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The Effect of Gaze Angle and Fixation Distance on the Responses of Neurons in V1, V2, and V4

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Summary

What we see depends on where we look. This paper characterizes the modulatory effects of point of regard in three-dimensional space on responsiveness of visual cortical neurons in areas V1, V2, and V4. Such modulatory effects are both common, affecting 85% of cells, and strong, frequently producing changes of mean firing rate by a factor of 10. The prevalence of neurons in area V4 showing a preference for near distances may be indicative of the involvement of this area in close scrutiny during object recognition. We propose that eye-position signals can be exploited by visual cortex as classical conditioning stimuli, enabling the perceptual learning of systematic relationships between point of regard and the structure of the visual environment.

Introduction

The locations of objects in the visual field provide important clues about their identity. Object distance, together with its retinal subtense, reveals the size of an animal and whether it is a possible food item or a potential predator. Some threatening animals, like raptors, tend to be located in the upper visual field, while others, like snakes, tend to creep in the lower visual field. The experience with their probable location will facilitate their identification and speed the initiation of life saving, protective responses. Similarly, different types of food sources tend to be located in different parts of visual space, and this knowledge will facilitate efficient foraging (Altmann, 1998). There is also a close association between the near response, consisting of convergence, accommodation, and pupillary constriction, and the behavior of scrutinizing during object recognition. This paper explores the influence of where the monkey is looking in 3D space on the responsiveness of neurons in V1, V2, and V4.

The presence of eye-position signals in visual cortex has been known since the 1970s. Profound spatial deficits found in clinical cases of damage to posterior parietal cortex motivated the search for and discovery of neurons, which were both responsive to visual stimuli and influenced by eye-position information (Andersen, 1994; Sakata et al., 1980). The success of this line of research and the associated coordinate transformation theory has influenced where subsequent research has looked for this phenomenon and how its functional relevance has been interpreted. In the interval since these seminal studies, further research has found similar eye-position modulation of neurons in earlier areas along the dorsal visual processing pathway, and more recently, studies have extended these findings to the earliest stages of cortical and subcortical visual processing (Buisseret and Maffei, 1977; Lal and Freidlander, 1990; Weyand and Malpeli, 1993; Trotter and Celebrini, 1999). Studies of the modulatory effect of distance cues on cells in both V1 and V4 have suggested that extraretinal signals related to vergence and accommodation are also present in areas along the ventral visual pathway (Dobbins et al., 1998). Our study explores the influence of all three spatial parameters, horizontal, vertical, and depth eye-position signals, and their interactions. It has been proposed that eye-position information in the dorsal pathway contributes to perceptual stability during eye movements as well as to the planning and coordination of such movements (Andersen and Zipser, 1988; Andersen et al., 1990; Milner and Goodale, 1996). Eye-position modulation may be related to different functions in the ventral pathway, which motivated us to examine its influence in V1, V2, and V4.

Results

In these studies, we created maps of mean neuronal firing rates for cells in V1, V2, and V4 as a function of horizontal (H), vertical (V), and depth (D) position of the point of regard for cells in V1, V2, and V4. Two monkeys, with recording chambers positioned to permit access to foveal and perifoveal V4, as well as V1 and V2, were trained to fixate a spot on a movable monitor. The fixation spot appeared randomly at a position in a $3 \times 3 \times 3$ array of possible horizontal, vertical, and distance locations as illustrated in Figure 1. Each of these 27 (H, V, and D) positions was repeated ten times in random order during the course of an experiment. Horizontal and vertical fixation spot positions could assume the values $-7.5°$, $0°$, and $7.5°$, where a horizontal position of $-7.5°$ indicates a position left of center, and a vertical position of $-7.5°$ indicates a position below center. These relatively small excursion eye movements are comparable to those used in scanning the page of a book or a monitor. The fixation spot could appear at distances of 22.5, 45, and 80 cm from the monkey. The monkey maintained fixation, and an optimized bar stimulus was presented in the receptive field of the neuron. Stimuli were scaled and translated with respect to point of regard in order to keep the retinal stimulus unchanged (see Experimental Procedures for details) and monkeys viewed the stimuli binocularly through an aperture, which masked off all but the display portion of the monitor. The data for a neuron recorded from V4 are illustrated three ways in Figure 2. The set of raster plots on the right illustrate the run-by-run response to stimuli presented in each of the 3×3 arrays at distances of

