



**Modulation of Neural Stereoscopic Processing in Primate Area V1 by the Viewing Distance**

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  13. Male Sprague-Dawley rats (280 to 320 g) were implanted under halothane (2%) anesthesia with lumbar polyethylene (PE-10) IT catheters according to a modified method originally described by T. L. Yaksh and T. A. Rudy [*Physiol. Behav.* **17**, 1031 (1976)]. IT injection studies were carried out 6 to 8 days after surgery and all agents were injected with IT in a volume of 10  $\mu$ l followed by 10  $\mu$ l to flush the catheter. CNQX, ASA, and S(+)- and (R-)-ibuprofen were prepared in a 5% solution of 2-hydroxypropyl- $\beta$ -cyclodextrin (cDex) and all other drugs were dissolved in physiological saline. Given separately, IT injections of saline and cDex had no effect by themselves.
  14. AMPA injected intrathecally produced thermal hyperalgesia. This was unexpected compared to previous reports that AMPA had no hyperalgesic effect after spinal administration [L. M. Aanonsen, S. Lei, G. L. Wilcox, *Pain* **41**, 309 (1990); T. J. Coderre and R. Melzack, *Neurosci. Lett.* **131**, 71 (1991)]. This difference may be accounted for by species differences (mouse versus rat) and our use of larger doses.
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  25. The algescic index is the percentage change from base line averaged over each of the time points tested between 15 to 60 min after the NMDA, AMPA, or SP injection. These values were cumulated [that is, the sum of (postdrug latency - base line)/(base line) for measurements at 15, 30, 45, and 60 min] and normalized (divided by the number of measurements) so that values of increasing negativity indicate progressively greater hyperalgesia, values of increasing positivity indicate increasing hypoalgesia, and a value of zero indicates a normal pain response.
  26. The treatment data are presented as the ratio of the means for the drug-treated group relative to those of the saline-treated group, which we defined as 100% (error bars, SEM). The variation of the means was estimated according to the formulas provided in R. J. Tallarida and R. B. Murray [*Manual of Pharmacologic Calculation with Computer Programs* (Springer-Verlag, New York, ed. 2, 1987), pp. 137-139].
  27. Supported by DA02110 (T.L.Y.)

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## Modulation of Neural Stereoscopic Processing in Primate Area V1 by the Viewing Distance

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Accurate binocular depth perception requires information about both stereopsis (relative depth) and distance (absolute depth). It is unclear how these two types of information are integrated in the visual system. In alert, behaving monkeys the responsiveness of a large majority of neurons in the primary visual cortex (area V1) was modulated by the viewing distance. This phenomenon affected particularly disparity-related activity and background activity and was not dependent on the pattern of retinal stimulation. Therefore, extraretinal factors, probably related to ocular vergence or accommodation, or both, can affect processing early in the visual pathway. Such modulations could be useful for (i) judging true distance and (ii) scaling retinal disparity to give information about three-dimensional shape.

Stereopsis allows the visual system to determine the position of an object relative to the plane of fixation. It relies on the horizontal retinal disparity between the images of an object projected on the two retinas (1), a parameter encoded by neurons in the visual cortex (2). However, stereoscopic information alone is not sufficient for accurate binocular depth perception. It has to be combined with information about the viewing distance (derived from cues such as vergence or accommodation, or both). We have addressed the question of what happens to the response properties of individual neurons when the distance of fixation is changed. Three predictions can be made. First, retinal disparity sensitivity could remain the same, despite the distance of fixation (this would entail a purely stereoscopic mechanism). Second, the response properties of cells could be qualitatively modified: Altering the fixation distance could transform a neuron that was in the "far" category to the "near" category; such cells could be directly involved in encoding

absolute depth. Finally, the amplitude of the neural discharges could show modulations as a function of the distance of fixation. This could be an intermediate step in encoding absolute depth. Our results show that this last possibility is typical of what actually occurs in neurons of area V1. Changing the viewing distance also produced changes in the amount of the spontaneous firing rate (which is often associated with, but which occurs independently of, the modulation of visual responsiveness).

