

Distance Modulation of Neural Activity in the Visual Cortex

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Humans use distance information to scale the size of objects. Earlier studies demonstrated changes in neural response as a function of gaze direction and gaze distance in the dorsal visual cortical pathway to parietal cortex. These findings have been interpreted as evidence of the parietal pathway's role in spatial representation. Here, distance-dependent changes in neural response were also found to be common in neurons in the ventral pathway leading to inferotemporal cortex of monkeys. This result implies that the information necessary for object and spatial scaling is common to all visual cortical areas.

Under normal viewing conditions, humans make accurate judgments of object size for distances of as much as 100 feet (30 m). This perceptual capacity, known as size constancy, has been demonstrated by experiments that require humans and monkeys to report the size of objects located at different distances (1, 2). To represent the size of an object in a distance-invariant manner, an estimate of distance is necessary to compensate for the diminution of image size with distance. A key question is whether the cues to distance act on early representations of size and form or on higher representations of objects.

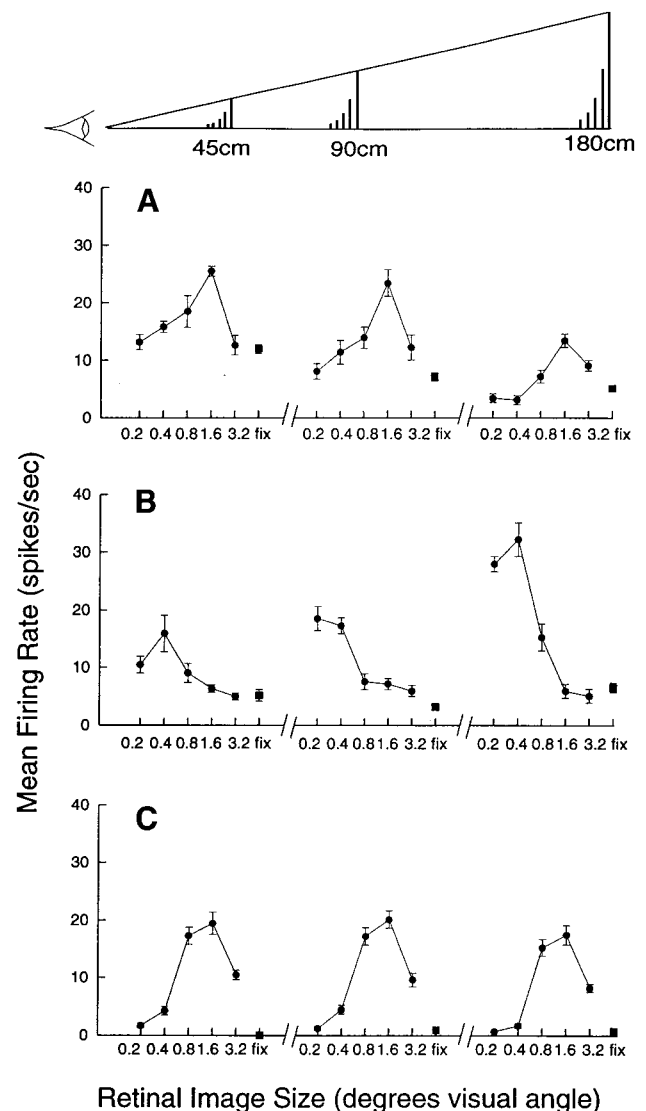
Viewing distance and angle of gaze are known to modulate neural responses in parietal cortex and on the dorsal pathway to parietal cortex beginning in cortical area V1 (3–6). It has been firmly established that parietal cortex is involved in visuospatial coding (7). However, lesions to parietal cortex do not disrupt size constancy judgments in monkeys (2), suggesting that the visuospatial information used for size constancy is encoded in nonparietal areas. Area V4 is at an intermediate level in the ventral visual cortical pathway to inferotemporal cortex and contains a large proportion of size-selective neurons (8). Thus, we were interested in investigating the neural coding of size and distance in V4 of awake monkeys (9).

