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Author(s): Steven P. Wise and Robert Desimone

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# Behavioral Neurophysiology: Insights into Seeing and Grasping

STEVEN P. WISE AND ROBERT DESIMONE

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**One marvels at a batter's ability to hit a baseball traveling at 150 kilometers per hour or a monkey's skill in snatching a flying insect. Indeed, the ability of many animals to reach out, grasp, and manipulate objects is a feat of biological engineering unmatched by even state-of-the-art robots. But how are the objects of our attention chosen and how are the eyes and hands directed to it? Recent progress in behavioral neurophysiology has clarified some of the brain mechanisms at work.**

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**I**N OUR EVERYDAY ACTIVITIES WE REGULARLY EXAMINE objects with our eyes, hands, and minds. In this article, we survey some recent progress in understanding how the central nervous system directs attention to one among several objects, moves the eyes to an object of interest, and generates the limb movements necessary to grasp and manipulate it.

## Attention

In a typical visual scene a myriad of shapes, colors, and textures impinge on the retina. Just as we cannot make an eye or limb movement to all objects at once, so also we cannot fully attend to more than one or two objects at a time. Much unwanted information must be filtered out by the central nervous system. The first stage in this filtering and selection process is largely automatic and involves distinguishing figures from their background (figure-ground separation). A red apple on a green field or a fly moving against a wall are examples of objects that "pop out" from their backgrounds on the basis of differences in color, shape, texture, distance, or motion (1). The neural mechanisms underlying figure-ground separation most likely begin with simple lateral inhibition in the retina, which serves to reduce neuronal responses to regions of uniform luminance. These processes continue as visual information is relayed through the thalamus to the cerebral cortex, where neurons are especially responsive to stimuli that differ from their backgrounds in form, color, or motion, just the features that produce pop-out phenomena perceptually (2).

Even after figure-ground separation, a processed visual scene will still be very complex, typically containing many different figures. Thus, a second stage of object or feature selection is necessary. Unlike the mechanisms for figure-ground extraction, which operate in parallel across an entire visual scene, this second stage, attention, is thought to operate serially on one or two objects at a time.

In studies of attention, a subject is typically instructed about where to focus attention pending the subsequent presentation of visual stimuli. For example, the subject looks at a screen, holding the

eyes steady. A cue, such as a small dot, comes on to indicate where attention should be directed, without making eye movements. If an array of different stimuli is then briefly presented on the screen, the subject will best remember the stimulus at the cued location. In a different experiment, when a "go" stimulus appears on the screen, the subject must respond as quickly as possible by pressing a key. If a prior cue directs the subject's attention to the go-stimulus location, movements begin sooner than if attention is drawn to a different location. Thus, attention serves both to control access to memory and to facilitate behavioral responses (3).

*Neurophysiology of attention.* Research in primate behavioral neurophysiology has shown that attention can have powerful effects on the responses of individual neurons. In some cases attention leads to an enhancement of neuronal responses to attended items; in others it leads to suppression of responses to unattended items. We discuss some effects of attention in the visual system, but analogous effects occur in other sensory systems as well (4).

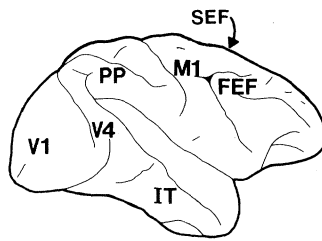
The primary visual cortex (V1), also known as the striate cortex, appears to be the source of two major cortical pathways (5). Each pathway relays information through several additional visual cortical fields (Fig. 1), collectively known as the extrastriate cortex. One pathway is directed into the temporal cortex and appears to be critical for object recognition. The other pathway is directed into the posterior parietal cortex (PP) and appears to be important for visuomotor performance, visuospatial perception, and spatial attention.

*PP and the control of spatial attention.* Neurons in PP appear well suited for a role in spatial perception and attention rather than form or object recognition; changes in their discharge rates reflect more the location of a stimulus and whether it is attended to than the features of a stimulus, such as its shape or color. PP neurons have "receptive fields" in the sense that a given neuron will respond to stimuli only within a certain restricted portion of the visual field (6). A stimulus appearing within the receptive field of a PP neuron, if it triggers a behavioral response, will elicit a much larger neuronal response than if the monkey ignores it; in some cases, ignored stimuli do not cause any neuronal response at all. For most, perhaps all, PP cells, the nature of the behavioral response does not matter: eye or arm movements toward the stimulus, or even generalized responses triggered by but not directed toward the stimulus, are associated with equally potent enhancements of the neuronal response. These findings suggest that the enhancement seen in PP reflects the monkey's attention to a specific location in space rather than any aspect of the motor response; therefore, it may be preferable to think of these cells as having an "attention field" rather than a receptive field.