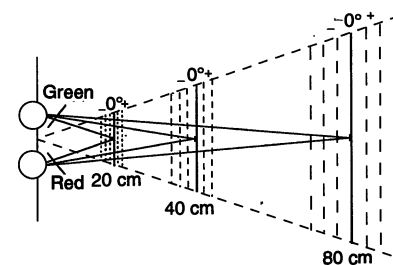
We have demonstrated these phenomena by recording the responses of individual neurons in cortical area V1 to the presentation of random dot stereogram (RDSs) (Fig. 1). Fifty visually responsive cells were tested at at least two viewing distances in monkeys trained to perform a fixation task (3). The visual responses of 41 cells (82%) were modulated by changes in the viewing distance. Changes in the spontaneous activity were also observed in 21 cells (42%).

Two examples of changes in visual responsiveness are shown in Fig. 2. Cell A was weakly visually responsive at 20 and 40 cm but at 80 cm showed a tuned excitatory response. However, at 40 cm there appeared to be a trend toward a mild retinal disparity (the same disparity for which the

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**Fig. 1.** Schematic representation of visual stimulation. At a given target fixation distance (20, 40, or 80 cm), static RDSs, generated through red-green filters, were presented on a color video monitor in the plane of fixation (0°, solid vertical lines) at two uncrossed horizontal disparities (+) and three crossed disparities (-), indicated by vertical dotted lines. The RDS pattern consisted of a 128 by 128 array of rectangular dots (density 10, 20, or 30%, according to the neuron's best response), which appeared as a large flat surface (width 18°, height 14°, of visual angle) floating in front of or behind a fixation point in the center of the screen. We changed the distance of fixation by physically moving the monitor on rails in a tunnel to fixed distances. The same pattern was used at each fixation distance, but, to keep the angular size of the stimulus constant, the physical size of the image was doubled each time the fixation distance was increased by a factor of 2, which resulted in a fixed angular dot size of 9 by 7 min of arc. The amount of luminance through colored filters was 1 candela per meter squared at the three distances of fixation.



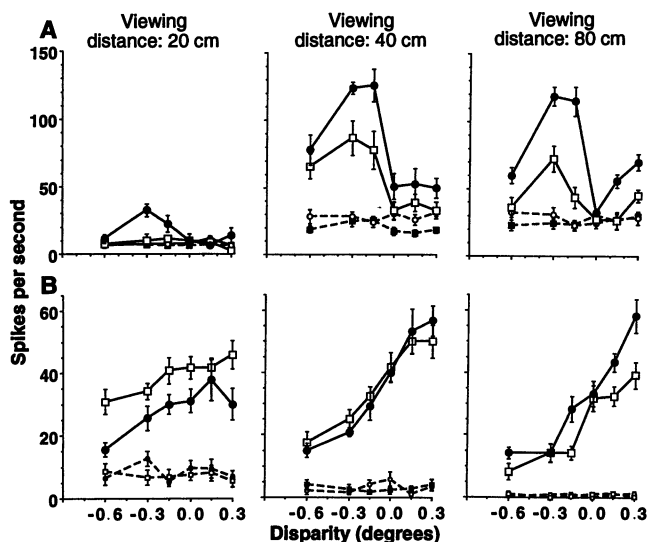
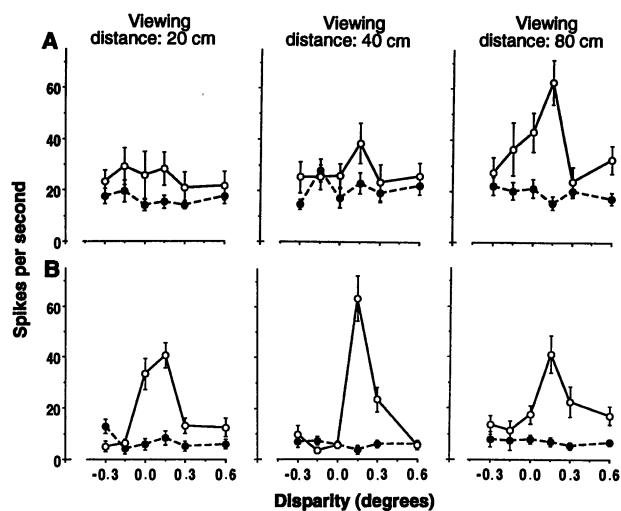
cell showed a significant visual response at 80 cm). Cell B showed a broadly tuned excitatory response to stimuli, with disparities close to zero at a distance of 20 cm. This cell was sharply tuned at 40 cm and much less disparity-selective at 80 cm. Because most neurons showed such modulations of their responsiveness (similar percentages in both monkeys), disparity selectivity emerged [22 out of 41 visually modulated cells (53.5%)] or was significantly sharper [11 out of 41 cells (27%)] at a certain distance of fixation (4). Disparity tunings were similar in peaks, although some features of the tuning curves may have changed. Non-disparity-sensitive cells—at least those considered as such on a viewing distance of up to 80 cm—also showed modulations in discharge magnitude after changes in the viewing distance [7 out of 13 nonselective cells (17% of the visually modulated cells)]. Qualitative changes in the response type occurred in only one neuron, a cell that was tuned excitatory with the fixation distance set at 20 cm and tuned inhibitory at 40 and 80 cm.