To address these issues—where in the visual pathway distance information is combined with retinal size information and how it is incorporated—we measured size tuning in

V1, V2, and V4 with respect to viewing distance in awake monkeys (*Macaca fascicularis* and *M. mulatta*). Two monkeys were trained to fixate a spot on a movable monitor while viewing stimuli of a variety of sizes. Stimuli were scaled with distance so that retinal image size and speed were unchanged

Fig. 1. Illustrative results. Measurements were made with octave spaced stimulus sizes (length and width) at octave spaced distances to maintain a fixed range of retinal size. Three common types of responses of cells were found in areas V1, V2, and V4. All of the cells shown are size-tuned and prefer the same retinal image size regardless of distance. (A) Nearness cell, which showed a monotonic increase in mean firing rate with increasing proximity of the stimuli. This cell also showed significant distance modulation to fixation only (squares to the right of each tuning curve). (B) Farness cell, which monotonically increased in mean firing rate with increasing distance. (C) Distance-independent cells. The cell shown in (A) was recorded from area V1, and the other cells are from area V4. Qualitatively similar distance modulation effects were observed in V1, V2, and V4. The spontaneous neural activity at each distance measured during fixation, but in the absence of a stimulus on the receptive field, is shown to the right of each graph.

with changing distance (10). We isolated and tested 178 cells in two monkeys. Distance was a crucial parameter governing neural response in more than half the cells tested. Figure 1 illustrates typical results. Figure 1, A and B are representative of cells that show response modulation with viewing distance, while Fig. 1C illustrates a cell in which response is independent of distance. The most commonly observed type showed increasing response with proximity (nearness cells), but the opposite type (farness cells) were also common (11). A small number of cells exhibited a nonmonotonic response (Fig. 2C) as a function of distance (for example, exhibiting a maximal or minimal response at an intermediate distance). Of the cells that had significant response modulation with viewing distance, 65% were nearness cells, 22% were farness cells, and the remaining 13% had nonmonotonic response profiles. Because viewing distance and stimulus distance were not varied independently, we could not distinguish viewing distance



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modulation from absolute distance tuning (12).

A two-way analysis of variance was used to examine the effects of stimulus size and distance on mean firing rate. Three-quarters of cells were size modulated (133/178, $P < 0.01$), and almost two-thirds showed modulation of responsivity with viewing distance (114/178, $P < 0.01$). In the absence of histological confirmation, we combined V1 and V2 cells for analysis (13). Sixty-five percent of V1/V2 cells (55/85) and 64% of V4 cells (59/93) exhibited a change in responsivity with viewing distance. Forty percent of V1/V2 cells (34/85) and 54% of V4 cells (50/93) showed statistically significant modulation for both size and distance. For both V1/V2 and V4, the fraction of cells exhibiting both size and distance effects is not significantly different than the product of the fraction of cells exhibiting each effect, implying that size and distance modulation have independent sources. Size and distance are combined from the outset in the visual cortex and could provide, in a distributed form, the necessary elements to achieve size constancy.

The standard viewing situation afforded the monkey an unobstructed binocular view of the monitor and room, providing a variety of cues to distance. Under similar viewing conditions, humans can exploit oculomotor as well as visual cues to distance such as linear perspective and occlusion (14). Under binocular full-field viewing, horizontal binocular disparity and most pictorial cues are constant with changes in monitor position. In contrast, changing viewing distance entails changes in (i) the angular subtense of the monitor; (ii) differential binocular occlusion of the background regions flanking the monitor; and (iii) differential perspective (horizontal gradient of vertical disparity) of the monitor (15). Each of these effects would be manifested as beyond-the-classical-receptive-field contextual influences on the foveal and perifoveal units in our sample, and each would be eliminated under restricted field viewing, leaving only extraretinal cues (16). To distinguish the contributions of visual and extraretinal cues, we performed the experiment under two additional viewing conditions. Measurements were repeated through either binocular or monocular apertures that restricted the animal's view to the monitor screen, excluding the monitor frame and re-