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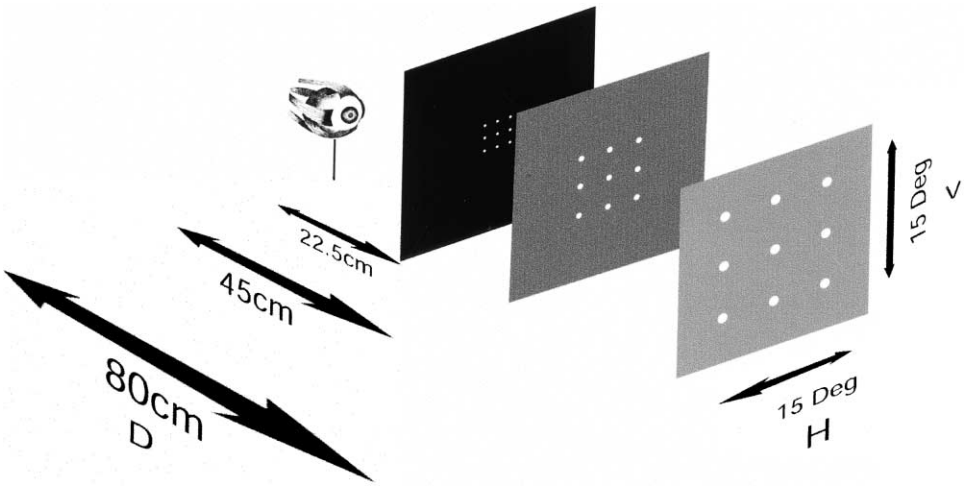

Figure 1. Experimental Setup

The top figure is a schematic of the experimental design. Monitor is mounted on a computer controlled positioning device, which can place the monitor at three different distances from the subject (represented by the eye) viewing the monitor through an aperture. At each of these distances, the fixation spot can appear at one of three horizontal positions and one of three vertical positions. Fixation spot size and position are scaled with distance so as to keep retinal stimulus and position constant with respect to distance.

22.5, 45, and 80 cm. The set of panels in the center illustrates the mean firing rate during fixation only periods (FO, blue) and during stimulation periods (S, red) for each fixation point in the 3 × 3 array at each distance. Error bars indicate the standard deviation of the mean over the ten repetitions of the experimental condition.

On the right are color-coded maps of the firing rates superimposed on the viewing screens at the three distances. This V4 neuron showed a strong preference for stimuli near the center of the 22.5 cm plane. Figure 3 shows data recorded from three additional neurons represented in the same way as the central panels in Figure