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S. P. Wise is in the Laboratory of Neurophysiology, National Institute of Mental Health, P.O. Box 289, Poolesville, MD 20837. R. Desimone is in the Laboratory of Neuropsychology, National Institute of Mental Health, Building 9, Room 1N-107, Bethesda, MD 20892.

**Fig. 1.** Lateral view of macaque brain showing locations of some visual and motor areas. Abbreviations: FEF, frontal eye field; IT, inferotemporal cortex; SEF, supplementary eye field; PP, posterior parietal cortex; M1, primary motor cortex; V1, primary visual (or striate) cortex; and V4, fourth visual area.



Since PP lesions in humans often impair the ability to disengage attention from one location and shift it to another (7), it is tempting to suggest that its neurons play a causal role in shifting attention. In this view, the responses of a PP neuron reflect the mechanism of redirecting attention to its “receptive” field. One argument against this notion is that the receptive fields of parietal neurons are very large, in some cases a quadrant or more of the visual field. However, as we argue later, broad spatial tuning by individual neurons need not lead to poor spatial resolution, if the neurons are part of an appropriate neuronal network.

*Effects of attention on the cortical system for object recognition.* The second major visual pathway in the primate cortex, the one that is necessary for object recognition, is directed into the temporal rather than the parietal lobe (Fig. 1). Information in this temporal pathway is transmitted from V1, through areas V2, V3, and V4 into the inferior temporal cortex (IT) (8). Unlike neurons in the parietal pathway, neurons in the temporal pathway are concerned with the features of objects, such as color, orientation, texture, and shape.

Recently, it has been shown that attention affects visual processing at the later stages of this pathway, although not quite in the same way as in PP. Neurons in areas V4 and IT have receptive fields so large that many stimuli will typically fall within them. One might expect that the responses of such cells would reflect the properties of all stimuli inside their receptive fields. However, it has been found that when a monkey restricts its attention to one location within a V4 or IT cell’s receptive field, the response of the cell is determined primarily by the stimulus at the attended location, almost as if the receptive field “shrinks” around the attended stimulus (9). For example, consider a cell that responds strongly to red stimuli and not to green when only a single stimulus appears inside its receptive field. If red and a green stimulus appear simultaneously at different locations within the field, and the animal focuses its attention on only the red one, the cell will respond strongly. If, however, the animal attends to only the green stimulus, the cell will respond weakly or not at all to the red stimulus, even though the red stimulus is still inside the receptive field and the retinal stimulation is identical to the previous condition (Fig. 2). Thus, the cell selectively processes information about the stimulus at the locus of attention, inside its receptive field, at the expense of information about unattended stimuli. In addition to the effects of attention on stimuli at different locations, attention to one aspect of a stimulus, such as the orientation of a vertical red grid, also modulates neuronal responses in extrastriate cortex (10), possibly reducing the processing of unattended information even further. Together, these results may explain why we perceive and remember the properties of a particular stimulus out of the many that may be impinging on the retina at a given moment.

Surprisingly, unlike in PP, the attention effects observed in V4 depend on both the attended and ignored stimuli being located within a recorded neuron’s receptive field, which is typically only a few degrees in size (9). If the animal attends to a stimulus outside a cell’s receptive field, the response to an ignored stimulus inside the field is as strong as when the animal attends to it. Thus, in V4, attention to a stimulus serves to attenuate responses to nearby

stimuli only. By contrast, attentional effects cover a larger spatial range in IT, where receptive fields are much larger, in some cases as large as the entire visual field. These results suggest at least two stages of filtering unwanted information: the first stage works over a small spatial range in V4 and the second stage works over a much larger range in IT. No such effects of attention have yet been found in either V1 or V2, suggesting that V4 is the first area along the temporal pathway in which attention profoundly influences visual information processing.