The second effect of changing the viewing distance concerned the amount of spontaneous neural activity that was produced (Fig. 3). In most cases, it was usually higher when the animal was fixating at shorter distances [15 out of 21 cells (71.5%)]. This could be related to the increased muscular effort required to fixate stimuli closer to the animal.

The modulation of disparity sensitivity that occurred (41 cells) could have resulted from changes in the level of excitability, as suggested by the example in Fig. 3A and as observed in eight cases. However, the cell in Fig. 3B was much more disparity-selective at a far viewing distance (40 or 80 cm) than at a near viewing distance (20 cm), despite having a higher level of spontaneous firing at 20 cm. Similar examples were seen in 12 cases, where the two main effects on visual responsiveness and on spontaneous activity were present but not related to each other. Moreover, changes in visual responsiveness without changes in background activity were present in 21 cells, which again indicates that both phenomena occurred independently of each other.

Although every effort was made to maintain the pattern on the retina constant despite the changes in viewing distance, controls were performed to ensure that the modulation of disparity selectivity could not have resulted from small artifactual shifts in dot position on the retina and thus in the receptive fields. First, blocks of trials were interleaved at different distances, but the pattern of responses at a particular distance was unchanged. Second, disparity sensitivity was tested at the three distances

**Fig. 2.** Effects of the viewing distance on disparity coding. Retinal disparity tuning curves (solid lines) of two neurons [(A) top row, and (B) bottom row] were obtained at three target fixation distances (20, 40, and 80 cm). Dotted lines indicate the spontaneous activity measured for a period of 400 ms preceding the RDS presentation of 300-ms duration. Vertical bars indicate standard errors (12 to 15 runs). The first neuron in (A) is only disparity-sensitive at one distance (80 cm). The second neuron in (B) shows a sharpening of the disparity tuning curve and a higher response when the RDSs were presented at a viewing distance of 40 cm. These two examples are representative of the modulation of disparity sensitivity in cortical area V1 by the target fixation distance.



**Fig. 3.** Two examples of the effects of viewing distance on both visual responsiveness and spontaneous activity in two visual stimulus conditions. The two cells (A and B) were tested at three distances (20, 40, and 80 cm) with the use of two different dot densities, 20% (filled symbols) and 10% (open symbols). Visual responsiveness (solid lines) and the corresponding spontaneous activities (dotted lines) are shown.

for a given dot pattern (for example, 20% of dot density) and repeated for another pattern (for example, 10% of dot density). Two examples of such a control are shown in Fig. 3. Cell A was poorly visually responsive to both patterns at 20 cm but was clearly a near-type neuron at 40 and 80 cm, no matter which dot pattern was present (5). Cell B was very poorly disparity-selective at 20 cm but showed similar disparity selectivity at far distances (40 and 80 cm) for both patterns. Tests of all nine neurons demonstrated that the effects of fixation distance and dot pattern occurred independently of each other. Therefore, changes in the neural activity of area V1 produced by

changes in the viewing distance were not related to the pattern of retinal stimulations.

