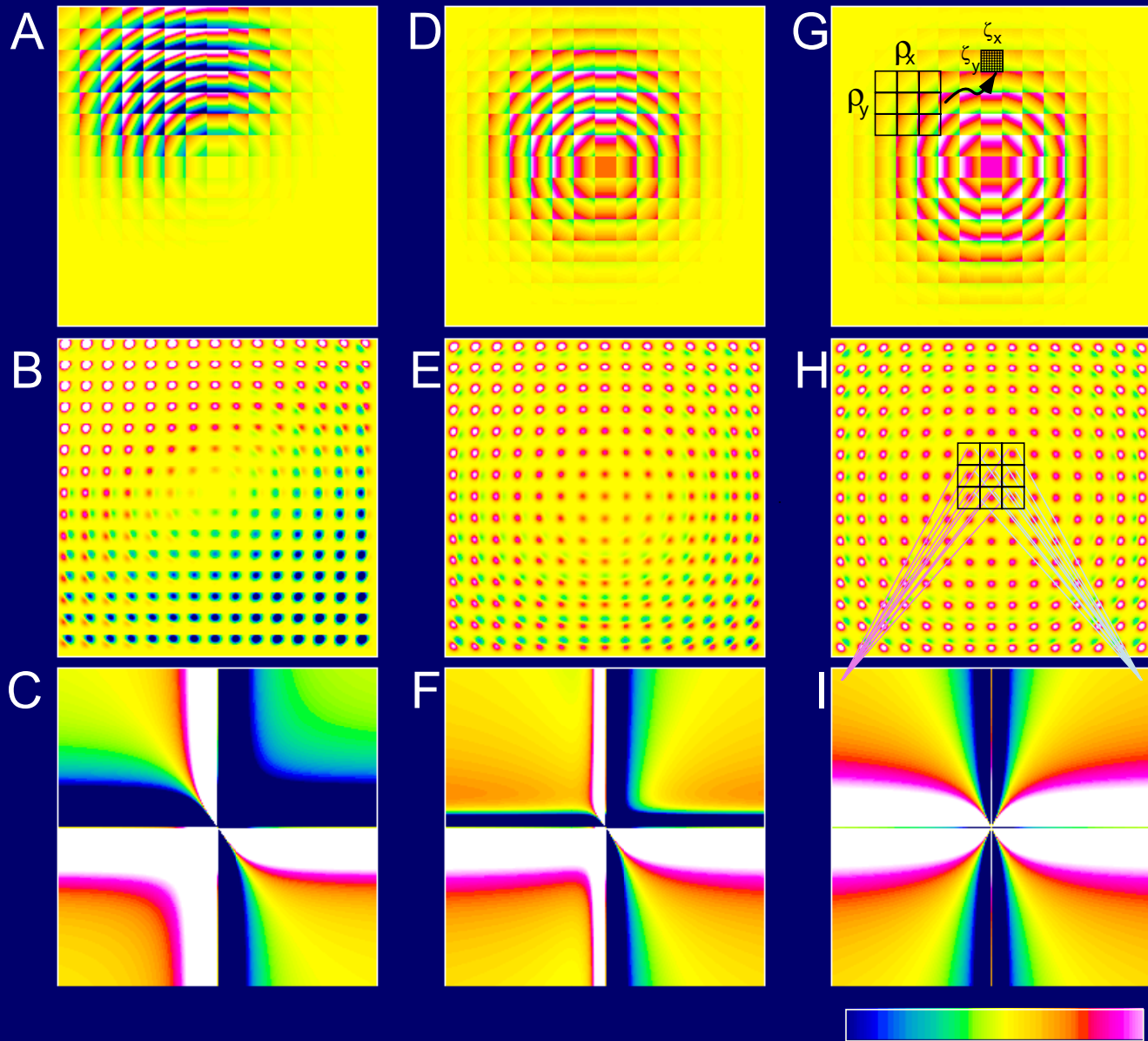
The results thus far demonstrate that the neural activity of angle of gaze cells can be summed in parallel

to form a linear representation of visual space. This linear signal is not purely in terms of head position; it is also dependent on eye position. The dependence on eye position might seem to lead to difficulties in using this signal in guiding motor movements, as there is no unique firing activity to indicate the absolute location of an object in space. It is suggested here that in order to account for behaviors that use a map of visual space, it is not necessary to have such an absolute spatial map. The linear signals provided by the center of mass computation on the angle of gaze cells could in themselves serve as a distributed *linear* representation to guide eye movements. To demonstrate the utility of such a signal, this section sketches a guidance system for eye movements. First, the general topographic mapping of area 7a neurons onto the cortex is given. Second, the tuning of the area 7a neuron is described. Third, the mapping of the parameters defining the area 7a neurons response onto the cortex is described. Fourth, the integration by the neurons that receive area 7a neuron output is described. Finally, the integrated response of the area 7a neurons is used to guide eye movements.