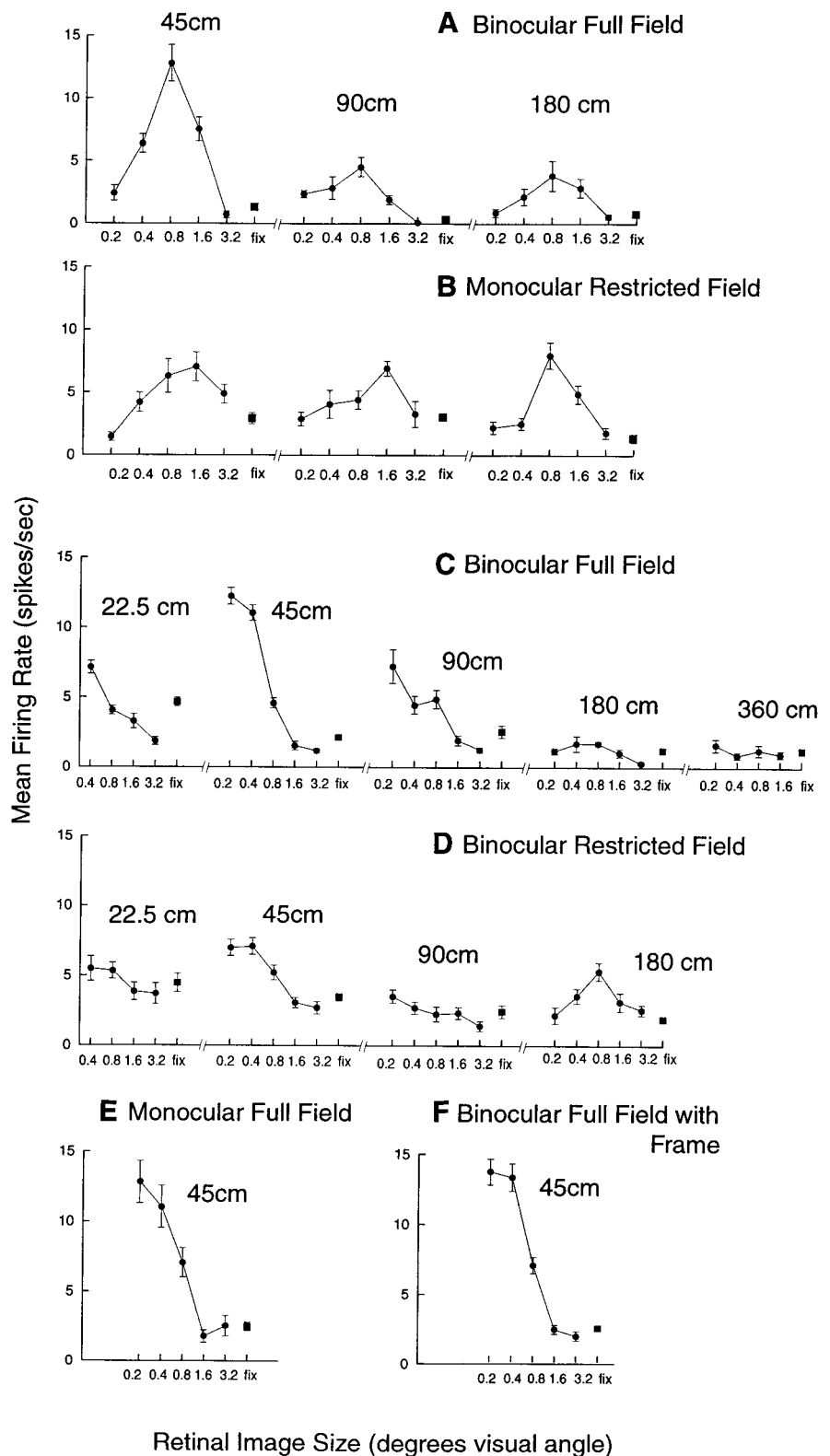


Fig. 2. Visual distance modulation. A V4 cell was tested under (A) binocular full-field and (B) monocular restricted-field conditions. In (B), distance modulation is abolished under monocular restricted-field viewing. These graphs combine three alternating (two binocular, one monocular) blocks of measurements. The effect of distance modulation was statistically significant in both binocular blocks ($P < 0.01$), but not in the monocular block. (C) through (F) shows a V4 cell that is dependent on visual context. (C) Under binocular full-field viewing, response is greatest at a viewing distance of 45 cm. (D) Distance modulation disappears under binocular restricted-field viewing. [(E) and (F)] To determine whether binocular or monocular contextual cues were responsible, two additional measurements were performed at the preferred viewing distance. (E) Under monocular full-field viewing, response strength was similar to binocular full-field viewing. (F) Similarly, binocular full-field measurements at 45 cm with a mask covering the monitor to simulate the appearance of the monitor screen and frame at a viewing distance of 180 cm did not affect the response strength at the preferred viewing distance.

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remainder of the room (17).

Figures 2 and 3 compare responses under full and restricted field viewing conditions. Combining binocular and monocular restricted-field viewing conditions (combining V1/V2 and V4), 49% (27/55) of the cells maintained distance modulation under restricted viewing conditions. This suggests that for these cells, extraretinal signals related to ocular state are sufficient to mediate distance modulation. However, neurons may depend

on both visual and extraretinal cues, as is suggested by the cell in Fig. 3, C and D in which distance modulation is diminished but not abolished under monocular restricted-field viewing. Under binocular restricted-field viewing, a majority of cells (63% or 12/19) retained significant distance modulation (an example is shown in Fig. 3, A and B). A somewhat smaller proportion of cells (45% or 15/33), retained significant distance modulation under monocular restricted-field view-