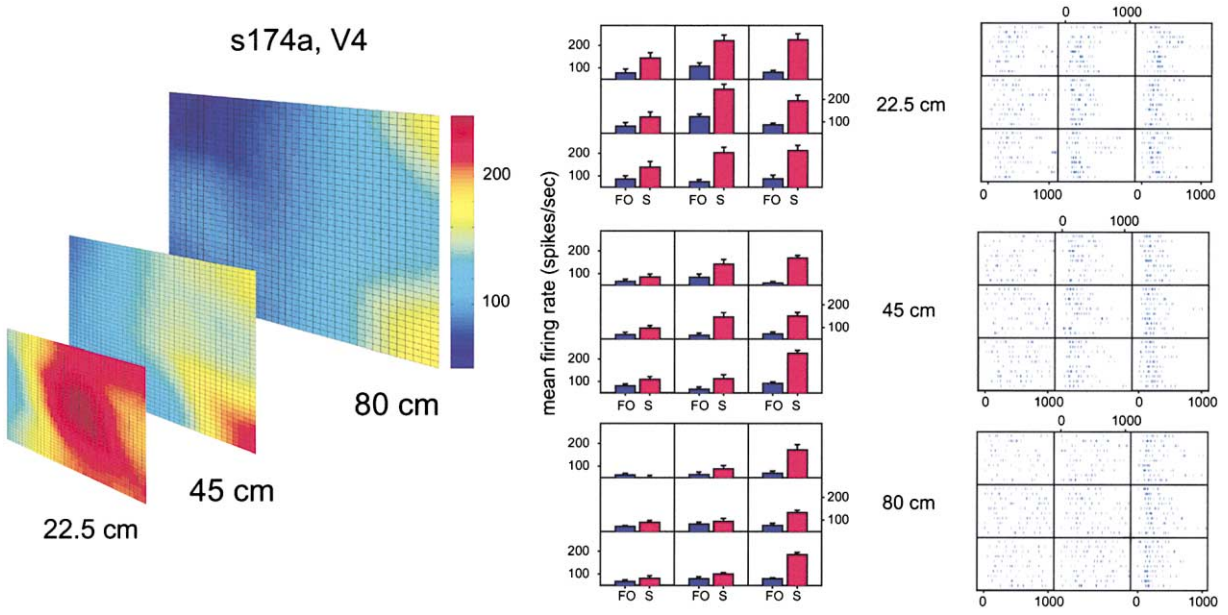

Figure 2. Three Representations of an Example Cell from V4

The rightmost figure represents the spike rasters of the S period for each of the 27 experimental conditions. These conditions are split into three panels, one for each of the monitor distances. Within each panel, rasters for each of the nine (H, V) fixation conditions are represented as a 3 × 3 grid of graphs. Zero indicates the time of stimulus onset in each raster plot. The center figure represents the mean firing rates for this cell during both the fixation period (FO, blue bars) and the stimulation period (S, red bars). The error bars show one standard deviation. The arrangement of the 27 graphs is the same as described for the spike rasters. The leftmost graphs show the mean firing rate data during the stimulation period using an interpolated color plot. Each of the planes represents a monitor viewing distance. A hot color scale was used with red representing high firing rates, and blue representing low firing rates. Only the firing rate during the S period is represented in the left and right figures.

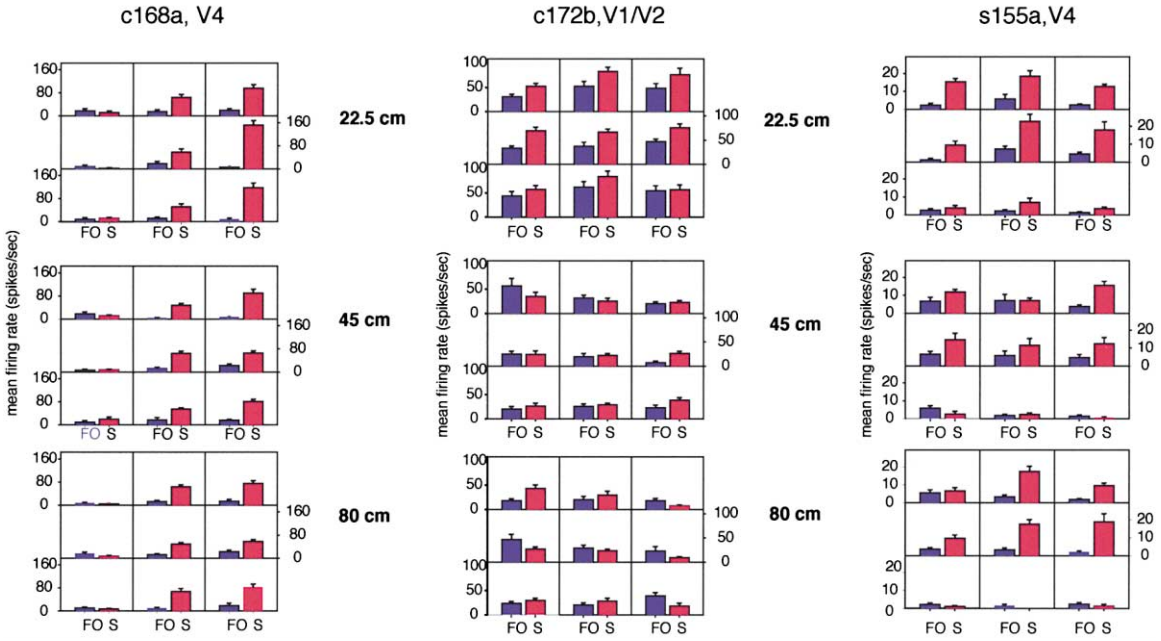

Figure 3. Examples of Different Types of Modulation of Mean Firing Rate with Respect to Point of Regard