Putative Topographic Maps. It was proposed above that a topographic mapping between the different parameters defined the angle-of-gaze cells in area 7a. Two possible mappings are possible in area 7a. First, the eye-position tuning may be embedded within the retinal map in a homology as to the embedding of orientation within the retinotopic map in striate cortex (Fig. 5A). Second, the retinal map could be embedded within the eye-position map (Fig. 5B). A comparison of Figs. 5A and 5B shows how the proposed retinotopic map and the eye-position map would interact to modulate the responses of the cortex. The response of each of the neurons is the same in the two panels; what differs is their mapping onto cortex.

Individual Neuronal Response. It is assumed that the tuning of individual area 7a neurons is described by Eq. (13). Equation (13) indicates that the response of the neuron is a linear function of eye position and a humped function of retinotopic position. Implicit in Eq. (13) is the eye-retina proportion (ζ) between the receptive field center and the intercept of the eye-position signal ($\rho_x = \zeta_x \cdot \beta_x$). This linear relationship results in the integral of a set of area neurons linear with eye position and world coordinates (Eq. (14b)).

An alternative would be the use of Eq. (15) in which the receptive field center and the gain field are linearly



Siegel, Figure 5

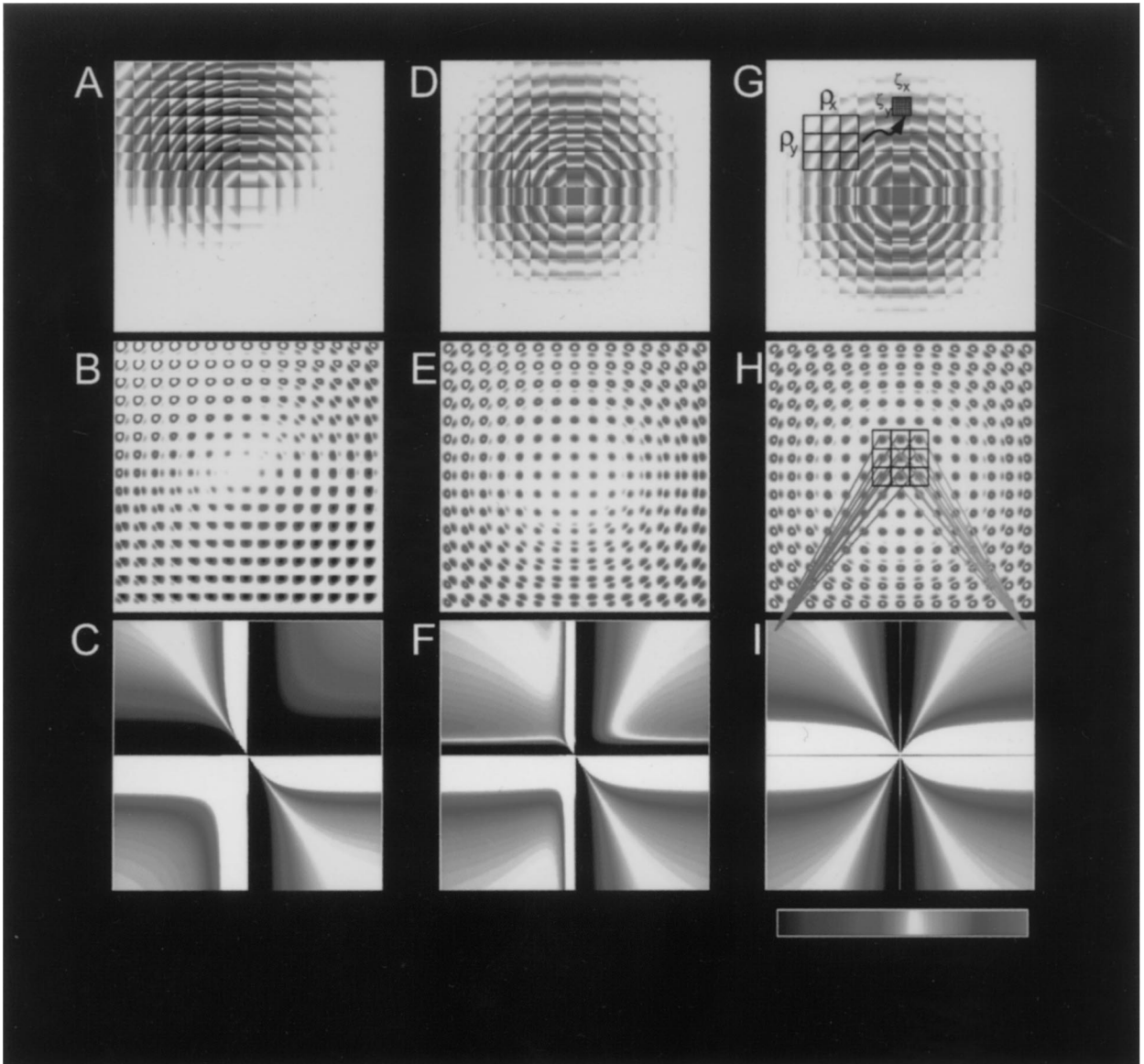


Figure 5. Putative mapping of area 7a and frontal eye fields. Each of the nine panels is a representation of neural activity that might be found on the surface of the cortex. The horizontal and vertical portions of each of the panels represent excursions along the surface of the cortex. (The depth of the cortex is not taken into account.) The upper six panels are representations of activity that could be found in area 7a. The lower three panels are representations of activity found in a cortical region that receives projections from area 7a (for example, frontal eye fields). There are two possible ways to topographically represent eye and retinotopic tuning. In the top row of three panels (A, D, G), it is assumed that the retinotopic map is distributed across the extent of cortex with an eye-position map embedded within it. The middle row of three panels (B, E, H) assume that the eye-position map is distributed across the extent of cortex with the retinotopic map embedded within it.

The three columns illustrate the effect of changing eye position with the stimulus at a fixed world-based coordinate of (10 deg, -20 deg). In the first column (A, B, C), the eye is at the primary position (0 deg, 0 deg). In the second column of panels (D, E, F) the eye is at (7 deg, -14 deg). In the third column of panels (G, H, I), the eye is at (10 deg, -20 deg).

The slope of the eye-position gain function is 2 Hz per deg; the receptive field space constant λ is 20 deg. The color scale is similar to that for heated metals. (Blue indicates low firing rate, while white indicates high firing rates.) The range of values corresponding to the color bar is ± 30 Hz for the upper six panels, while it is $\pm 50,000$ Hz² for the lower three panels. The firing integrated firing rate has units of Hz² as the integration is not normalized.