Although attention appears to filter unwanted information by causing suppression of V4 and IT neuronal responses to ignored stimuli, other results indicate that attention can also cause enhancement of responses to stimuli when the amount of attention, or cognitive effort, devoted to an already attended stimulus is increased. For example, extrastriate neurons show different degrees of responsiveness depending on whether the monkey is idle, engaged in an easy detection task, or engaged in a difficult discrimination task (11). Further, V4 neurons respond more vigorously and are more tightly tuned to the orientation and color of stimuli when a monkey uses the stimuli in a difficult discrimination task than when it uses the same stimuli in an easier version of the same task (12). This enhanced processing does not appear to be due to nonspecific factors, such as arousal, because neuronal responses to irrelevant stimuli presented concurrently with the attended stimuli are not enhanced. Similarly, behavioral data indicate the monkey’s discriminative abilities improve when it is engaged in a more difficult task. Thus, when an animal is challenged by a difficult task, it appears to concentrate its attention, of which two neural correlates are enhanced neuronal responsiveness and sharpened selectivity.

## From Attention to Action

After attention brings an object to the focus of the brain’s information processing system, the next step in exploring an object is usually to direct the eyes to the item of interest, a process called foveation or a gaze shift (13). Indeed, more than eye movements are typically performed to “look at” an attended item. Coordinated movements of the eyes, head, and body bring foveal scrutiny to bear on the object of interest, allowing the greatest possible amount of visual information to be gathered and promoting accurate reaching (14).

*Gaze control.* Several cortical and subcortical structures play important roles in the control of eye movements, and we will not attempt to review this vast literature here. But it is clear that among the areas participating in oculomotor control, the PP, the frontal eye fields (FEF), and the superior colliculus (SC) are especially important in higher order aspects of target selection and gaze control. Of these three structures, FEF and SC appear to be critical. Since combined lesions of those two structures severely impair the generation of saccadic eye movements. Interestingly, ablation of either structure alone causes minimal impairment of eye movements, except for short-latency movements, which suggests a high degree of parallel function in the two structures (15).

The enhancement of visual responses, like that seen in PP for any attended stimulus, also occurs in FEF (16) and SC (17), but only when the stimulus is to be a target of a saccadic eye movement and not when it is merely the focus of attention. Neurons in these two structures have “motor fields,” rather than strictly sensory receptive fields, which specify eye movements of a given amplitude and direction, independent of the initial eye position (18, 19).

*Limb movement control.* Directing attention, then the fovea, to the point or feature of interest does little to affect the environment or achieve any goal beyond parsing and acquiring information. Influ-

encing the environment requires use of the limbs or mouth for most mammals, and for primates, in particular, it often means moving the hand to the object. Much of the central nervous system is devoted to the control of movement, but we will focus here on the motor cortex.

Like the visual cortex, the motor cortex consists of a number of functionally distinct cortical fields (20, 21), and, like the visual cortex, and the SC, most motor areas are organized topographically. However, the details of topographic organization in the motor fields are not as well understood as in visual areas (22). It is accepted, though, that in the primary motor cortex (M1), the hindlimb is represented medially, the head and face laterally, and the forelimb in between. Much work on the cerebral control of movement has focused on that "forelimb representation" (21), and it was there that practical behavioral neurophysiology began (23).

Motor cortex cells begin discharging, on average, about 100 ms in advance of a limb movement and more than 50 ms before the earliest increases in electromyographic (EMG) activity in the muscles that will move the limb. In primates, at least some of these cells project through the pyramidal and corticospinal tracts to terminate directly on spinal motor neurons. Physiological and anatomical studies show that they contact several different motor pools with excitatory synapses (24). Thus, there is a direct causal link between the discharge of at least some M1 neurons and motor neuron excitation.