The three columns represent three different cells. The three rows represent the three viewing distances. Each panel is divided into nine bar graphs representing the nine (H, V) pairs. FO is the mean firing rate during the FO period of the trial. S is the mean firing rate during the stimulation period of the trial. The leftmost figure represents a cell, which is modulated with respect to H. The middle figure is an example of modulation with respect to D. This cell is a nearness cell. The rightmost figure is an example of modulation with respect to V. This cell is an upness cell.

2. The neuron illustrated on the left was strongly modulated in the horizontal dimension (H); the neuron in the center panel was modulated mainly by distance (D); the neuron on the right was strongly modulated in the vertical dimension (V).

We recorded from 88 cells (41 in V1/V2 and 47 in V4) in two monkeys. Each cell in our sample population was tested for modulation with respect to H, V, D and all possible interactions between these variables using both an ANOVA analysis and nonparametric statistics. We found that 85% of the cells we recorded from had a statistically significant amount of modulation during ($p < 0.01$) (S) period with respect to at least one of the experimental variables H, V, or D, and 40% of these cells showed significant modulation during the FO period. The presence of modulation during the FO period makes it unlikely that these effects are the result of fixation error or mislocation of the receptive field stimulation. The presence of potentiation of activity during the prestimulus period was noted early in the research on eye-position modulation in parietal visual areas (Sakata et al., 1980), and more recently in V1 and V4 (Dobbins et al., 1998). Activity of this type found in primary motor cortex is postulated to reflect preparation for response to a later stimulus or preparatory set activity (Evarts and Tanji, 1976).

The percentage of the population having each of the different types of modulation is shown in Figure 4. The distribution of the different types of modulation varies significantly both with respect to visual cortical area (V1/V2 and V4) and with respect to trial period (FO/S). The largest population of cells was that modulated with respect to D. The amount of modulation during the S period is consistently larger than that found during the FO in both V1/V2 and V4. As shown in Figure 5, when the fixation firing rate is factored out by either subtraction or division, about half of the neurons still show significant modulation. This indicates that these results can only be partially explained by simple additive or multiplicative models of gain modulation by eye position. Among the notable differences between the distribution for area V1 and the distribution for area V4 is the relative paucity of modulation with respect to V in V1/V2. This result confirms earlier findings (Trotter et al., 1992) and contrasts with V4 where the amount of modulation with respect to V is comparable to the amount of modulation with respect to H.

The modulation of each cell can be classified according to whether the mean firing rate is monotonically increasing, monotonically decreasing, or nonmonotonic with respect to the experimental variables. For the D experimental variable, this gives rise to categories called nearness, nonmonotonic, and farness. For the V experimental variable, this gives rise to categories called upness, nonmonotonic, and downness. For the H experimental variable, this gives rise to categories called leftness, nonmonotonic, and rightness. The percentage of cells falling into each of these categories is shown in Figure 6. In V1/V2, for each experimental variable, the numbers of neurons falling into each of the three categories is about evenly split. In V4, there are significantly more neurons classified as nearness cells than farness cells. This is consistent with experimental results showing a bias in the disparity tuning of V4 cells for disparities