related. However, this would be a poor choice as there are eye positions for which there would be no dependence of the integrated neuronal response on the location of the object in world coordinates (Eq. (16b)). Therefore, Eq. (15) is not investigated further.

Mapping of Neuronal Parameters onto Cortex.

Given the assumed implementation of Eqs. (13) and (14b), it then becomes necessary to map the position parameters of Eq. (14a) across the cortex. Based on experimental data (Andersen et al., 1990b; Read and Siegel, 1997), it is assumed that the receptive field center (ρ) varies over a range of (-20 deg, 20 deg). The gain field slope (β) is fixed at 2 Hz/deg; the receptive field width (λ) is 15 deg. All that is left is to describe how the gain field intercept varies with position—that is, the eye-retina proportion. One possibility is that there is one value of the eye-retina proportion. Then the gain field intercept β would be given as $\beta = \zeta\rho$ for all neurons. However, there is no evidence that this strict relationship is held for all area 7a neurons. A second possibility is that the linearity ζ varies with location on the cortex as was proposed in Eq. (13). A reasonable range of values for eye-retina proportion is $(0, 2)$ as the gain field intercept would vary from $(-40, 40)$ Hz. The mapping of the receptive field center and eye-retina proportion parameters are shown in Fig. 5G and 5H. Now, given the location of the eye in the orbit as well as the retinal location of the object, the strength of the response can be computed. Figure 5G illustrates an eye position of $(10$ deg, -20 deg) with a retinal locus of the visual stimulus centered at $(0$ deg, 0 deg) (that is, the eye is fixating the visual target). Note how the receptive field is mapped across the cortex in 5G and repeatedly within the cortex in 5G.

Integration by Recipient Neurons. It is now possible to illustrate the response of neurons that would sum the activity of area 7a neurons. According to the assumptions leading to Eq. (14b), a linear response in world and eye coordinates is found in neurons that integrate cells with the same value of the eye-retina proportion (ζ). The connections between the cells in Figs. 5H and 5I indicate this selective summation. Each neuron in the recipient cortex illustrated in Fig. 5I receives input from all the neurons within area 7a that have the same values of (ζ_x, ζ_y) . Thus a neuron in panel I receives inputs from a collection of neurons in the area 7a that are all have the same retinotopic tunings but different

eye position tuning. This connectivity continues for all locations in parietal cortex. Such patchy connectivity patterns are known to exist between area 7a and area 45 in the frontal eye fields and the supplemental eye fields (Andersen et al., 1985a; Selemon and Goldman-Rakic, 1988; Andersen et al., 1990a). The response of any neuron in the recipient cortex is then linear in eye position and world position. However, the spatial dependence of the integrated neuronal firing across the recipient cortex varies as $1/\zeta$ to $1/\zeta^2$ (Eq. (14a)).

This inverse dependency on the eye-retina proportion can be removed if the normalizing factor of the center-of-mass equation (Eq. (8)) is used. This could be implemented biologically by using first performing a summation of the inputs from area 7a. This signal could be normalized by another summed signal in the absence of a gain field. The division could be implemented via silent synapses (Koch et al., 1990).