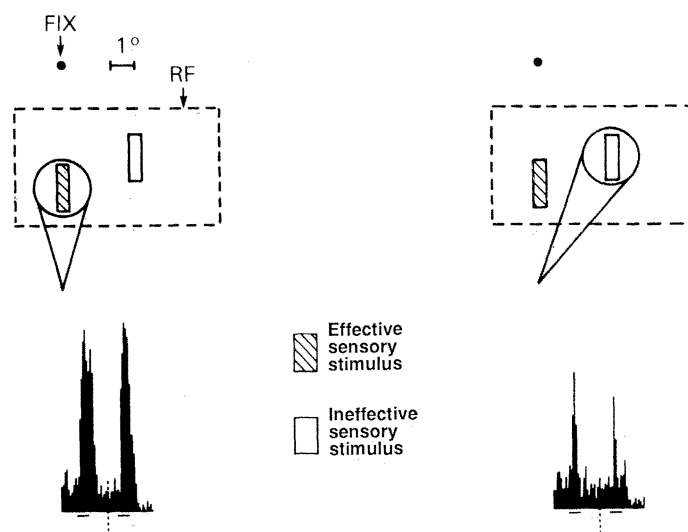
## Population Coding

Little has been said up to this point about how neurons code highly accurate eye, head, and limb movements. One conceivable mechanism would be to assign individual "command" neurons to code individual inputs or outputs, but theoretical work indicates greater precision can be achieved by neural networks in which the individual elements are coarsely tuned (25). As a simple illustration, assume a collection of eight neurons, each of which either responds totally or is silent. If each neuron responds to a stimulus at only a single location, only eight different locations can be coded. However, if each neuron responds to stimuli at any of 128 locations, and the set of locations is unique for each neuron, then 256 different locations (that is, 8 bits) could theoretically be coded by the network with the use of a binary coding system. The spatial specificity of the network is increased, whereas the specificity of the individual neural elements is decreased. Although such binary coding schemes are not actually used by the nervous system, a significant coding efficiency could similarly be achieved by broad, overlapping tuning functions or large, overlapping receptive and motor fields. In such coarse coding schemes, the neural code for a stimulus or response is not localized to a specific neuron, but rather is distributed across the population. In addition to coding efficiency, population codes have other useful properties such as resistance to the effects of local damage. Population codes appear to be the codes actually used by the vertebrate nervous system (26).

*Population vectors and gaze shifts.* In accord with the concept of coarse coding, the motor fields of individual FEF neurons appear to be broadly tuned: activity at half the peak discharge frequency can extend over about 50 degrees of visual space (18). Similarly, broad motor tuning curves are observed in SC (27). At first glance, the breadth or coarseness of the motor tuning curves seems paradoxical: saccades are accurate to within a few degrees, at worst, and electrical stimulation of SC or FEF causes eye movements similarly restricted in amplitude and direction (18, 28). Recent work (29) has clarified this problem by showing that a broad region of SC contributes to an eye movement, not just the focal region in which cells respond optimally before that movement. Deactivation of small regions of

SC with lidocaine does not eliminate the "optimal" eye movements coded by cells at the focus of the injection, but rather decreases their velocity and increases their duration. Further, when the same region is inactivated, saccades to targets other than the optimal one are inaccurate. If the optimal movement for the inactivated region is a horizontal saccade to the left, and the target is 45 degrees up and to the left, then the eye movement will miss the target by being too far to the right, as if some "pull" to the left is lacking. Such a result would be expected if an eye movement is caused by an averaged response of cells with a wide range of preferred eye movement vectors, distributed throughout much of SC. Although the precise manner in which SC neuronal responses are averaged has not yet been worked out, the averaging does not appear to be linear (29). Models positing linear summation predict that when the zone making the largest contribution to that vector is inactivated, all eye movements would undershoot the intended target, whereas experimentally observed eye movements after deactivation sometimes overshoot the target.

Whereas distributed population codes are efficient, they suffer from interference effects when two or more stimuli must be coded simultaneously, a difficulty termed the binding problem in network theory (25). Combining the codes for two stimuli is no solution, because that would result in a third code, one specifying a completely different location. One possible mechanism for solving the binding problem is selective attention, which, by filtering out certain stimuli and enhancing others, could control access to both sensory and motor networks. Yet, it may be objected that the attentional filtering of neuronal responses is never complete. Stimuli that are unattended and that will not be the target of an eye movement nevertheless may elicit at least weak neuronal discharges.



**Fig. 2.** Effect of selective attention on responses of a neuron in V4. At the attended location (circled), two stimuli, sample and test, were presented sequentially and the monkey was required to respond differently depending on whether they were the same or different. Irrelevant stimuli were presented simultaneously with the sample and test but at a separate location in the receptive field (RF). In the initial mapping of the RF, the cell responded well to red bars but not at all to green bars. A red bar (the effective stimulus) was then placed at one location in the field and a green bar (the ineffective stimulus) at another. When the animal attended to the location of the red bar at the time of presentation of either the sample or test, the cell gave a good response (left), but when the animal attended to the location of the green bar (right), the cell gave only a small response, even though the sensory conditions were identical to the previous condition. Horizontal bars under the histograms indicate the 200-ms period when the sample and test stimuli were on. FIX, the fixation point during all stimulus presentations. [Adapted from J. Moran and R. Desimone (9)]

If large populations of neurons code sensory stimuli and motor responses, would not even weak responses interfere with the population code? The answer seems to be that unattended or untargeted items in the visual field can indeed cause a certain amount of interference with both recognition of (3), and eye movements to (30), an attended item. According to Findlay, under certain conditions

... when two targets are presented simultaneously in the visual field, saccades land at a position intermediate between the two. It appears that the saccade system does not completely resolve the individual targets, and even voluntary effort cannot entirely overcome this tendency.

