

# Microstimulation of a Neural-Network Model for Visually Guided Saccades

Sabrina J. Goodman and Richard A. Andersen

Massachusetts Institute of Technology

## Abstract

Microstimulation of many saccadic centers in the brain produces eye movements that are not consistent with either a strictly retinal or strictly head-centered coordinate coding of eye movements. Rather, stimulation produces some features of both types of coordinate coding. Recently we demonstrated a neural network model that was trained to localize the position of visual stimuli in head-centered coordinates at the output using inputs of eye and retinal position similar to those converging on area 7a of the posterior parietal cortex of monkeys (Zipser & Andersen 1988; Andersen & Zipser 1988). Here we show that microstimulation of this trained network, achieved by fully activating single units in the middle layer, produces "saccades" that are very much like the saccades produced by stimulating the brain. The activity of the middle-layer units can be considered to code the desired location of the eyes in head-centered coordinates; however, stimulation of these units does not produce the saccades predicted by a classical head-centered coordinate coding because the location in space appears to be coded in a distributed fashion among a population of units rather than explicitly at the level of single cells.

## Introduction

A fundamental problem for achieving motor coordination under visual guidance is how to transform information from visual coordinates to body-centered coordinates. The visual scene is imaged on the retina and defined in retinal coordinates. A more or less point-to-point mapping of these inputs at the lower levels of the visual system maintains this retinotopic representation. However, movements are made to locations in space. Thus, at some point in the nervous system, the location of the eyes in the orbits and location of the head on the body must be integrated with visual inputs of retinal location to code the location of the stimulus with respect to the body. Since information is also available to the motor system about the position of the limb, motor commands can then be formulated to move the limb to the correct location of a visual target in space.

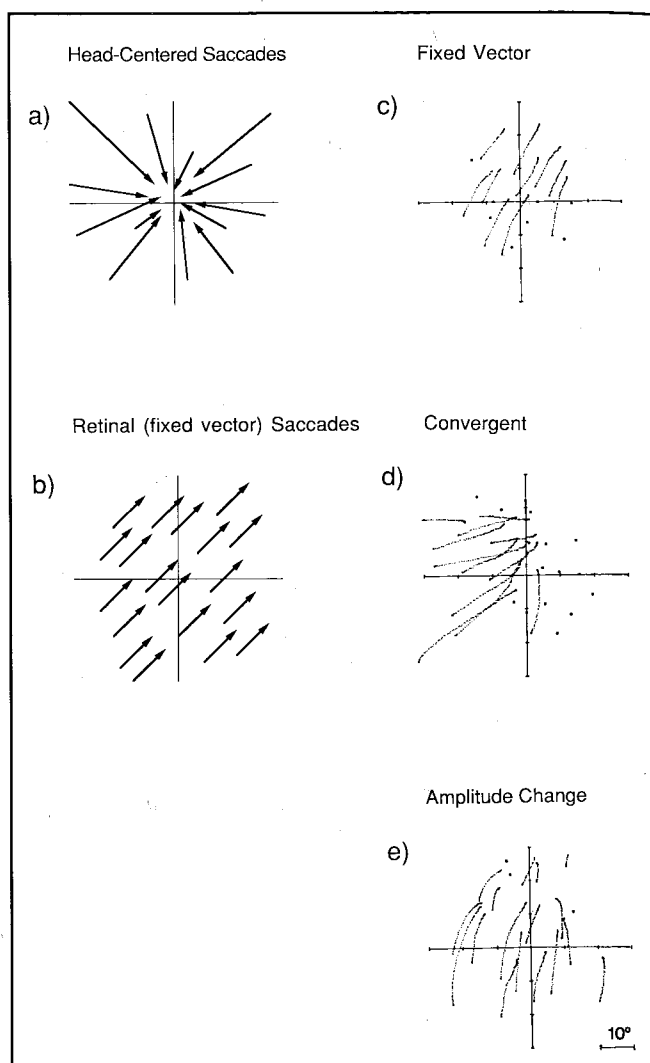
In the present study we have concentrated on the saccade system, a simpler system than the one responsible for limb movements. However, the problem of coordinate transformation is still fundamentally the same; visual

targets for eye movements are provided in retinal coordinates, yet the motor command must specify the desired locations of the eyes in the orbits. Thus, the programming of visually guided saccades requires a transformation from retinal to head-centered coordinates by combining retinal and eye position information. We have employed two variations of our neural network model of area 7a neurons (Zipser & Andersen 1988; Andersen & Zipser 1988) and have stimulated them varying only the eye position information. We have compared our network results with recording data and have found significant similarities. Finally, we have examined the interactions of the hidden units to gain insights regarding how the brain computes transformations from retinal to head-centered coordinates using a distributed processing code.

The classical head-centered coordinate coding scheme of Robinson (1972, 1975) predicts that microstimulation of saccade centers in the brain that code desired location of the eye in orbital (head-centered) coordinates should produce eye movements that drive the eye toward a single orbital position regardless of the initial eye

position. For instance, stimulating a small number of cells coding for the straight-ahead position should move the eye to the left if the animal is looking right and to the right if the animal is looking left, i.e., the direction of the eye movement can actually reverse at different initial orbital positions (see Figure 1a.) On the other hand, cells coding eye movements in strictly retinal (oculocentric) coordinates should produce eye movements to stimulation that are always of the same direction and amplitude (fixed vector) regardless of initial eye position (Figure 1b and c). In fact, stimulation of some saccade centers, including the superior colliculus parafoveal representation (Robinson 1972; Schiller & Stryker 1972) and the frontal eye fields (Robinson & Fuchs 1969), produces eye movements that have been interpreted to be of this fixed-vector type. Stimulation of other areas such as the supplementary eye fields (Schlag & Schlag-Rey 1987; Mann et al. 1988), posterior parietal cortex (Shibutani et al. 1984), cerebellum (Noda 1988), and peripheral field representation of the superior colliculus (Seagraves & Goldberg 1984) in the monkey, and the primary visual cortex (McIlwain 1988), cerebellum (Ohtsuka et al. 1987), and superior colliculus (Roucoux & Crommelinck 1976; Guitton et al. 1980; Roucoux et al. 1980; McIlwain 1986) in the cat, produces eye movements that do change direction and amplitude as a function of eye position. However, these eye movements usually do not behave in a manner fully consistent with the above predicted head-centered coordinate representation. While these eye movements may converge on a single location in head-centered space, their movements rarely reverse direction (Figure 1d). At initial eye positions where one would predict the direction of movement should reverse, often the eye does not move at all (Figure 1d). For other stimulation sites, the directions of the eye movements do not change but the amplitude does. Usually the saccades become smaller in amplitude as the saccades are made from more eccentric eye positions that are in the direction of the evoked eye movements (Figure 1e). McIlwain (1988), in his study of cat primary visual cortex, found change in amplitude effects to be more common than change in direction.