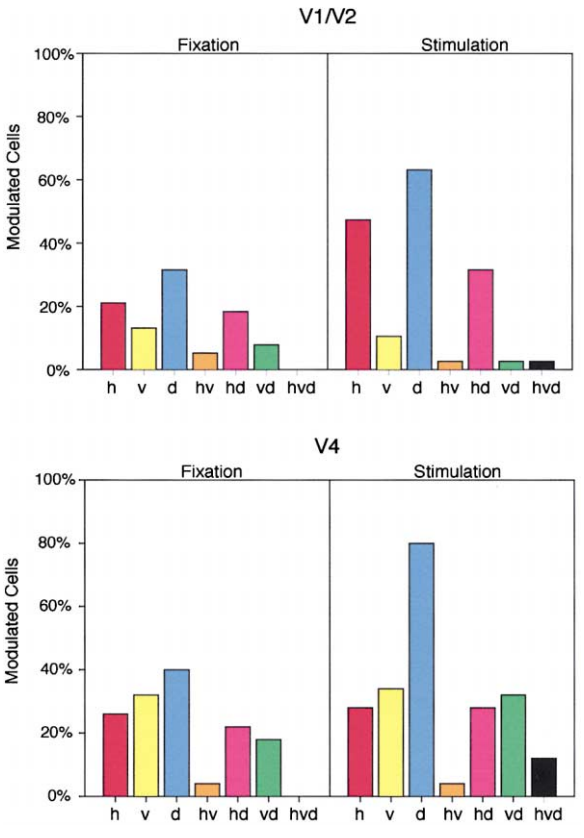

Figure 4. Summary Results of Three-Way ANOVA Analysis for FO and Stimulation Periods for Each Cell

Percentage of cells that had significant ($p < 0.01$) amount of the variance in mean firing rates accounted for by modulation with respect to H, V, and D, or interactions between these experimental variables. Results for V1/V2 and V4 are shown separately.

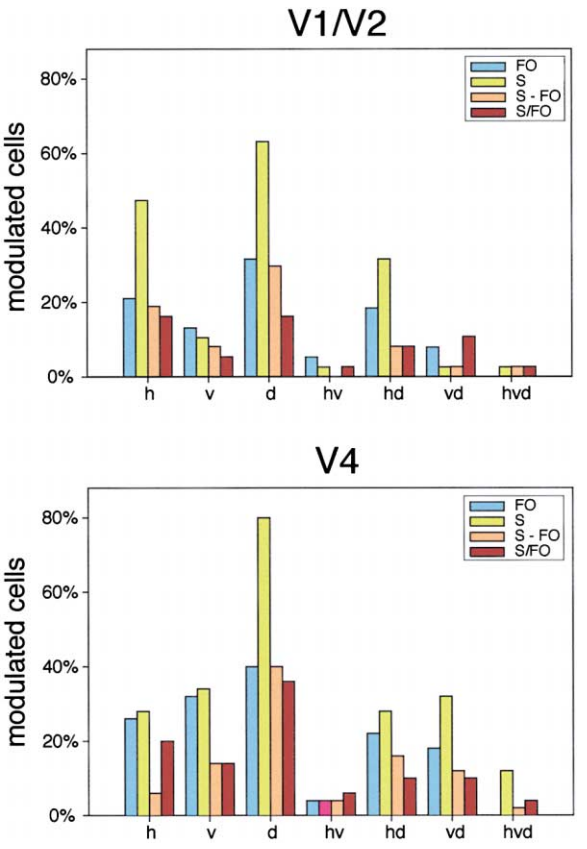

Figure 5. Summary Results of Three-Way ANOVA Analysis for Stimulation Firing Rates with Fixation Firing Rates Factored Out through Both Subtraction and Division

Percentage of cells that had significant ($p < 0.01$) amount of the variance in mean firing rates accounted for by modulation with respect to H, V, and D, or interactions between these perimental variables. Results for V1/V2 and V4 re shown separately.

corresponding to positions in front of the fixation point (Hinkle and Connor, 2001). Calculation of the size of intersections between categories revealed that there were significantly fewer cells falling into the far and down intersection than other intersections (Figure 6, bottom). The fact that there are unusually few neurons falling into both the far and down categories might be due to the fact that this is a relatively unusual viewing situation. It is more common to look down and near than down and far away.