Attention, therefore, appears to ameliorate the binding problem, but in itself is not sufficient to overcome it. A special case of the binding problem occurs when a stimulus appears in the peripheral visual field, but an animal wants to continue looking at (or fixating) a central target. If the peripheral stimulus causes a neuronal response in SC and FEF, should not that activity lead to a small saccade in its direction? It appears that the nervous system has evolved special circuits to circumvent this problem. In the cat SC there is a tension between maintaining fixation on a stimulus and breaking fixation to produce targeted saccades (31). Neurons representing central space, that is, near the fixation point, discharge maximally when the cat attentively fixates a stimulus. Neural activity is reduced when the animal's attention is directed away from the fixation point and ceases altogether just before the saccade. If these cells inhibit the neurons involved in saccade generation "downstream" from the SC, as they are thought to (31), then eye movements to unattended stimuli could be prevented and the binding problem could be circumvented.

**Population vectors and arm movements.** Before and during arm movements made in either two- or three-dimensional space, M1 neurons show a coarse tuning analogous to those in FEF and SC (32, 33). As with eye movements, the coarseness of tuning observed for individual neurons contrasts with the high degree of accuracy with which arm projection movements can be made. A typical example of an M1 directional tuning curve is shown in Fig. 3. The cell is active before all movements to the left, with a peak activity modulation before and during movements between 135 degrees and 225 degrees. The tuning of the cell for direction is similar to the directional tuning mentioned above for FEF neurons (18). Although the tuning of each individual cell is very broad, the vector-

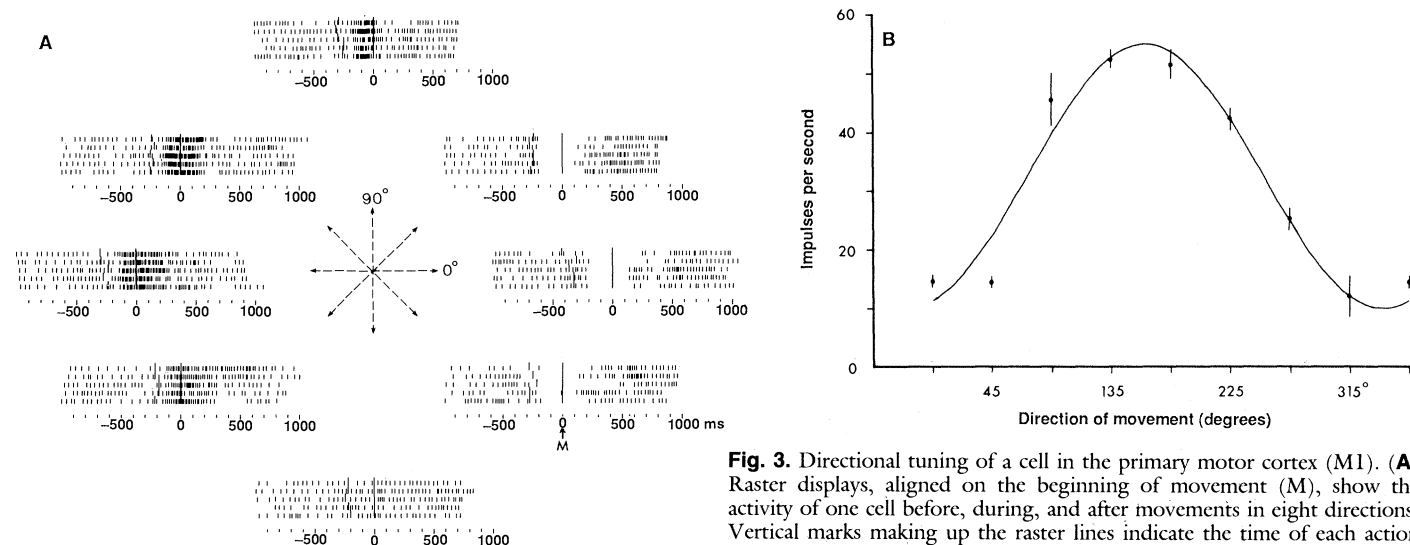
averaged activity of a population of such cells correlates closely with movement direction. To calculate such a population vector, each of the cells in M1 can be considered to represent a vector specifying its "preferred" direction, defined as the arm-movement direction correlated with the greatest discharge modulation. When each neuronal vector is weighted by its activity, the calculated M1 population vector corresponds well with the experimentally observed direction of limb movement, typically within less than 15 degrees (34). Population activity of M1 cells also correlates better than single-cell activity with the force generated by the limb (35, 36).