ing (an example is shown in Fig. 3, C and D). For those cells in which distance modulation was abolished under restricted-field viewing conditions (Fig. 2, B and D), factors other than the extraretinal ones are implied (18).

It is known that humans can perceive stereo depth differences on the basis of differential occlusion and that differential perspective can be used for depth scaling, but only for objects sufficiently large (15) ($>20^\circ$, which corresponds to viewing distances of 90 cm and less in our experiments). In most of the cells studied, it is not possible to distinguish among the visual factors contributing to distance modulation. However, Fig. 2, C through F depicts a cell in which distance modulation is abolished under restricted-field viewing conditions but is conserved under monocular full-field viewing (19). For this cell, the binocular contextual cues—differential occlusion or differential perspective—are not necessary, but the visibility of the ambient scene is, implicating pictorial cues. Therefore, in some neurons, one function of the nonclassical receptive field surround may be to provide a context-dependent modulation related to object and spatial scaling.

Models in which extraretinal signals related to gaze direction and distance act on retinal representations via gain modulation are capable of transformations from eye- to head-based coordinates and for representing distance (20). These models were conceived as models of computations in parietal cortex, because the early evidence of gaze-dependent neural response modulation was found there. However, our findings—in combination with an earlier report of changes in responsivity with viewing distance in V1 neurons responsive to random dot stereograms (5, 6), and a report of changes in responsivity with gaze direction in cat striate cortex (4)—imply that the substrate for computations related to object and spatial constancy is already present in primary visual cortex.