In summary, a linear signal in eye and head position can be obtained by integrating angle of gaze cells if the center of the receptive field is proportional to the baseline-firing rate. We propose that each neuron will have a gain field with its intercept proportional to the receptive field center (as in Fig. 5). If this assumption is true, then a cell that sums up the activity of an appropriate subset of parietal neurons has a response proportional to the position of the stimulus in world coordinates and proportional to the eye position (from Eq. (14b)). Such a convergent computation would then result in a single cell that encodes both eye position and world coordinates. The output representation could be distributed if there were a distributed set of ζ . Then each neuron in the output representation (lower panels of Fig. 5) would have a different *linear* relationship between its response and its object and eye position.

In the recipient region, this mapping of ζ is repeated resulting in a distributed and linear representation of the position of an object in world coordinates and eye position. This hypothetical organization has the advantage of generating an output representation that is distributed and linear with changes in eye and object position. A change in the position of the object or the eye linearly alters the response in the second tier. However, the changes in activity across the cortex do not vary linearly with the position of the neuron in the cortex. This is because the dependence of activity on ζ is nonlinear (see Eq. (14a) and Fig. 5I)—that is, roughly $1/\zeta^2$. Nonetheless, this representation can be used to guide eye movements as shown below.

Guidance of Eye Movements. To understand how the recipient cortex that integrates area 7a output might guide eye movements, the effect of different eye positions on the parietal and recipient cortex needs to be considered. Each of the three columns of panels of Fig. 5 indicates three different eye positions with the object position kept fixed at a location (10 deg, -20 deg). The leftmost column of panels is for an eye position of (0 deg, 0 deg). The center column is for an eye position of (7 deg, -14 deg). The left column is for an eye position of (10 deg, -20 deg). As the eye is progressively brought to bear on the target position, the location of the activity in the retinotopic map shifts from the upper right visual field to the foveal representation. At the same time it can be seen that the activity in the neurons receiving the projections from the angle of gaze cells (Figs. 5C, 5F, 5I) becomes symmetrical.

Such patterns of activity can be used to drive motor neurons. For example, consider motoneurons for controlling horizontal and vertical eye movements. Activation from neurons in the recipient cortex of neurons on the appropriate motor neurons would result in movements of the eye. One can then consider the sequence of events. A target appears resulting in activation of the area 7a neurons. Their output passes to the second tier of neurons, whose distributed activity indicates the size and direction needed to move the eye toward the target. The horizontal eye movements could be guided by simply computing the difference between the activity from a patch in the upper right quadrant from the lower left quadrant. Similarly, differencing the activity in the upper left quadrant from the lower right quadrant could control vertical eye movements.

These signals could pass to the motoneurons that lead to eye movements. With the appropriate gain values, the eye movement can be made in one step and would represent a saccade to a target. Once the eye is on target, the activity in the area 7a is still complex; however, the activity in the recipient is spatially symmetric and no further eye movements occur. If the target moves to a new position, this process continues. Indeed, the succession of eye positions from the primary position (Fig. 5A) to that foveating the target (Fig. 5G) was performed in two steps using this simple algorithm.

At no time has this model of area 7a and its recipient cortex ever explicitly computed retinotopic position, eye position, or object position. These three measurements are implicitly found in the distributed representation of area 7a and the regions that receive its

projections. However, the signal present in the region that receives input from area 7a is linear in each of these three measures. Linearity would aid in the control process of making a saccade. In summary, area 7a neurons can be demonstrated to be able to guide eye movements to a target. However, as is more fully discussed below, no provision for determining one target out of many is given as there is insufficient data from the cortical measurements in the behaving monkey to suggest a useful algorithm.

Discussion

The center of mass model described here is based on two main assumptions about the properties of area 7a neurons. First, the receptive fields of area 7a neurons are assumed to be linearly modulated by the position of the eye in the orbit. Second, it is assumed there is a relationship between the parameters of the area 7a neurons that describe the eye-position dependence and the receptive field location. The proposed algorithm makes a prediction that there should be grouping of outputs from neurons in area 7a to regions involved in eye movements. If the algorithm utilizing parallel computation from population of area 7a neurons is implemented between areas 7a and a recipient region to guide eye movements, then a further prediction can be made. For those neurons that project to a restricted recipient region, *the center of the receptive field should vary in direct proportion to the intercept of the gain field*. To test this hypothesis, it will be necessary to combine comprehensive quantitative mapping of area 7a with small injections of retrogradely transported substances in the same animal. Two possible recipient regions are area 45 and the supplemental eye fields. Such studies should find that neurons that project to a limited region in area 45 should all have the same relationships between the receptive field center and the intercept of the gain field. Such maps could be obtained either by using 2-DG (Tootell et al., 1985) or by optical mapping in behaving monkeys (Grinvald et al., 1991).