To measure the magnitude of modulation, the fractional gain of each cell was calculated with respect to each of the experimental variables. This measure is defined as the difference between the maximum and minimum firing rates normalized by the maximum firing rate, which can range from 0 to 1, with 0 indicating no modulation. The range of fractional gains found indicates the presence of a continuum in the population of cells from those that are little influenced by eye-position signals to those that are heavily influenced. Fractional gain values were distributed normally with a mean of 0.4. The distributions did not significantly differ when separated out by cortical area, trial period, or experimental variable. Table 1 shows a strong correlation between the strength of modulation with respect to one experimental variable and the strength of modulation with respect to the others. Cells that are strongly modulated with respect to one experimental variable tend to be as strongly modulated with respect to the others. These correlations are much stronger during the FO period than during the S period. The correlation may be more evident during the FO period due to lack of a superimposed stimulus driven response.

Discussion

While these experiments do not directly address the question of where the modulatory signals originate, the presence of modulation during the FO period strongly suggests that the modulatory signals are related to eye position. Tracing experiments have demonstrated an input to V2 and V4 from the small saccade part of the frontal eye fields (sFEF) (Stanton et al., 1995; Bullier et al., 1996). The frontal eye fields (FEF) are an important component of the cerebro-ponto-cerebellar pathway involved in governing voluntary eye movements, including vergence and ocular accommodation (Gamlin et al., 1996). There is a population of cells in FEF that display a tonic firing rate related to vergence angle and accommodation (Gamlin et al., 1996). Stimulation of either FEF

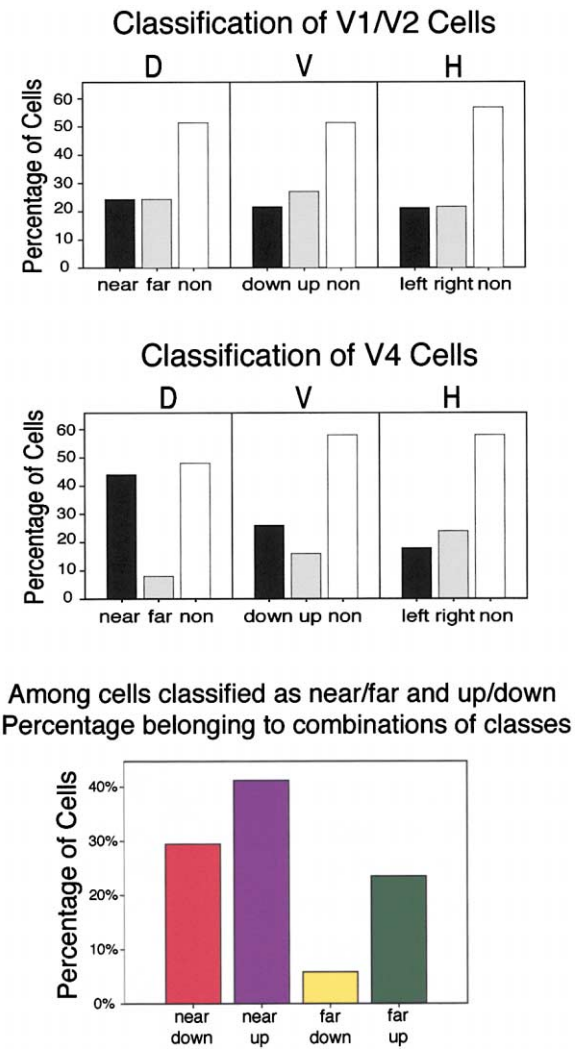

Figure 6. Distribution of Different Types of Modulation

Top two graphs show histograms for V1/V2 and V4, respectively, for groups near, far, and nonmonotonic. The nonmonotone group aggregates the two different ways of being nonmonotone in this paradigm. Bottom shows histogram for intersection of classes related to distance and vertical position for monotonic cells for all areas.

or V4 produces vergence and accommodation (Jampel, 1960). Thus, the modulation seen in V2 and V4 may arise from efference copies of commands arising in the frontal eye fields. The modulation seen in V1 may result from indirect relay from frontal eye fields via V2. The lack of cells showing interaction between parameters H and V may be indicative of an independence of the sources of the signals producing the H and V modulations. The difference between V1 and V4 in the number of cells showing modulation with respect to V may be an indication that information regarding V is not available to V1 and only enters the visual processing stream at the later stage of V4. This is further evidence of the independence of the sources of information regarding H and V. In contrast, the coupling between the H and D modulations found in V1 may be indicative of a common source for the modulation with respect to these two parameters. This signal may be the result of an integration of the separate premotor conjugate and vergence eye movement commands of the type hypothesized by Hering (1942).