A retinal coordinate coding of eye movements is a relative coding in that it indicates only the direction and amplitude of a movement necessary to foveate a target. However, at some point in the oculomotor system the eye movement must be coded in absolute position of the eye in the orbit. As Westheimer (1973) and Nakayama (1975) have pointed out, the oculomotor system must inevitably be position-based because it obeys Listing's Law (see Nakayama 1975): the eye's orientation for a given gaze position can be described by a rotation around an axis lying in the frontal plane passing through the eye's center of rotation. In other words, two dimensions specify the eye's position completely. This limitation on eye movements is not imposed by the muscles, since the six extraocular muscles allow the eye three degrees of freedom to rotate. In an awake animal, however, the eye



**Figure 1.** (a) A schematic diagram of predicted saccades resulting from stimulation of a brain area representing space in head-centered coordinates. The lighter axes represent eye position in head-centered coordinates. In some of the animal experiments in which the head is fixed, these axes also define the coordinates of the tangent screen on which points of light are projected for fixation prior to electrical stimulation. The arrows show the predicted amplitude and direction of saccades for different initial eye positions. (b) A similar schematic diagram as in (a), but for predicted saccades resulting from stimulation of a brain area representing space in retinal coordinates. Parts (c-e) illustrate actual recording data resulting from stimulation of the supplementary eye fields of macaque monkeys (Schlag and Schlag-Rey 1987). These results are typical of those found in many other areas of monkey and cat brain and are reviewed in the text. Stimulation produces fixed-vector saccades like those predicted by stimulation of a retinal coordinate representation (c), but also produce converging (d) and amplitude change (e) saccades. The converging saccades rarely reverse direction and the single points represent positions in which stimulation produced no movement at all. The change in amplitude saccades had smaller amplitude eye movements for eye positions in the direction of the saccade.

moves with only two degrees of freedom. The exact path of the eye to a given position does not affect its orientation, or the neural activity to the six extraocular muscles, once it is in that final position. If eye movements were specified in a relative code, such as retinotopically, then changes in orientation along a path would accumulate. For the same final eye position reached by two different series of movements, the orientation of the eye and the pattern of firing rates to the extraocular muscles often will be different in the relative coding scheme. Therefore, the brain must be coding eye movements as a final orbital position, that is, in head-centered coordinates. Mays and Sparks (1980) showed that stimulation of the superior colliculus during an intended eye movement, which momentarily drives the eye in a different direction, does not affect the final fixed position of the saccade. These results likewise indicate that the brain is coding the final position of the eye in the orbit and is not using a relative movement code.

Coding in head-centered coordinates requires combining eye position and retinal position information. These signals are combined in a complex fashion in area 7a of the posterior parietal cortex in macaques (Andersen et al. 1985; Andersen & Zipser 1988). Head-centered position is only partially represented in the activity of single cells; rather, computational studies have shown that the spatial location can be coded in the population response (Zipser & Andersen 1988). An important feature of encoding was discovered in these physiological experiments in the parietal lobe: if retinal position was held constant at a location in the visual receptive field of a neuron, the total activity of most area-7a neurons varied linearly as a function of horizontal and vertical eye position. This linear behavior of the combined response of the eye position and visual signals at different eye positions occurred even though the interactions between the two signals was often complex and nonlinear. The activity of these "gain fields" in the monkey could be modeled by a plane in most cases. The visual receptive fields of these neurons were found to be very large and complex. In a companion set of theoretical studies, the hidden units of a neural network simulation trained to combine retinal and eye position inputs and map to locations in head-centered coordinates showed responses much like those recorded from area-7a neurons (Andersen & Zipser 1988; Zipser & Andersen 1988). The hidden units showed similar planar gain fields, receptive fields, and nonlinear interactions of eye and retinal position.

Recently we have discovered an area in the lateral bank of the intraparietal sulcus, the lateral intraparietal area (LIP), which appears to play a role in the processing of saccadic eye movements (Andersen et al. 1985; Andersen 1987, 1989). This area lies adjacent to area 7a in the posterior parietal cortex, but unlike area 7a has strong connections to the superior colliculus and frontal eye fields. Eighty-five percent of the cells in this area have saccade-related responses and 59% of the saccade-

related responses are presaccadic (Barash, Bracewell, Fogassi, Gnadt & Andersen 1989, personal communication). Many of the cells that respond to saccades here also respond to visual stimuli. Eye position activity is also prominent in this area as well, and the saccade and visual responses interact in ways similar to those seen in area 7a (Andersen et al. 1988; Andersen & Gnadt in press). Thus, the same algorithm that operates in area 7a may operate in area LIP to convert retinal visual signals to desired location of the eyes in head-centered coordinates. Interestingly, stimulation of area LIP produces saccades that modify their direction and amplitude characteristics as a function of initial eye position (Shibutani et al. 1984). As seen with stimulation to other brain regions, these eye movements do not produce a reversal in direction as would be predicted by head-centered representation schemes.