An additional anatomical prediction can be made. It may be recalled that the model predicts that the intercept of the gain field is proportional to the receptive field center. The "intercept of the gain field parameter" is the background rate of neural firing for an area 7a neuron. Higher background activity has been proposed to underlie increased cytochrome-oxidase activity. For example, cytochrome-oxidase blobs in area 17 are

correlated with increased background activity (Wong-Riley and Carroll, 1984; Livingstone and Hubel, 1984). Thus, there should be a pattern of cytochrome-oxidase activity in area 7a. Furthermore, the regions of highest cytochrome-oxidase activity should have a fixed relationship to the afferent projections to the next tier in the visual hierarchy such as the frontal eye fields.

These predictions arise from experimental data collected under the controlled conditions of fixed head position and the presentation of single stimuli in a plane. In more natural conditions, the head is often free to move and is not fixed in space. Objects can be found anywhere in three-dimensional space, not just in a plane. Objects can vary in number and in size. What implications do these natural conditions have for the utility of the center of mass computations in extracting position in space?

Unfortunately, quantified single unit studies have not been published in the inferior parietal cortex when the animal's head is free to move. However, anatomical evidence suggests that head position signals are available to parietal neurons (Andersen et al., 1990a). Therefore, it is possible that the neurons of area 7a that have the angle-of-gaze signal also have an additional angle of head signal. Indeed, if area 7a neurons were insensitive to head position and its signals were not combined at all with head and other extraocular signals, then insufficient information would be available to determine location in space. If head coordinates linearly modulate the neurons in area 7a, then it could be possible to extend the center of mass computation to include head position.

In all the above derivations, an object is assumed to reside on a world always equidistant from the observer, and the effect of moving the object in depth is unknown. Early studies where an object was moved in depth indicated that area 7a neurons were selective to this stimulus dimension (Sakata et al., 1980), although the source was not clear, and any quantified data about the type of tuning were not available. More recently, it has been shown that area 7a neurons utilize a number of different cues (such as disparity accommodation, and vergence) to code the location of an object in depth (Gnadt and Mays, 1995). Such results can be included in the present formulation by writing Eqs. (1) and (2) to include the depth (z) dimension and by performing the integrals of the center of mass equation in x , y , and z . The integrated activity of such neurons would be linear for the location of the position for all three coordinates.

Clearly, the visual world does not consist of single, pointlike objects. Objects that are located in space vary in size and shape. The proposed mechanism would be expected to always compute the center of mass of an object or collection of objects. This result is in accord with the effect of object shape, size, and number of eye movements (Matin and Matin, 1972). Subjects asked to perform an eye movement to a complex object or objects will move to the approximate center of mass of the object.

However, it is more difficult to explain how a subject can select one out of a collection of objects. It is an outstanding experimental problem (Mountcastle et al., 1981; Moran and Desimone, 1985; Fuster, 1990) as to how subjects are able to focus our attention on any single object in a collection and make appropriate eye movements to it. In the present context, only one comment can be made. The activity of area 7a neurons is known to be modified by the locus of an animal's attention (Mountcastle et al., 1981). Such an attentional mechanism could serve to increase the cell's response to a selected target and thus bias the center of mass computation toward the selected target. Further experiments are needed as to the coordinate system in which the attentional mechanism functions prior to further theoretical work.

An additional question these studies raise is why is there a mixed representation in area 7a. A possible reason for the mixed reference frame is that it is the easiest to create using simple biological mechanisms. One can imagine that the response of neurons with large receptive fields is simply altered by a neuromodulator (such as GABA or dopamine), which could alter the responsiveness of the area 7a neuron to its visual input. Such an argument has evolutionary roots. First, the ability to represent images in retinal coordinates evolved followed by the ability to modulate this retinal response by eye and head position forming the mixed representations. Prior treatments of this issue in Andersen et al. (1985b, 1990b) are noted.

Other Neural Applications of the Center of Mass Equation

As outlined above, the center of mass computation can be used under conditions that are more realistic than the original experimental conditions under which it is derived. All of the theoretical results hinge on the similarity of the tuning of area 7a neurons to the center of mass equation. Now it may be that this similarity

is fortuitous. However, similar relationships are found in other cortical areas (Hubel and Wiesel, 1977; Van Essen et al., 1981; Maunsell and Van Essen, 1983; Albright et al., 1984; Georgopoulos et al., 1986, 1989). Thus, it is suggested that the center-of-mass principle might be applicable to these other regions.

Motor cortex neurons have a relationship between the vector of an intended movement of the arm in three-dimensional space and the response of the cell (Georgopoulos et al., 1986, 1989). These cells are broadly tuned for the angular space of movement. The problem arises how such broadly tuned cells can be used to make a precise map of arm movements.