Interestingly, although much M1 activity reflects maintained postures and the production of forces in the absence of movement (21, 37), for the majority of M1 cells, movement-related changes in discharge rate are not significantly affected by the starting position of the limb (38). Most M1 neuronal modulation and the M1 population vector as calculated by Georgopoulos and his colleagues (38) correlate with the direction of limb movement (or force production) rather than final limb position. This finding is reminiscent of those in FEF and SC, where gaze-shift vectors are specified in relative terms, producing the same movement regardless of the initial eye position (28).

## Coordinate Systems for Movement

Because we perceive the environment as stable while moving our eyes and body, many neurophysiologists have searched for a neural representation of space that remains invariant over eye, limb, or body movement. A retina-centered coordinate system does not have this property, because the retinal coordinates of objects vary with gaze. Although a fixed reference system may seem attractive, or even necessary, it has been shown that movements can be made without reference to such a coordinate system in many circumstances. Indeed, as described above, neurons in the FEF have been argued to code only relative movement vectors (28).

Nevertheless, neurons in other structures may specify movements in a fixed coordinate system. There is evidence that some neurons may code eye movements in a head-centered coordinate system, others code limb movements in a body-centered coordinate system, and still others code body movements in an environment-centered (allocentric) coordinate system. For example, a recently discovered



**Fig. 3.** Directional tuning of a cell in the primary motor cortex (M1). (A) Raster displays, aligned on the beginning of movement (M), show the activity of one cell before, during, and after movements in eight directions. Vertical marks making up the raster lines indicate the time of each action potential. The equal-amplitude movements began at the center of a circle. A

visual stimulus presented the target of each limb movement 200 to 300 ms before movement onset. (B) The mean activity during the period from target presentation to the end of the movement is plotted against movement direction (mean  $\pm$  SEM,  $n = 5$ ). [From A. P. Georgopoulos *et al.* (32), with permission]

cortical field, the supplementary eye field (SEF), may be involved in directing fixation to a particular location in space. The SEF (Fig. 1) lies immediately rostral to, or as some would argue is the rostral part of, the supplementary motor area. Eye movements can be evoked with intracortical stimulation of SEF and its cells discharge in relation to eye movements (39, 40). Many of the eye movements that can be evoked from the SEF converge on a given orbital position, regardless of the eye's initial position in the orbit (41). Studies of single-unit activity in SEF also indicate that the activity is related to head-centered spatial locations, rather than being strictly linked with movements of a given amplitude and direction (40), as is typically the case in FEF. Premotor cortical areas (20) may similarly provide a body-centered coordinate system for goal acquisition by arm movements (40, 42). And, finally, cells in the hippocampus, at least in rats, are thought to code an animal's location in an allocentric coordinate system (43).

How could a head- or body-centered neural representation of space be constructed? There is evidence that PP may be important in this function. The responses of many neurons in PP reflect not only the position of a stimulus on the retina but also the position of the eye in the orbit. Zipser and Andersen (44) have developed a three-layer neural network model that shows how spatial maps can be constructed out of neurons with those properties. Cells in the output layer of their network specify spatial location, cells in the input layer specify the position of the eye in the orbit and the retinal coordinates of a stimulus, and cells in the middle layer "learn" (through the adjustment of "synaptic" weights) to associate inputs with the appropriate outputs. Importantly, the "cells" in the middle layer of the theoretical network develop response properties remarkably similar to those of PP neurons.