The neural network model used in our previous studies provides a good correspondence to the actual recording data not only from area 7a but also from area LIP. The effects of eye position on the visual and saccade responses of area LIP neurons are predicted by the area 7a neural network model (Andersen et al. 1988, 1989). Would simulated microstimulation of a trained network also predict the results of the studies of brain microstimulation at different eye positions cited above? The experiments described in this article have been designed to answer this question. Microstimulation can be simulated in the model by adding directly to the activation of a hidden unit in the network and examining changes in the resulting output. The initial output of the model is the desired location of the eyes in head-centered coordinates, while the change in output following stimulation can be considered the evoked "saccade." We find that the model, using a *linear* (monotonic) frequency of firing code at the output, produces the same three types of saccades found as a result of stimulation of the various eye-movement areas of the brain, that is, fixed vector, converging, and amplitude-change saccades. In contrast, using a *gaussian* format for coding the head-centered location at the output produced much more complicated patterns of movement. By examining in detail the network using the linear output format, we can explore why the network, and perhaps the brain, produces these three saccade patterns as a result of stimulation.

## Method

The neural network simulations were trained using back-propagation learning (Rumelhart et al. 1986). Each network has three layers: one containing the input it was given, one hidden layer for internal representations, and one producing the output to which it is trained. The activation of each input unit is multiplied by a weight representing the strength of the connection between that unit and each hidden unit and the resulting values are added to the inputs of the hidden units. All inputs are

connected to all hidden-layer units, which in turn are connected to all output units. There are no connections within a layer or back to previous layers. Each unit in the hidden layer takes the sum of its weighted inputs, together with a bias which can be fixed in advance or trained like the weights, and puts out a number between 0 and 1 representing a function of its inputs equal to  $[1/1 + e^{-(\text{net input} + \text{bias})}]$ . A total input of zero would produce an output of 0.5 from a unit with bias 0; numbers less than  $-7$  or greater than  $7$  become vanishingly close to 0 and 1 respectively. These output values are then passed on to the next level, that is, multiplied by their corresponding weights to be added to the input of each unit in the output layer, which then computes its output in the same way. The resulting output pattern of the output layer is subtracted from the desired output during training to produce an error vector, which is used to correct the weights by the backpropagation procedure (Rumelhart et al. 1986).

Two different formats were used for the head-centered output position, but all networks had the same retinal and eye position inputs. The retinal input was represented by an  $8 \times 8$  (64-unit) array. Each retinal input unit's activation represents the value of a gaussian function at the point where the "light" falls on the "retina"; the input units were considered to be a grid of points separated by ten degrees of visual angle, and their gaussian functions had a  $1/e$  spread of fifteen degrees. The possible values for each input ranged from 0 to 1. The other 32 input units represented the position of the eyes. These units' activations were monotonic functions of eye position similar to those seen from neurons found to code eye position in the parietal cortex. Because each unit represents position, mostly in the same range, this is a highly redundant distributed coding. Each network contained 12 hidden units.

The first network's output was a set of monotonic functions of either horizontal or vertical position of the visual stimulus in head-centered coordinates. These units were identical to the eye-position input units but coding the location of the visual stimulus with respect to the head. The second network's output layer was an array of gaussians identical in format to the retinal input but coding location in head-centered coordinates rather than retinal coordinates. Both were trained by backpropagation to give the correct outputs representing the eye-position-independent, head-centered location of the visual stimulus represented by the "retinal" stimulus seen at the given eye position. Training consisted of presenting patterns of randomly chosen eye and retinal input positions several hundred times until the average output error was reduced to less than ten degrees of visual angle (i.e., less than the space between the retinal input units) for all input patterns. The neural network outputs were more accurate closer to the straight ahead location (in head-centered coordinates) than at more peripheral angles, and average error over locations out to 40 degrees ranged from

roughly 5 to 15 percent in the networks described here. Longer training has been found to reduce error to increasingly smaller amounts without any appreciable differences in the general parameters of the network (Zipser & Andersen 1988).

The microstimulation experiment involved moving the "eye" to several different eye positions, stimulating the network by saturating the activation of one or more of the hidden units, and recording the resulting change in eye position as the stimulation-induced "saccade." The "eye" was moved to each new initial eye position by applying an eye-position signal at the input with no retinal input signal present, and the location represented by the output was considered to be the eye position prior to stimulation. In the networks with monotonic output formats, the output eye position represented by each of the thirty-two monotonic units was calculated, and the results (16 vertical and 16 horizontal) were averaged to give one horizontal coordinate and one vertical coordinate of the output position. For the gaussian output, the position was calculated as a weighted average of the retinal locations of the four units with the highest activations. With no retinal input, the monotonic output networks generally gave an output position very close to the input eye position. The gaussian output networks gave slightly less similar input and output eye positions when no retinal position was applied at the input.

Stimulating a hidden unit consisted of increasing its activation after an eye position input pattern had been propagated forward through the network, and recomputing the output. Since each unit's activation is constrained to values from 0 to 1, simply adding a fixed amount to the output could result in a value exceeding 1 and therefore would not be appropriate. Instead, the input to the hidden unit was increased and resulted in the new total output being close to 1. The result was multiplied by the appropriate weights and added to the inputs of the output-layer units in the usual way.

In order to study how stimulation-induced changes in output varied with eye positions, a set of input patterns was made (with no retinal input) for eye positions at regularly spaced points on a  $6 \times 6$  grid separated by 10 deg. Each hidden unit was stimulated for each of these positions, and the change in output position was regarded as a saccade vector. This method simulates the earlier animal experiments in which the animal changes his direction of gaze and stimulation is delivered to different eye movement centers.

## Results

### The Monotonic Format Network

In the networks with the monotonic output format, the saccades were mostly parallel. Of a total of sixty hidden units from five simulations trained to monotonic output (see Table 1), seven produced no appreciable saccades

Table 1

PERCENTAGES OF HIDDEN UNITS BY CATEGORY		
Category	Linear Output (total 60 units)	Gaussian Output (total 24 units)
Fixed vector (e.g., Figure 2)	7 %	0
Amplitude change (Figures 3 and 7b)	82 %	38 %
Complex (such as Figures 7a and 8a)	0	42 %
Little or no movement (Figure 8b)	12 %	21 %