A numerical analysis of the problem suggested a way to use this neural representation (Georgopoulos et al., 1986). This approach was based on computing a weighted vector sum of the response of neurons in a population. To compute this weighted sum, each cell was represented by a best direction of movement (in their terminology the unit vectors \vec{C}_i for the i th cell). The strength of the response of each cell can be constructed from its tuning curve as $T(\vec{M} - \vec{C}_i)$ where \vec{M} is the intended movement vector. They then test the hypothesis that the weighted sum $\sum_i C_i \cdot T(\vec{M} - \vec{C}_i)$ over all cells would yield the required movement vector \vec{M} . In their articles, this sum is generated from the exemplar cells that they recorded in cortex. It was found that this sum is equal to the movement vector. This result is then used to support the argument for the utility of these cells in mapping movement space.

However, the weighted sum that is given, $\sum_i \vec{C}_i \cdot T(\vec{M} - \vec{C}_i)$, can be recognized from Eq. (7) as the discrete summation form of the center of mass equation. *If the tuning functions T are all identical, this sum must be proportional to the movement direction \vec{M} .* Simulations of this problem with a random set of tuning widths and amplitudes can be made to show that there is not a strict requirement for all the cells to have precisely the same receptive field size. Clearly, from the elegant and graphic studies of Georgopoulos et al. (1986), the motor cortex has neurons with properties that can be used for mapping movement space. The weighted summation computation that was proposed by them can also be described and analyzed analytically using the center of mass principle.

Comparison to Other Models That Extract Space from Parietal Neurons

Other studies have addressed the representations in area 7a. Some of these studies have addressed how the area

7a neurons properties are formed (Salinas and Abbott, 1996). Others address the issue of how space may be obtained from area 7a neurons. In one, a back-propagation model was devised to mimic the overall scheme of combining retinotopic receptive fields and eye position signals to form a head-centered spatial coordinate system (Zipser and Andersen, 1988a, 1988b). This model, using a teacher-based method, has a middle layer that provides neurons with similar receptive fields to those studied in area 7a in that both retinotopic and eye position modulates the response of the neurons. The model is then examined to show that although the receptive fields are large, reasonable spatial precision may be obtained.

Recently, an elegant computational study examines how location may be represented with area 7a neurons (Pouget and Sejnowski, 1994, 1997). This work differs from that of Zipser and Andersen (1988a, 1988b) in that it proposes a *versatile principle* whereby the area 7a neurons are used. This principle is the use of basis functions. These functions provide a basis set that can be combined to represent an arbitrary function. In these studies, the basis functions are formed by the product of the retinal and eye position fields. It is assumed that both the receptive field and gain fields are nonlinear and are used to obtain various re-representations of the parietal responses. The authors note that although the basis method is quite powerful, "a ... potentially large number of units may be needed ... as the dimensions of the representation increases" (Pouget and Sejnowski, 1997). Earlier treatment (Pouget and Sejnowski, 1994) shows how the same basis function principle may be used to extracting depth using a distributed set of depth tuned neurons.

The current computational study is similar in approach to those of Pouget and Sejnowski (1994, 1997) in that all three studies derive a *principle* for computation based on the properties of area 7a neurons. The current work differs in terms of the principle that is derived. We use the center-of-mass equation and emphasize the linearity of the gain field signal. The earlier studies use basis functions and emphasize the nonlinearities of the eye-position signal. As noted in the Introduction both linear and nonlinear neurons are found in area 7a. It may be that the cortex exploits both principles depending on whether linear gain fields or nonlinear gain fields are best for a particular sensorimotor transformation. Alternatively, the center-of-mass principle could be used for finer-scale spatial judgments in which the linear nature of the angle-of-gaze signal would predominate. The basis function principle could

be used for coarser spatial judgments in which nonlinearities would predominate. Further comparisons between center-of-mass and basis functions may be found elsewhere (Salinas and Abbott, 1994; Mussa-Ivaldi and Giszter, 1992; Snippe, 1996; Abbott, 1994).

These theoretical studies taken together indicate that it is certainly possible to extract head-centered coordinates from area 7a neurons. Further experimentation is needed to differentiate between these possibilities. Although additional measurements of the distribution of properties (such as linear versus nonlinear gain field) could be made, it may prove to be more useful determine experimentally how the area 7a neurons area combined. A first step would be to determine the anatomical and functional architecture both within area 7a and in terms of its projection to other cortices. The current study makes predictions for this mapping of neuronal properties onto the visual cortex as well as the projection patterns. Further experimentation using optical recording methods as well as combined anatomical and physiological measures will be necessary to further constrain the range of possible models.

Thus, the processing performed in area 7a can be explored with the concept of the center of mass. These computations may also apply to other cortical representations that combine more than one sensory and/or motor representation. The present work presents hypotheses to be tested that follow logically from the assumption that the cortex does indeed use this computational device in a parallel fashion. Careful mapping of area 7a with respect to the location of a cell in the cortex, its projection pattern, and the determination of the slope, gain and retinal receptive field centers will establish whether or not the center of mass implementation is used in this system. Such analysis may also suggest additional new principles. Its utility in subcortical and other cortical systems remains to be seen.