Table 1. R Values of the Correlation Between the Magnitudes of Modulation with Respect to Each of the Experimental Variables

	H and V[1]	H and D[1]	V and D[1]
Fixation Period	0.84	0.85	0.83
Stimulation Period	0.50	0.64	0.61

[1] Top headings indicate pairs of modulation indices.

Our results may contribute to a better understanding of the functional differences between the ventral and dorsal pathways in the visual cortex of primates. A basic distinction in these pathways is between the ventral specialization for object identity and the dorsal specialization for manipulation of objects in visual space (Gross, 1973; Milner and Goodale, 1996). This distinction probably arose in the evolution of the extrastriate visual areas because the more ventral path proceeds from the foveal visual field representation in V1, whereas the dorsal path lies adjacent to the lower visual field representation where the hands are located during the manipulation of objects (Maunsell and Van Essen, 1987; Previc, 1990). Location in visual space is crucial for the performance of both ventral and dorsal functions, but in different ways. For example in V4, a main component of the ventral path, object distance probably contributes to the mechanism of size constancy (Dobbins et al., 1998), which is crucial in discriminating object identity. The ability to accurately judge the size of objects at a distance requires gradual learning of the relationship between retinal size, object distance, and object size during early childhood (Allman, 1998; Zeigler and Leibowitz, 1955). Lesion experiments producing deficits on size constancy tasks indicate that this learning may occur in V4 and its downstream target IT (Humphrey and Weiskrantz, 1969; Ungerleider et al., 1977). Such learned associations between eye-position signals and sensorimotor contexts would have significant adaptive value.

Signals from a variety of sources indicating eye position, threat, and reward are potentially present in visual cortex (Amaral and Price, 1984; Chun and Phelps, 1999; Morrison et al., 1998; Hollerman and Schultz, 1998). These signals often precede and are indicative of a change in behavioral or sensory context (Land and Furneaux, 1997; Maunsell, 1990). As a result of learning mechanisms present in cortex, such predictive signals would tend to influence neuronal responses (Sejnowski, 1999; Ahissar et al., 1992). Ivo Kohler's studies with prisms have demonstrated psychophysically that the visual system is indeed capable of adapting in an eye-position-dependent manner, a phenomenon which he termed "situational or conditioned aftereffects."

Because modulatory eye-position signals exist in visual cortex prior to visual stimulation, they might function as conditioning stimuli. Retinal stimulus characteristics (unconditioned stimulus) produce sensory responses in visual cortical neurons (unconditioned response). Learning resulting from repeated pairing of eye-position signals (conditioned stimulus) with retinal stimulus characteristics (unconditioned stimulus) would tend to result

in the eye-position signal potentiating those neurons sensitive to the stimulus characteristics (conditioned response) prior to stimulus presentation (Ahissar et al., 1992), thus preparing visual processing for the expected stimulus. A functional linkage between point of regard (conditioned stimulus) and the responses of visual cortical neurons (unconditioned response) learned in this way could result in perceptual learning of systematic relationships between point of regard and statistical characteristics of the visual environment. While there are circumstances in which strong correspondences exist between eye position and stimulus characteristics, and in these circumstances the visual system is capable of adapting to the eye-position signal alone (Kohler, 1964), in natural behavior it is more likely that eye-position signals are but one of an array of extraretinal signals that, when taken together, are very informative about the current sensory and behavioral demands and strongly predictive of future sensory inputs. This array probably includes eye-position-related signals relayed from frontal eye fields, penalty-related signals from amygdala, and reward-related dopaminergic signals, which serve a critical role in learning (Hollerman and Schultz, 1998; LeDoux, 1996; Amaral and Price, 1984; Ahissar et al., 1992). All three of these extraretinal signals converge on layer one of V2 and V4 and the frontal eye field and dopaminergic inputs also converge on layers five and six of V2 and V4. Devices for human use, as simple as mirrors or bifocals, and as complex as a virtual cockpit explicitly based on a "what-you-see-depends-on-where-you-look" concept, create correspondences between point of regard and distinctive information sources and may be implicitly exploiting the natural talent humans have at learning such associations.