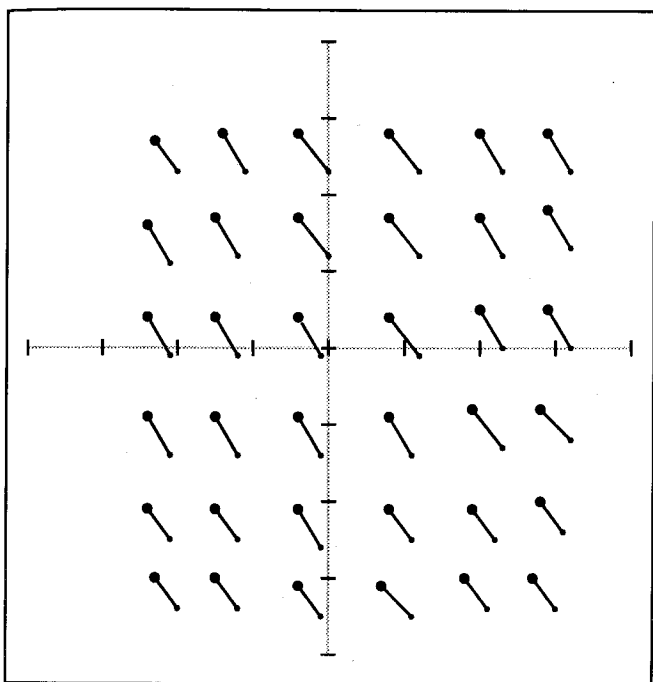


Figure 2. Fixed-vector saccades from a monotonic-output network. The large spots of each saccade represent the initial eye position and the smaller spot the final position of the output calculated after saturating the activity of a single hidden unit. The simulated eye movements are of nearly equal amplitude and direction regardless of initial eye position. The plot is in head-centered coordinates with 10 deg per division.

at all and four gave identical saccades from all eye positions (as in Figure 2). The remaining 49 converged toward one side of the simulated oculomotor range (Figure 3). These saccades were mostly parallel, but their length varied with starting position. The direction varied slightly as well, especially toward the edges of the visual field, but not nearly as much as the magnitude. The shortest saccades were those that started closest to the edge they pointed toward, so that the overall effect is of converging on one side (see Figure 3).

The slight variations in direction often added to the converging effect in the monotonic-output networks, so that all saccade vectors flowed toward one corner (e.g.,

Figure 3b). This slight change in direction was caused by the use of separate output units for horizontal and vertical position. When the output units for one direction were near saturation, so that saccades could not go much farther in that direction, they could still move in the other dimension. This asymmetrical saturation effect appeared to be the source of most, probably all, effects on saccade direction for stimulation of single units in the monotonic output networks. This directional convergence at extreme positions was caused at the output layer. Other convergence effects, in particular that of the saccades being shorter when they started closer to the direction they were going, were caused at the level of hidden units.

Sometimes a much higher degree of convergence is created by stimulating two hidden units at once. This result would be equivalent to that seen when a current is delivered to an electrode simultaneously activating two neurons (or two small populations of neurons) with different direction and amplitude tuning properties. Figure 4 is an example of such a convergence. In this case,

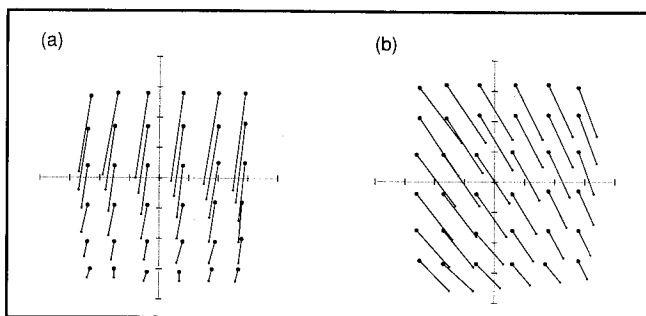
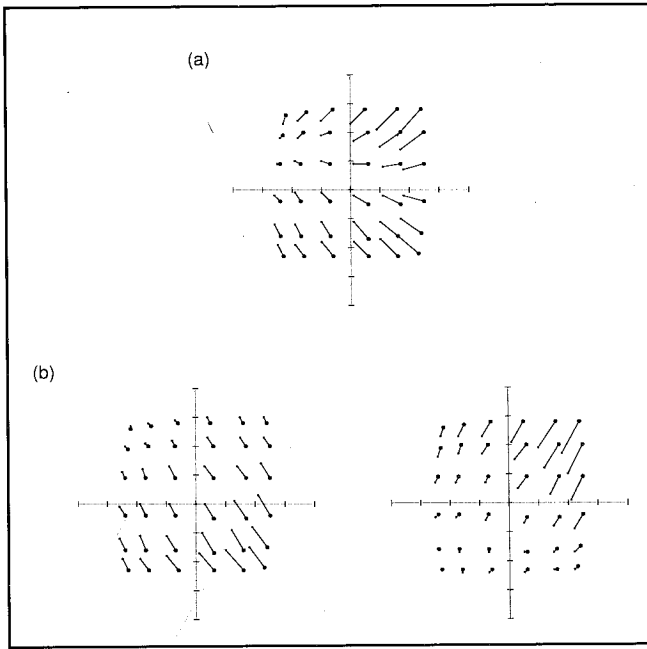


Figure 3. Two examples of saccades produced by stimulating single hidden units of a monotonic network that do not show fixed-vector behavior. (a) Example of stimulation that produced amplitude change with progressively decreasing amplitudes for initial eye positions in the direction of the eye movement. Note the similarity between this network result and the amplitude change results from brain stimulation studies (Figure 1e). (b) Example where the amplitude decreases in the direction of the eye movement and there is a small degree of direction change. Note that the convergence for this hidden unit stimulation is markedly less than the degree of convergence that often occurs with brain stimulation (Figure 1d).