Note added in proof: Recently, Duhamel et al. (1997) have demonstrated that a subpopulation of neurons in VIP that encode head-centered coordinates from moving stimuli. These neurons could be formed by a center-of-mass computation combining the response of area 7a neurons in a manner similar to that described here. Anatomical projections between the two regions exist that might underlie this computation.

Acknowledgments

This work was supported by the NEI 5 R01 9223 and Office of Naval Research Grant Number N00014-93-1-

0334. Part of this work was performed while the author was a visiting scientist at the IBM Thomas J. Watson Research Center.

References

- Abbott LF (1994) Decoding neuronal firing and modelling neural networks. *Q. Rev. Biophys.* 27:291–331.
- Albright TD, Desimone R, Gross CG (1984) Columnar organization of directionally selective cells in visual area MT of the macaque. *J. Neurophysiol.* 51:16–31.
- Andersen RA, Asanuma C, Cowan WM (1985a) Callosal and prefrontal associational projecting cell populations in area 7A of the macaque monkey: A study using retrogradely transported fluorescent dyes. *J. Comp. Neurol.* 232:443–455.
- Andersen RA, Asanuma C, Essick GK, Siegel RM (1990a) Cortico-cortical connections of anatomically and physiologically defined subdivisions within inferior parietal lobule. *J. Comp. Neurol.* 232:443–455.
- Andersen RA, Bracewell RM, Barash S, Gnadt JW, Fogassi L (1990b) Eye position effects on visual, memory, and saccade-related activity in areas LIP and 7a of macaque. *J. Neurosci.* 10:1176–1196.
- Andersen RA, Essick GK, Siegel RM (1985b) The encoding of spatial location by posterior parietal neurons. *Science* 230:456–458.
- Andersen RA, Essick GK, Siegel RM (1987) Neurons of area 7 activated by both visual stimuli and oculomotor behavior. *Exp. Brain Res.* 67:316–322.
- Andersen RA, Mountcastle VB (1983) The influence of the angle of gaze upon the excitability of the light-sensitive neurons of the posterior parietal cortex. *J. Neurosci.* 3:532–548.
- Colby CL, Duhamel JR, Goldberg ME (1993) Ventral intraparietal area of the macaque: Anatomic location and visual response properties. *J. Neurophysiol.* 69:902–914.
- Critchley M (1953) *The Parietal Lobes*. Hafner Press, New York.
- Duhamel JR, Bremmer F, BenHamed S, Graf W (1997) Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature* 389:845–848.
- Feynman RP, Leighton RB, Sands M (1963) *The Feynman Lectures on Physics*. Addison-Wesley, Reading, MA.
- Fuster JM (1990) Inferotemporal units in selective visual attention and short-term memory. *J. Neurophysiol.* 64:681–697.
- Galletti C, Battaglini PP, Fattori P (1993) Parietal neurons encoding spatial locations in craniotopic coordinates. *Exp. Brain Res.* 96:221–229.
- Georgopoulos AP, Lurito JT, Petrides M, Schwartz AB, Massey JT (1989) Mental rotation of the neuronal population vector. *Science* 243:234–236.
- Georgopoulos AP, Schwartz AB, Kettner RE (1986) Neuronal population coding of movement direction. *Science* 233:1416–1419.
- Gnadt JW, Andersen RA (1988) Memory related motor planning activity in posterior parietal cortex of macaque. *Exper. Brain Res.* 70:216–220.
- Gnadt JW, Mays LE (1995) Neurons in monkey parietal area LIP are tuned for eye-movement parameters in three-dimensional space. *J. Neurophysiol.* 73:280–297.
- Graziano MS, Hu XT, Gross CG (1997) Visuospatial properties of ventral premotor cortex. *J. Neurophysiol.* 77:2268–2292.