## Learning Visuomotor Relations

Even if eye and arm movements result from the activity of neuronal populations, it remains unclear how these populations are programmed to produce the exact motor signals needed to acquire a sensory target. Indeed, this is quite a problem in a developing organism: as the limbs grow, they change their inertial mass and the muscles become stronger. Those and a myriad of other developmental events change the relation between neural force commands and the resultant limb movements. There is evidence that accurate reaching depends on prior visuomotor experience. Development of visuomotor control requires experience with vision and movement together; animals reared without experiencing the visual effects of their own motions cannot perform accurate reaching movements until they obtain that experience (45, 46). Held and Bauer (46) concluded that for monkeys

... the ability to guide the hand visually with the normally achieved accuracy requires mapping of the coordinates of motor response onto the space for vision for which prior exposure seems essential.

Likewise, neural network models of visually guided movement, such as that developed by Kuperstein (47), use accumulated experience to adjust and maintain the spatial consistency between sensory input maps and motor output maps (48). His model posits that initially random motor signals produce movements, resulting in arm and hand positions that the system can observe. During learning, the errors in reaching a target are used to modify weightings between the sensory input maps, showing the target location in space, and the motor output maps necessary to acquire that target, something like Zipser and Andersen's model (44) of spatial mapping in PP. After a few thousand trials, the weightings adjust to the point that the motor and sensory maps are spatially consistent, at which

time the system makes an average error of about 4 percent or 4 degrees. The system generalizes over all reachable space, in accord with the finding that experience with visually guided reaching leads to such generalization, whereas lack of experience prevents it (46).

## Conclusion

We have, of course, only touched the surface of work currently taking place in the field of behavioral neurophysiology. But it occurs to us that the state of behavioral neurophysiology today resembles that of functional neuroanatomy in the early 1970s. At that time, new techniques and approaches, many taken from cell biology, led to a revolution in neuroanatomical practice, one built on the experience, thought, and strategies of the previous 20 years work with experimental fiber-tracing methods. Similarly, behavioral neurophysiologists have had, for about two decades, a method for exploring neuronal activity in alert, behaving animals. We expect that the experience and experimental strategies developed during that period, with the infusion of ideas from psychophysics, neural network theory, and engineering, will serve as the foundation for a new era in neurophysiology.

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# Perspectives on Cognitive Neuroscience

PATRICIA S. CHURCHLAND AND TERRENCE J. SEJNOWSKI

**How is it that we can perceive, learn and be aware of the world? The development of new techniques for studying large-scale brain activity, together with insights from computational modeling and a better understanding of cognitive processes, have opened the door for collaborative research that could lead to major advances in our understanding of ourselves.**

NEUROSCIENCE AND COGNITIVE SCIENCE SHARE THE GOAL of trying to understand how the mind-brain works. In the past, discoveries at the neuronal level and explanations at the cognitive level were so distant that each often seemed of merely academic significance to the other. Symbol processing models based on the digital computer have been unpromising as a means to bridge the gap between neuroscience and cognitive science, because they did not relate to what was known about nervous systems at the level of signal processing. However, there is now a gathering conviction among scientists that the time is right for a fruitful convergence of research from hitherto isolated fields. The research strategy developing in cognitive neuroscience is neither exclusively from the top down, nor exclusively from the bottom up. Rather, it is a coevolu-

tionary strategy, typified by interaction among research domains, where research at one level provides constraints, corrections, and inspiration for research at other levels (1).

## Levels

There are in circulation at least three different notions of the term "levels," as it is used to describe scientific research, each notion carving the landscape in a different way—levels of analysis, levels of organization, and levels of processing.

*Levels of analysis* concern the conceptual division of a phenomenon in terms of different classes of questions that can be asked about it. A framework articulated by Marr and Poggio (2) drew upon the conception of levels in computer science and identified three levels: (i) the computational level of abstract problem analysis, decomposing the task into its main constituents (for example, determination of the three-dimensional structure of a moving object from successive views); (ii) the level of the algorithm, specifying a formal procedure to perform the task by providing the correct output for a given input; and (iii) the level of physical implementation. Marr (3) maintained that computational problems of the highest level could be analyzed independently of understanding the algorithm that performs the computation. Similarly, he thought the algorithmic problem of the second level was solvable independently of understanding its physical implementation.

Some investigators have used the doctrine of independence to conclude that neuroscience is irrelevant to understanding cognition.

P. S. Churchland is in the Department of Philosophy at the University of California at San Diego, La Jolla, CA 92093. T. J. Sejnowski is at The Salk Institute, La Jolla, CA 92093, and in the Department of Biology, University of California at San Diego, La Jolla, CA 92093.