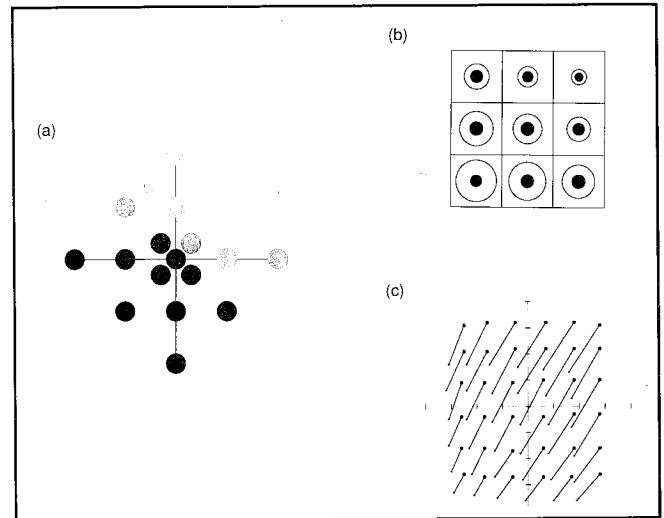
**Figure 4.** Eye movements recorded when two hidden units of a monotonic-output network are stimulated simultaneously. Note the much higher degree of convergence than that typically recorded with single hidden-unit stimulations (Figure 3b) and the greater similarity to the convergence behavior that is often recorded with brain stimulation. (b) Eye movements recorded when each of the two hidden units is stimulated alone. Note that the result of simultaneous stimulation, illustrated in part (a), is more or less the vector addition of the two saccade fields that result from stimulation of the individual units.

the convergence is caused by saturation of the hidden units rather than the output units. In most cases, however, the pattern of saccades produced by probing two units at once looks similar to that produced by one unit, because most of the hidden units did not reach saturation in positions where the output units would not be saturated as well.

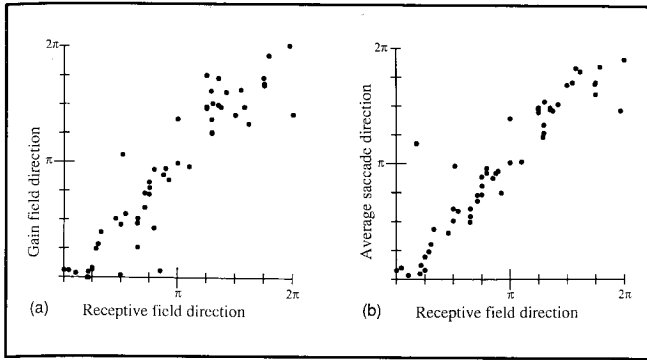
Examination of the properties of the hidden units reveals the eye-position effects upon the saccade behavior. In Figure 5a, the visual receptive field of such a hidden unit is plotted with each circle representing its response to a visual stimulus at that location, with darker shading representing higher activity. The seventeen sample points correspond to the seventeen receptive field locations sampled in recording experiments in area 7a (Andersen et al. 1985; Andersen & Zipser 1988) and are distributed across an area 80 degrees in diameter. Note that the receptive field is large with greatest sensitivity for locations down and left. Figure 5c shows that the best saccade direction was also down and to the left. This similarity in best directions for the motor (saccade) and receptive fields was generally found for all hidden units in the monotonic format network (see Figure 6b). This similarity in best directions of the motor and receptive fields also has been found in recording experiments in

area LIP (Barash et al. in press) and the superior colliculus (see Schiller 1984 for review).

Figure 5b shows the gain field of this unit. The diameter of the inner dark circle is proportional to the response evoked by the visual stimulus at the most responsive retinotopic location in the visual field tested at nine different eye positions. The eye positions are separated by 20° with the center position at straight ahead. The outer circle's diameter is proportional to the total activity and thus the annulus is proportional to the eye-position signal. It can be seen in Figure 5b that the eye-position signal for fixating down and left nearly saturates the output of the hidden unit while fixation up and right produces only a minimal response. Note that the gain field is planar; that is, the activity can be fit by a plane with the positive gradient directed down and to the left — the same best direction as the motor and visual receptive



**Figure 5.** Receptive field, gain field, and saccade field of a single hidden unit trained to a monotonic output. (a) The response to the visual input was tested at 17 positions within an 80-deg diameter area with the eye-position signal always kept at straight-ahead fixation (0,0). Each sample location's response is represented by a shaded circle with the darker shading representing a more vigorous response. This method was chosen because it mimics the methods used to map visual receptive fields of area 7a neurons in previous physiological experiments (Andersen et al. 1985, Andersen & Zipser 1988). (b) The gain field was mapped by presenting a visual stimulus at the same retinal location, in the most responsive area of the receptive field, at nine different eye positions. Each set of circles represents the response at a particular eye position; eye positions were spaced by 20 deg in a 3 × 3 array with the central eye position at location (0,0). This protocol mimics the one used to map gain fields in the animal recording experiments (Andersen et al. 1985; Andersen & Zipser 1988). The inner, dark circle of each set has a diameter proportional to the activity generated by the visual input and the annulus diameter is proportional to the eye position contribution to activity. (c) The saccade field for this unit was generated in the same way as in the previous figures (Figures 2, 3, and 4). Note that the receptive field, gain field, and saccade response all have approximately the same best direction.



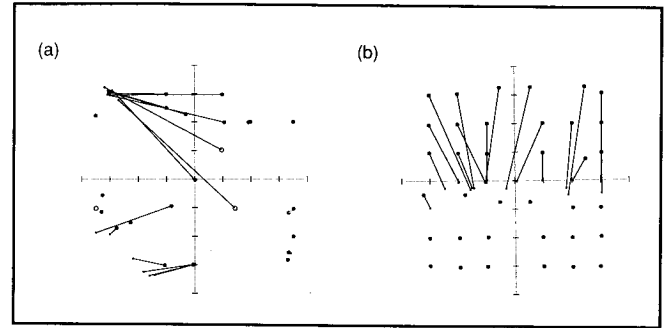
**Figure 6.** (a) Plot comparing the direction of the gain fields and receptive fields for all of hidden units. The best direction of the gain field was determined by the gradient of the planar gain field and was calculated as the inverse tangent of the ratio of the vertical and horizontal slopes. The receptive-field best direction was the direction of the vector calculated by averaging the set of vectors defined by the location of the visual target from the fixation point and weighted by the firing rate. (b) Plot comparing the best directions of the receptive fields and saccade responses. The saccade best direction was the average of all saccades produced at different eye positions. The two plots indicate that, as a rule, the receptive, saccade, and gain fields all had similar best directions for hidden units of the monotonic-output model.

fields. All gain fields in the model exhibited this planar behavior, as do most gain fields recorded from cells in areas 7a and LIP (Andersen et al. 1985, 1988). The similarity of best directions for the gain fields and the motor and receptive fields was a general finding for all monotonic format trained hidden units (Figure 6b).