Experimental Procedures

Training and Surgery

Two macaque monkeys were trained to reliably fixate a small spot on a computer monitor for a juice reward. Two aseptic surgeries were performed. Prior to training, a head post was implanted to permit head restraint for fixation training. Fixation was monitored monocularly with a noninvasive infrared video-based eye tracker (ISCAN, RK-716PCI) with an accuracy of 0.05°. Following fixation training, the second aseptic surgery was performed to implant a recording chamber over perifoveal V1, V2, and V4 to allow insertion of microelectrodes.

Recording

To record the activity of single neurons, the intact dura was penetrated with sterile glass insulated platinum-iridium microelectrodes. Single neurons were isolated with a window discriminator and spike activity recorded with a PC. The monitor was mounted on a computer controlled positioning device (Industrial Devices Corp.) with electrooptic switches mounted so that the monitor could be accurately positioned at 22.5 cm, 45 cm, and 80 cm from the monkey. All experimental conditions were randomly interleaved. Stimulus luminance was 160.96 $\pm$ 3.4 cd m-2. The luminance of the stimuli at the different test distances were measured using the methods detailed in Dobbins et al. (1998) and showed no appreciable difference over the distances used. This was further confirmed using measurements of pupil size, which was measured with the eye tracker. The white bars were flashed in the receptive field during fixation at the preferred orientation, length, and width for the cell, determined prior to the experiment with the monkey fixating at the central position at the farthest distance.

The monkey binocularly viewed the stimuli through an aperture, which masked all of the visual field except the display portion of the monitor screen even at the farthest distance. The display was used in its highest resolution mode (1280–1024 pixels) with a refresh rate of 75 Hz. Stimuli were generated on an SGI O2 using graphics programs written in Python and utilizing native SGI OpenGL. Whenever applicable, antialiasing routines were used to reduce pixellation effects. Both the dimensions of the bar stimuli and their offset from the fixation point were scaled with presentation distance so that the stimulus subtended the same retinal angle and was presented in the same retinotopic location regardless of fixation location. The flat monitor provides an accurate approximation of a spherical presentation for the small viewing angles used in these experiments requiring negligible correction.

Experimental Paradigm

A single successful experimental trial consisted of acquiring and maintaining fixation with accuracy of a quarter of a degree for approximately 500 ms before the bar stimulus flashed on in the receptive field for between 1500 and 2000 ms; the bar stimulus then flashed off and then the fixation spot went off. If, after acquiring fixation, the subject maintained fixation until the fixation spot went off, he received a reward of juice or water. If at any point after acquiring fixation and before the fixation spot went off, the subject broke fixation, the trial was immediately aborted, the screen blanked, and there was a short pause interval before the beginning of the next trial.

Analysis

Cells were assigned to a visual cortical area based on receptive field position, size, and properties and position relative to the lunate sulcus. In the absence of histological classification, we combined the data from V1 and V2 for quantitative analysis. Cells showed a linear relationship between mean and variance in the firing rates. Two different statistical tests were performed on the data from each cell to determine if there were significant differences in the data with respect to the experimental variables. A three-way ANOVA was performed on the data after a logarithmic transformation of the mean firing rates, which is the standard treatment of data in which means and variances are positively correlated. A p value of less than 0.01 was used as criterion threshold in all cases. In addition, a nonparametric variant of the Kruskall-Wallis Rank Sum test was performed on the data, with virtually identical results.

The magnitude of modulation of the mean response with respect to each of three dimensions was quantified by calculating the fractional gain between the highest and the lowest mean response values, normalized by the maximum mean response. The lowest possible fractional gain value is zero, which indicates that the mean response rate was unaffected by a change in the dimension in question. The highest possible value of 1.0 indicates that responses were absent for at least one value of the dimension in question.

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