- Grinvald A, Siegel RM, Bartfield E, Frostig RD (1991) High resolution imaging of functional architecture in striate cortex of behaving monkey. *PNAS* 88:11559–11563.
- Hubel DH, Wiesel TN (1977) Functional architecture of macaque monkey visual cortex. *Proc. Roy. Soc. Lond. (Biol.)* 198:1–59.
- Hyvarinen J (1982) *The Parietal Cortex of Monkey and Man*. Springer-Verlag, New York.
- Koch C, Douglas R, Wehmeier U (1990) Visibility of synaptically induced conductance changes: Theory and simulations of anatomically characterized cortical pyramidal cells. *J. Neurosci.* 10:1728–1744.
- Law MI, Constantine-Paton M (1981) Anatomy and physiology of experimentally produced striped tecta. *J. Neurosci.* 1:749–759.
- Lehky SR, Pouget A, Sejnowski TJ (1990) Neural models of binocular depth perception. *Cold Spring Harb. Symp. Quant. Biol.* 55:765–777.
- Livingstone MS, Hubel DH (1984) Specificity of intrinsic connections in primary primate visual cortex. *J. Neurosci.* 4:2830–2835.
- Lynch JC (1980) The functional organization of the posterior parietal cortex. *Behav. and Br. Sci.* 3:485–534.
- Matin E (1982) Saccadic suppression and the dual mechanism theory of direction constancy [letter]. *Vision. Res.* 22:335–336.
- Matin L, Matin E (1972) Visual perception of direction and voluntary saccadic eye movements. *Bibl. Ophthalmol.* 82:358–368.
- Matin L, Pearce D, Matin E, Kibler G (1966) Visual perception of direction in the dark: Roles of local sign, eye movements, and ocular proprioception. *Vision. Res.* 6:453–469.
- Maunsell JH, Van Essen DC (1983) Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed and orientation. *J. Neurophysiol.* 49:1127–1147.
- Mishkin M, Lewis ME, Ungerleider LG (1982) Equivalence of parieto-preoccipital subareas for visuospatial ability in monkeys. *Behav. Brain. Res.* 6:41–55.
- Moran J, Desimone R (1985) Selective attention gates visual attention processing in extrastriate cortex. *Science* 229:782–784.
- Mountcastle VB, Andersen RA, Motter BC (1981) The influence of attentive fixation upon the excitability of the light sensitive neurons of the posterior parietal cortex. *J. Neurosci.* 1:1218–1235.
- Mountcastle VB, Lynch JC, Georgopoulos A, Sakata H, Acuna C (1975) Posterior parietal association cortex of the monkey: Command functions for operations within extra-personal space. *J. Neurophys.* 78:871–908.
- Mussa-Ivaldi FA, Giszter SF (1992) Vector field approximation: A computational paradigm for motor control and learning. *Biol. Cybern.* 67:491–500.
- Olson CR, Gettner SN (1995) Object-centered direction selectivity in the macaque supplementary eye field. *Science* 269:985–988.
- Poggio T, Koch C (1985) Ill-posed problems in early vision: From computational theory to analog networks. *Proc. R. Soc. Lond.* B226:303–323.
- Pouget A, Sejnowski TJ (1994) A neural model of the cortical representation of egocentric distance. *Cerebral Cortex* 4:314–329.
- Pouget A, Sejnowski TJ (1997) Spatial transformations in the parietal cortex using basis functions. *J. Cognitive Neurosci.* 9:222–237.
- Read HL, Siegel RM (1997) Modulation of responses to optic flow in area 7a by retinotopic and oculomotor cues in monkey. *Cerebral Cortex* 7:647–661.
- Robinson DL, Goldberg ME, Goldberg GB (1978) Parietal association cortex in the primate: Sensory mechanisms and behavioral modulations. *J. Neurophysiol.* 41:910–932.
- Salinas E, Abbott LF (1994) Vector reconstruction from firing rates. *J. Comput. Neurosci.* 1:89–107.
- Salinas E, Abbott LF (1996) A model of multiplicative neural responses in parietal cortex. *Proc. Natl. Acad. Sci. U.S.A.* 93:11956–11961.
- Sakata H, Shibutani H, Kawano K (1980) Spatial properties of visual fixation neurons in posterior parietal association cortex of the monkey. *J. Neurophysiol.* 43:1654–1672.
- Sanes DH, Constantine-Paton M (1983) Maltered activity patterns during development reduce neural tuning. *Science* 221:1183–1185.
- Selemon LD, Goldman-Rakic PS (1988) Common cortical and subcortical targets of the dorsolateral prefrontal and posterior parietal cortices in the rhesus monkey: Evidence for a distributed neural network subserving spatially guided behavior. *J. Neurosci.* 8:4049–4068.
- Snippe HP (1996) Parameter extraction from population codes: A critical assessment. *Neural Comput.* 8:511–529.
- Sparks DL, Mays LE (1983) Spatial localization of saccade targets. I Compensation for stimulation-induced perturbation. *J. Neurophysiol.* 49:45–63.
- Tootell RB, Silverman MS, Switkes E, De Valois RL (1985) On the mathematical structure of the visuotopic mapping of macaque striate cortex. *Science* 227:1065–1066.
- Van Essen DC, Maunsell JH, Bixby JL (1981) The middle temporal visual area in the macaque: Myeloarchitecture, connections, functional properties and topographic organization. *J. Comp. Neurol.* 199:293–326.
- Westheimer G (1957) Kinematics of the eye. *J. Opt. Soc. Am.* 47:967–974.
- Wong-Riley M, Carroll EW (1984) Effect of impulse blockage on cytochrome oxidase activity in monkey visual system. *Nature* 307:262–264.
- Zipser D, Andersen RA (1988a) A back-propagation programmed network that simulates response properties of a subset of posterior parietal neurons. *Nature* 331:679–684.
- Zipser D, Andersen RA (1988b) The role of the teacher in learning-based models of parietal area 7a. *Brain. Res. Bull.* 21:505–512.