The properties of the hidden unit gain fields and motor fields account for the effects of eye position on the saccade responses. Generally the eye-position-related activity of a unit increased in the direction of the gain field (see Figure 6b). As the eye-position activity increased, the unit became more saturated and the stimulation produced smaller saccades. The similarity in best directions accounts for the decrease in amplitude generally occurring for eye positions in the direction of the eye movement (compare parts b and c of Figure 5). The converging changes in direction occur when the horizontal or vertical components of the eye position saturate the response asymmetrically at the output.

The examination of the hidden-unit responses shows that they are already producing a partial solution for spatial location in the middle layer. For instance, the unit in Figure 5 will respond best if a stimulus appears in the lower-left visual field or if the eyes are pointed down and to the left; that is, this hidden unit is generally responding to locations down and left in head-centered coordinates. As Figure 6a indicates, all of the hidden units show this similarity in receptive-field and gain-field directions.

It is also interesting to note that the receptive fields often appear planar in the middle layer (for example, Figure 5a). The network and the nervous system are pre-

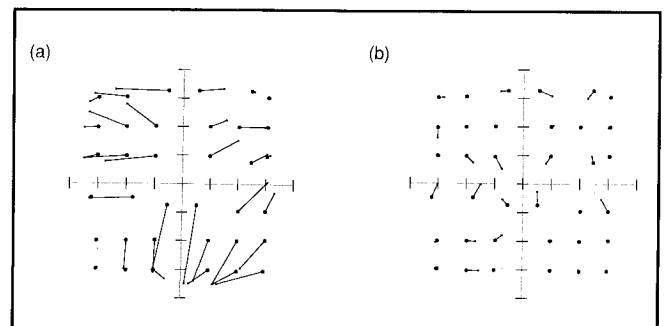


**Figure 7.** Saccades from a Gaussian-output network that appear to converge in some parts of the field. (a) The saccades for this hidden unit converge in the upper-left corner for some eye positions, but not for others. (b) The saccades in this example converge along the horizontal axis when eye positions are located up, but the eye does not move with stimulation when the eye position is down.

sented with a format problem at the input of combining eye-position signals, which are largely linear, with visual receptive fields, which are largely Gaussian. One solution would be to linearize the receptive fields by weighting their convergence at the input to the hidden units and then add the planar receptive field to a planar eye-position input sloped in the same direction. Although the model, and the brain itself, do have features of this solution, there are two major exceptions; the receptive fields are often peaked (Zipser & Andersen 1988; Andersen & Zipser 1988) and, more importantly, the gain fields generally demonstrate strong nonlinear (often multiplicative) interactions between the eye position and retinal position signals. These nonlinearities are due, in the model, to the nonlinear nature of the sigmoidal logistic function used to compute the outputs of the units. The similar nonlinear interactions arising from parietal neurons raise the possibility that they also have a sigmoidal input-output transfer function.

### The Gaussian-Format Network

Unlike the linear output model, the networks trained to output Gaussian arrays showed no consistent patterns of



**Figure 8.** Gaussian-output networks for saccades that do not appear to converge.

saccades (Table 1). A few (4 out of 24) looked extremely goal-directed, at least if only a portion of possible eye positions were examined, as in the upper left-hand part of Figure 7a. From other eye positions, however, the same unit produced saccades going in an entirely different direction. Saccades resulting from stimulating 5 of the 24 units went outward from central areas or lines (e.g., Figure 8a); another 5 produced small movements with no discernable pattern at all (Figure 8b). Nine of the 24 hidden units in these two networks produced saccade patterns like that shown in Figure 7b, with saccades going to one side. Even these patterns, which most closely resembled the patterns produced by the monotonic networks, were much less consistent in direction.

The directions of the saccades were nearly constant in the monotonic networks. Stimulating gaussian-output networks, by contrast, produced saccades going almost every direction, but this variation was never consistent as a function of position or magnitude. The magnitude of saccades was a very clear and usually linear function of starting position in the monotonic output networks. In the case of the gaussian output, position sometimes seems to have imposed a limit on how far saccades could go, but there are often small saccades among the longer ones. The gaussian output format, then, did not predict the usual stimulation-induced saccade behavior seen in the brain.

## Discussion

The results of this study show that stimulation of a network that contains a distributed representation for converting retinal coordinates to head-centered coordinates in a linear output format produces similar eye-position-dependent saccade behavior to that recorded in brain stimulation experiments. It is interesting to note that stimulation of some of the units produced "fixed vector" behavior, a pattern that has normally been considered to be consistent only with a retinal coordinate representation. The convergent saccade patterns did not reverse direction, similar to the experimental data. In fact, stimulation of single elements never produced movements to a single location in head-centered space. Such goal-directed patterns were not found because the network units specify location in space in a distributed manner, rather than explicitly at a single-unit level.

It should be emphasized that our network is not intended to be an exhaustive model for a single brain region. Rather, it shows one way that groups of neurons could process coordinate transformations for visually directed saccades. These simulations show how single cells would behave in such a distributed system, and in fact, the network predicts planar gain fields, overlap of motor and sensory fields, and the microstimulation behavior that has been observed in neurophysiological experiments. Since the network is a mathematical abstraction, it does not necessarily specify a single area of the brain.

The fact that microstimulation and recording data consistent with this model have been found in several brain regions suggests that this algorithm for coordinate transformation may be used in several neural systems, or alternatively, that a single system involved in coordinate transformation for saccades may be comprised of more than one brain region. An interesting observation relating to the latter possibility is that similar receptive fields and gain fields are found in networks using more than one layer of hidden units. In order to make it tractable, this model is limited in scope. For instance, it addresses the kinematic, but not dynamic, aspects of saccade generation. Further work will lead to modification and elaboration of the model.