A great deal of evidence supports the presence of spatial processing in the parietal cortex and object processing in the inferotemporal cortex (21). A more recent proposal holds that spatial information is used for different purposes in the dorsal and ventral streams (22), and recent evidence from a human functional imaging study supports a dorsal/ventral dichotomy which depends on whether the observer is performing a landmark identification (dorsal) or survey (ventral) spatial task (23). Our results demonstrate that distance-dependent modulation of visual response is a common property of neurons in V4 in the ventral visual cortical pathway. Consequently, spatial modulation is present in both dorsal and ventral visual cortical streams and appears to be a fundamental feature of the visual cortex. The existence of a common set of distance modulation func-

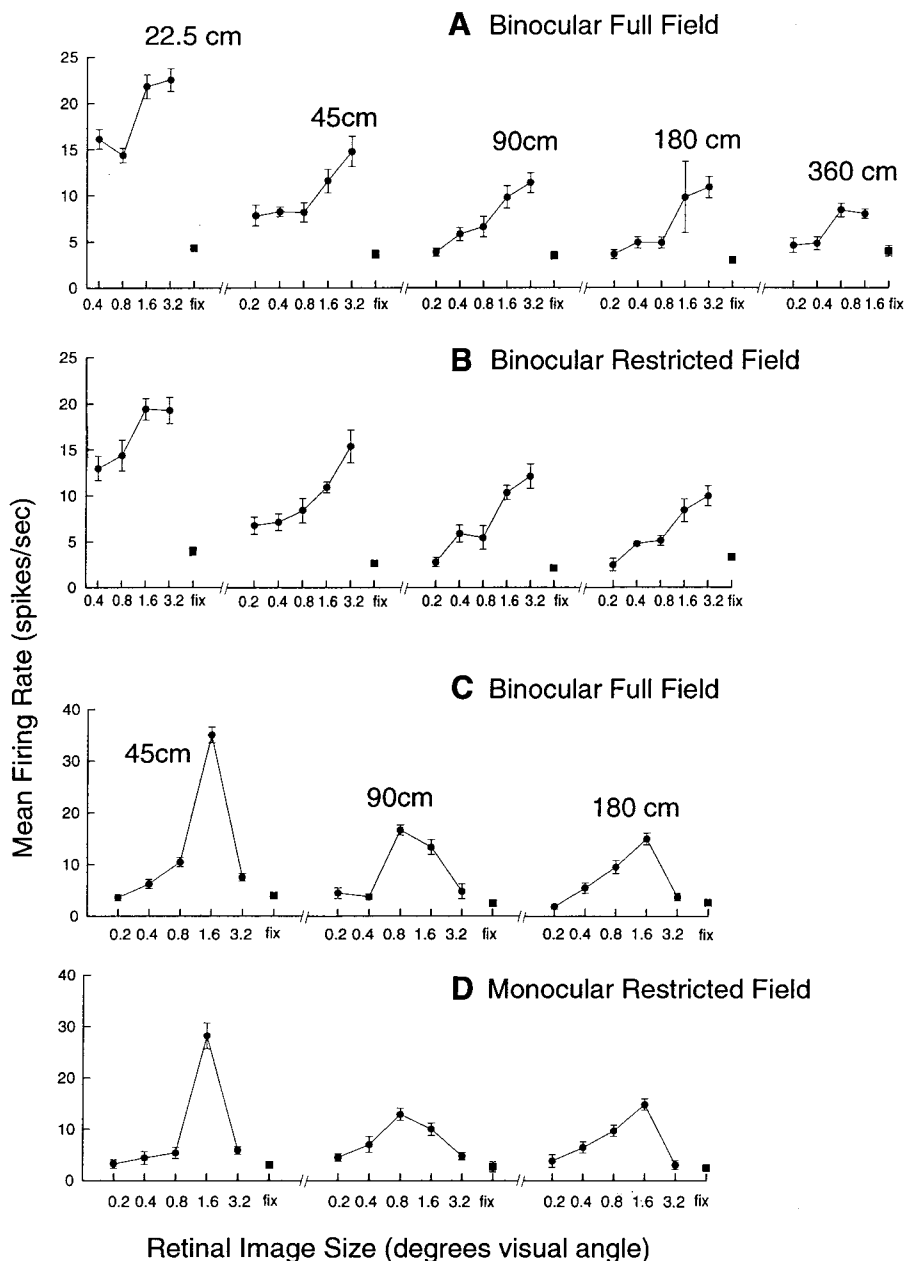


Fig. 3. Extraretinal distance modulation. (A) A V4 cell in which distance modulation does not depend on the visual context. (B) Responses are similar under binocular full-field and binocular restricted-field viewing conditions ($P < 0.01$). (C) A nearness cell in V4 in which distance modulation is conserved under monocular restricted-field viewing. (D) The slight diminution of the effect in the monocular restricted-field condition suggests that multiple cues may contribute to distance modulation in this cell. The graphs combine data of four alternating (two binocular, two monocular) blocks of measurements at the three distances. In all four blocks, the effect of distance modulation was statistically significant ($P < 0.01$).

tions in all visual cortical areas could underlie a three-dimensional spatial code for addressing and binding of computations carried out in different cortical compartments.

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9. Recording chambers were positioned to permit access to foveal and perifoveal V4 as well as V1 and V2. Two macaque monkeys were trained to reliably fixate a small spot on a computer monitor for a juice reward, and fixation was monitored monocularly with a noninvasive infrared video-based eye tracker [J. Barbur, W. Thomson, P. Forsyth, *Clin. Vision Sci.* **2**, 131 (1987)].