In this study we have been concerned with properties of the final, trained network rather than with the learning procedure that generated the network. The backpropagation learning technique we used is not biologically plausible without modification since it requires that information travel rapidly backward down axons and across synapses and it requires specific error signals at every synapse. Recently we have found that a more biologically plausible reinforcement learning rule (Barto & Jordan 1987), which does not require backward transmission and uses a more global error signal, produces similar results when applied to our network (Mazzoni, Andersen, & Jordan, personal communication). These results suggest that the same algorithm for coordinate transformation will develop independent of the exact learning rule used for training. Supporting this conjecture is our preliminary mathematical analysis, which suggests that the algorithm is largely constrained by the architecture of the network and the problem it solves. Any learning rule that converges on a solution would therefore generate the same algorithm, resulting in similar receptive field properties and microstimulation behavior.

The distributed coding has interesting implications for the recording data. To date, representation of location in head-centered space independent of eye position has never been shown to exist explicitly at a single-cell level anywhere in the nervous system. Rather, eye-position signals appear to interact with retinal-position signals with the eye-position signal often gating or modifying the response of the retinal receptive field. These nonlinear interactions of eye- and retinal-position signals in the brain are very similar to those produced in the network middle layers (Zipser & Andersen 1988). The summed output of the network does code explicitly the locations in head-centered coordinates. In the monotonic network, the output representation is a frequency of firing code for the extraocular muscles. Of course, these signals are found in motor neurons projecting to the eye muscles. Thus, in this model, the only explicit representation of head-centered coordinates is the behavior of making the eye movement to the appropriate location in head-centered space. The representation of location in space is a product of the entire network, and any single element



of the network contains only a portion of the coded information. A similar highly distributed representation may also be found in the brain and would account for the fact that individual cells coding head-centered location independent of eye position have never been found.

The gaussian output representation may be considered a representation appropriate for *perception* of spatial location rather than *movement to* a spatial location. Sensory areas generally code in receptive field formats like the gaussian format, whereas motor areas code in a frequency of firing format like the linear format. However, both formats may exist in a single area. For example, Zipser and Andersen (1988) demonstrated two general types of gain fields in their network model of area 7a. Although both the monotonic and gaussian outputs produced both types of gain field, the gain fields where the eye position and visual responses covaried were found largely for the monotonic output, whereas the gaussian output model produced largely noncovarying gain fields. Since both types of gain fields are recorded from area 7a (Andersen et al. 1985; Andersen & Zipser 1988; Zipser & Andersen 1988), these experiments suggest that both representations may exist in area 7a.

Generally two types of saccadic patterns have been reported for stimulation of different brain centers. Stimulation of the frontal eye fields and the foveal and parafoveal representations of the superior colliculus has been reported to produce only fixed vector saccades in the monkey (Robinson & Fuchs 1969; Robinson 1972; Schiller & Stryker 1972). On the other hand, stimulation studies of the supplementary motor field (Schlag & Schlag-Rey 1987; Mann et al. 1988), posterior parietal cortex (Shibutani et al. 1984), cerebellum (Noda et al. 1988), and peripheral field representation of the superior colliculus (Seagraves & Goldberg 1984) in the monkey and visual striate cortex (McIlwain 1988), cerebellum (Ohtsuka et al. 1987), and superior colliculus (Roucoux & Crommelinck 1976; Guitton et al. 1980; Roucoux et al. 1980; McIlwain 1986) in the cat report eye-position effects including convergence and amplitude change. An important question is why some areas of the brain, those exhibiting "fixed vector" behavior, would code saccades in retinal coordinates while other areas would code them in head-centered coordinates. The largely fixed-vector saccades produced by our model with a head-centered coordinate system suggest this pattern of saccades does not necessarily indicate a retinal coordinate representation.

Interestingly, stimulation of the peripheral field representation of the superior colliculus in both the cat and the monkey produces converging and amplitude-change saccade patterns. It has been proposed that the more peripheral locations are coding in head-centered coordinates because at these more peripheral locations the animals produce combined eye and head movements either to electrical stimulation or to natural conditions in the environment (Roucoux & Crommelinck 1976; Guitton et al.

1980; Roucoux et al. 1980). The eye-movement patterns produced by stimulation of the foveal and parafoveal representations of the superior colliculus do produce some convergence and amplitude change. However, these eye-position effects are only seen at more peripheral eye positions and are usually interpreted as resulting from the mechanical restraints occurring as the eyes approach the limits of the oculomotor range. It is assumed that orbital effects are compensated for at locations in the brainstem closer to the oculomotor nuclei.

If the superior colliculus is coding in retinal coordinates, why does its stimulation not also invoke the mechanisms correcting for orbital position to produce true fixed-vector movements? One possibility is that the eye-position corrections are made by a parallel pathway. Another interesting possibility is that the colliculus is coding in head-centered coordinates. Examination of the eye-movement traces of Robinson (1972) shows very similar patterns to those evoked by stimulation of single hidden units. Perhaps the more eye-position-dependent areas of the brain are using the same code as in the colliculus, but in a more complex local circuitry. Thus, stimulation of these areas would evoke eye movements similar to those produced by simultaneously stimulating two or more hidden units in the model; that is, movements that are more convergent and appear more head-centered.

Stimulation of single units in this neural network model did not produce classical head-centered movements, because the model represents spatial locations in a population of units rather than explicitly at the level of single units. In this distributed representation, no single unit responds directly to head-centered spatial location, although the network output is in absolute head-centered coordinates. This model, when trained with a monotonic output, produces patterns of "saccades" resembling those seen in stimulation studies of several parts of the brain. Examination of the network suggests some mechanisms that may be used by the brain for computing positions in head-centered coordinates.

#### Acknowledgments

This work was supported by Office of Naval Research Grant N00014-89-J-1236 and National Institutes of Health Grants EY05522 and EY07492.

Reprint requests should be sent to Richard A. Andersen, Massachusetts Institute of Technology, Department of Brain and Cognitive Sciences, 77 Massachusetts Avenue, E25-236, Cambridge, MA 02139.

#### References

- Andersen, R.A. (1987). The role of the inferior parietal lobule in spatial perception and visual-motor integration. In F. Plum, V.B. Mountcastle, & S.T. Geiger, (Eds.), *The Handbook of Physiology. Section 1: The Nervous System, Vol. IV. Higher Functions of the Brain, Part 2*, 483-518. Bethesda, MD: American Physiological Society.
- Andersen, R.A. (1989). Visual and eye movement functions of

- the posterior parietal cortex. *Annual Review of Neuroscience*, 12, 377–403.
- Andersen, R.A., Essick, G.K., & Siegel, R.M. (1985). Encoding of spatial location by posterior parietal neurons. *Science*, 230, 456–458.
- Andersen, R.A., & Gnadt, J.W. (in press). Role of posterior parietal cortex in saccadic eye movements. In R. Wurtz & M. Goldberg, (Eds.), *Reviews in Oculomotor Research*, Vol. III. Amsterdam: Elsevier.
- Andersen, R.A., Gnadt, J., Fogassi, L., Bracewell, M., Barash, S., Robertson, G., & Essick, G. (1988). Orbital position effects on saccade responses of area LIP neurons. *Neuroscience Abstracts*, 11.
- Andersen, R.A., & Zipser, D. (1988). The role of the posterior parietal cortex in coordinate transformations for visual-motor integration. *Canadian Journal of Physiology and Pharmacology*, 66, 488–501.
- Barash, S., Bracewell, R.M., Fogassi, L., & Andersen, R.A. (in press). Interactions of visual and motor-planning activities in the lateral intraparietal area (LIP). *Neuroscience Abstracts*.
- Barto, A.G., & Jordan, M.I. (1987). Gradient following without backpropagation in layered networks. *IEEE International Conference on Neural Networks*, Vol. II, 629–636. San Diego: SOS Printing.
- Guitton, D., Crommelinck, M., & Roucoux, A. (1980). Stimulation of the superior colliculus in the alert cat: I. Eye movements and neck EMG activity evoked when the head is restrained. *Experimental Brain Research*, 39, 63–73.
- Mann, S.E., Thau, R., & Schiller, P.H. (1988). Conditional task-related responses in monkey dorsomedial frontal cortex. *Experimental Brain Research*, 69, 460–468.
- Mays, L.E., & Sparks, D.L. (1980). Dissociation of visual and saccade-related responses in superior colliculus neurons. *Journal of Neurophysiology*, 43, 207–232.
- Mazzoni, P., Andersen, R., & Jordan, M. (1989). Personal communication.
- McIlwain, J.T. (1986). Effects of eye position on saccades evoked electrically from superior colliculus of alert cats. *Journal of Neurophysiology*, 55, 97–112.
- McIlwain, J.T. (1988). Saccadic eye movements evoked by electrical stimulation of the cat's visual cortex. *Visual Neuroscience*, 1, 135–143.
- Nakayama, K. (1975). Coordination of extraocular muscles. In G. Lennerstrand & P. Bach-y-Rita, (Eds.), *Basic Mechanisms of Ocular Motility and their Clinical Implications*, 193–207. New York: Pergamon Press.
- Noda, H., Murakami, S., Yamada, J., Tamaki, Y., & Aso, T. (1988). Saccadic eye movements evoked by microstimulation of the fastigial nucleus of macaque monkeys. *Journal of Neuroscience*, 60, 1036–1052.
- Ohtsuka, K., Edamura, M., Kawahara, K., & Aoki, M. (1987). The properties of goal-directed eye movements evoked by microstimulation of cerebellar vermis in the cat. *Neuroscience Letters*, 76, 173–178.
- Robinson, D.A. (1972). Eye movements evoked by collicular stimulation in the alert monkey. *Vision Research*, 12, 1795–1808.
- Robinson, D.A. (1975). Oculomotor control signals, Part III: Are saccades retinotopically or spatially organized? In G. Lennerstrand, & P. Bach-y-Rita, (Eds.), *Basic Mechanisms of Ocular Motility and their Clinical Implications*, 366–374. New York: Pergamon Press.
- Robinson, D.A., & Fuchs, A.F. (1969). Eye movements evoked by stimulation of frontal eye fields. *Journal of Neurophysiology*, 32, 637–648.
- Roucoux, A., & Crommelinck, M. (1976). Eye movements evoked by superior colliculus stimulation in the alert cat. *Brain Research*, 106, 349–363.
- Roucoux, A., Guitton, D., & Crommelinck, M. (1980). Stimulation of the superior colliculus in the alert cat. II. Eye and head movements evoked when the head is unrestrained. *Experimental Brain Research*, 39, 75–85.
- Rumelhart, D.E., Hinton, G.E., & Williams, R.J. (1986). Learning representations by back-propagating errors. *Nature*, 323, 533–536.
- Schiller, P.H., & Stryker, M. (1972). Single-unit recording and stimulation in superior colliculus of the alert rhesus monkey. *Journal of Neurophysiology*, 35, 915–924.
- Schiller, P.H. (1984). The superior colliculus and visual function. In J.M. Brookhart, V.B. Mountcastle, I. Darian-Smith, & S.T. Geiger, (Eds.), *The Handbook of Physiology. Section 1: The Nervous System, Volume III. Sensory Processes, Part I*, 457–505. Bethesda, MD: American Physiological Society.
- Schlag, J., & Schlag-Rey, M. (1987). Evidence for a supplementary eye field. *Journal of Neurophysiology*, 57, 179–200.
- Seagraves, M.A., & Goldberg, M.E. (1984). Initial orbital position affects the trajectories of large saccades evoked by electrical stimulation of the monkey superior colliculus. *Society for Neuroscience Abstracts*, 10, 59.
- Shibutani, H., Sakata, H., & Hyvarinen, J. (1984). Saccade and blinking evoked by microstimulation of the posterior parietal association cortex of the monkey. *Experimental Brain Research*, 55, 1–8.
- Westheimer, G. (1973). Saccadic eye movements. In V. Zikmund, (Ed.), *The Oculomotor System and Brain Functions*. Bratislava, Czechoslovakia: Publishing House of Slovak Academy of Sciences.
- Zipser, D., & Andersen, R.A. (1988). A back-propagation programmed network that simulates response properties of a subset of posterior parietal neurons. *Nature*, 331, 697–684.