10. The computer monitor was on a movable platform that could be set at 22.5, 45, 90, 180, or 360 cm from the monkey. Interleaved blocks of trials were obtained at three to five of the viewing distances with multiple blocks at each distance. Stimuli were presented in blocks consisting of randomly interleaved presentations of bars of varying size (aspect ratio, 4:1 or 8:1) and scaled with distance so that the bar size was of fixed retinal image size (lengths: 0.2, 0.4, 0.8, 1.6, and 3.2°). At 22.5 cm, the smallest bar (0.2°) was omitted, and at 360 cm, the largest bar (3.2°) was omitted because of physical limitations of the monitor and pixel size. Stimulus intensity was $160.96 \pm 3.4 \text{ cd} \cdot \text{m}^{-2}$. The bars were swept over the receptive field during fixation at the preferred orientation, direction, and color for the cell. Speed and length of excursion were scaled proportionally with distance to keep retinal speed and excursion constant.
11. Distance modulation and disparity modulation are distinct properties, therefore we use the terms "nearness" and "farness" to distinguish monotonic distance modulation from cells showing near and far binocular disparity-tuning as described by G. F. Poggio and B. Fischer [*J. Neurophysiol.* **40**, 1392 (1977)]. Classification of cells as monotonic (nearness or farness) is not completely certain, because a maximum or minimum could conceivably occur at an unsampled distance. A study of distance and disparity in V1 appears to show that for disparity-selective cells, farness cells are more common than nearness cells (6), but differences in stimuli, methods, and analysis preclude direct comparison with our results.
12. Tuning for absolute distance (at least for nearness) has been reported in the ventral intraparietal area of posterior parietal cortex [C. L. Colby, J. R. Duhamel, M. E. Goldberg, *J. Neurophysiol.* **69**, 902 (1993)] and in ventral premotor cortex [M. Gentilucci *et al.*, *Exp. Brain Res.* **50**, 464 (1983); L. Fogassi *et al.*, *J. Neurophysiol.* **76**, 141 (1996)]. However, a study that manipulated viewing distance and binocular disparity in V1 did not find the systematic shifts in preferred disparity with viewing distance that absolute distance tuning would predict (5, 6). Moreover, a cell tuned to an intermediate absolute distance would not show monotonic response with viewing distance, as the majority of cells here do. Nonmonotonic cells could be tuned for absolute distance, but these cells made up only 13% of our sample.

13. Cells were assigned to a visual cortical area based on receptive field position, size, and properties, and position relative to the lunule sulcus. Uncertainty about whether certain cells were in V1 or V2 led us to combine V1 and V2 for quantitative analysis.
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16. To ensure that ocular artifacts were not significant, a number of precautions were taken. Both monkeys were refracted by an optometrist using slit retinoscopy to establish that they were capable of accommodation over the range of distances used in the experiment (uncertainty <0.25 diopters). During the experiments, the monitored eye varied its position with distance consistent with the appropriate change of vergence. Pupil radius was measured with the eye tracker and did not vary with distance in either monkey ($2.33 \pm 0.01 \text{ mm}$; $1.73 \pm 0.02 \text{ mm}$). The monkeys were required to maintain fixation within a 0.25° square fixation window during the trial.
17. If viewing distance affected neural response, the measurements were repeated under either binocular or monocular restricted-field viewing conditions. Measurements were then repeated under the initial viewing conditions. The monkey viewed the stimuli through either monocular or binocular apertures (6.5° diameter). The remainder of the scene was masked such that only the monitor screen was visible to the monkey.
18. Because all receptive fields were in or close to the fovea (<2.5° eccentric in all cases), horizontal disparity of stimuli relative to the fixation point would be expected to be very close to zero at all distances. However, if the monkeys made vergence errors during fixation that varied systematically with distance, the responses of disparity-selective neurons could vary with viewing distance during binocular viewing.

In the absence of binocular disparity, this argument does not apply, and 15 of 33 neurons maintained distance modulation under monocular restricted-field viewing, demonstrating that distance modulation cannot be attributed to fixation-induced disparity. An independent line of evidence on this point is provided by the modulation of spontaneous activity observed in the absence of a stimulus in half the neurons studied (88/178, $P < 0.01$).

19. For this cell, manipulating the frame size had no effect (Fig. 2E; see figure legend for details), ruling out a center-surround artifact. Local image variations with viewing distance, such as slight changes in brightness or contrast, or changes in pixellation, are common to all the viewing conditions and cannot account for the difference between full-field and restricted-field responses. Nor can fixation disparity-induced horizontal disparity be responsible, because distance modulation is not dependent on binocular viewing. Therefore, local image variation with viewing distance cannot account for distance modulation.
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24. We thank A. Leonardo for contributions to the experiments; E. Dobbins, M. Lewicki, J. Mazer, and D. Rosenbluth for reviewing the manuscript; T. Annau, M. Lewicki, and J. Mazer for assistance with software tools; R. Desimone for providing data collection software; T. Joe for optometric assistance; and H. Weld and J. Baer for veterinary care. All methods of animal care conform to the guidelines of the Caltech Institutional Animal Care and Use Committee and the NIH.

19 February 1998; accepted 8 June 1998

“Inordinate Fondness” Explained: Why Are There So Many Beetles?

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The phylogeny of the Phytophaga, the largest and oldest radiation of herbivorous beetles, was reconstructed from 115 complete DNA sequences for the 18S nuclear ribosomal subunit and from 212 morphological characters. The results of these analyses were used to interpret the role of angiosperms in beetle diversification. Jurassic fossils represent basal lineages that are still associated with conifers and cycads. Repeated origins of angiosperm-feeding beetle lineages are associated with enhanced rates of beetle diversification, indicating a series of adaptive radiations. Collectively, these radiations represent nearly half of the species in the order Coleoptera and a similar proportion of herbivorous insect species.

When the British biologist J. B. S. Haldane was asked by a group of theologians what one could conclude as to the nature of the Creator from a study of His creation, Haldane is said to have answered, “An inordinate fondness for beetles” (1). Haldane’s remark reflects the

numerical domination of described species by the insect order Coleoptera (2), the diversity of which exceeds that of any other known animal or plant group. Because over half of all beetles are herbivorous and because the diversity of the remainder is comparable to that of other large, young, and nonherbivorous insect orders (3), a reconstruction of the phylogeny of beetle herbivory would contribute substantially to an understanding of

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