In conclusion, because changes in the response category rarely took place (1 out of 50 cells), it is unlikely that neurons whose activity is modulated by fixation distance could directly encode absolute depth. Rather, such cells could constitute an intermediate step in the computation of true depth, as suggested by neural-network models (6).

Our findings show that the visual responsiveness of neurons in cortical area V1 is affected by the viewing distance. The signals involved in such modulations are

presumably extraretinal in origin. However, it is still unclear whether these signals are derived from cues such as vergence angle or accommodation, or both, although psychophysical data suggest an important role for vergence (7). In both cases, the relevant information could be obtained from either corollary discharges or proprioceptive feedback; indeed, this second extraretinal signal contributes to the localization of objects in space (8).

The most surprising aspect of our study is the finding that the responses of disparity-selective neurons can be modulated by extraretinal factors, even at the level of the primary visual cortex. One might expect to find such units in higher order cortical areas, such as the parietal cortex, where neurons have been shown to integrate signals from the angle of gaze (9). However, our findings imply that stereoscopic processing in area V1 might no longer be considered only in relation to the pattern of light falling on the retina but also as a site in which a range of retinal and extraretinal signals involved in three-dimensional space perception are integrated.

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2. For a review, see G. F. Poggio and T. Poggio [*Annu. Rev. Neurosci.* **7**, 379 (1984)]. Disparity-sensitive cells were first discovered in the primary visual cortex of the anesthetized paralyzed cat. These cells respond to stimulation of disparate points on the two retinas, a stimulus condition that normally occurs only if an object is in front of or behind the fixation plane [H. Barlow, C. Blakemore, J. D. Pettigrew, *J. Physiol. (London)* **193**, 327 (1967); T. Nikara, P. O. Bishop, J. D. Pettigrew, *Exp. Brain Res.* **6**, 353 (1968); D. E. Joshua and P. O. Bishop, *ibid.* **10**, 389 (1970)]. Under normal conditions of binocular vision in behaving monkeys, distinct categories of cells exist in area V1: cells responding preferentially to stimuli in front of the fixation plane ("near" cells), behind the fixation plane ("far" cells), or around the fixation plane ("tuned" cells) [G. F. Poggio and B. Fischer, *J. Neurophysiol.* **40**, 1392 (1977)]. More recently, evidence for the existence of disparity-sensitive neurons was provided with the use of RDSs [G. F. Poggio, B. C. Motter, S. Squatrito, Y. Trotter, *Vision Res.* **25**, 397 (1985); G. F. Poggio, F. Gonzalez, F. Krause, *J. Neurosci.* **8**, 4531 (1988)].
3. We ensured fixation during the presentation of the stimuli by placing the monkeys (two *Macaca mulatta*) in darkness, with their heads fixed, and training them to fixate a small bright target that appeared at the center of the video monitor along the straight horizontal optical axis. The monkeys had to detect a slight dimming of the target at random times (between 500 ms and 4 s) after the start of fixation. For correct detections, the monkeys were rewarded with a drop of water. The training was performed at each of the three distances. The stability of the fixation of each eye was measured independently of the other and verified with the use of infrared oculometers. An examination of the refraction of the eyes (skiascopy) revealed no optical abnormality. Cortical recordings were made with insulated tungsten microelectrodes in area V1, in the representation of the central part of the visual field. During the fixation period, an RDS with one of the six disparity values was flashed on for a duration of 300 ms. At each fixation distance and for all disparity values, the RDSs were presented 9 to 15 times, randomly interleaved.
4. Of the 113 neurons tested with the viewing distance set at 40 cm, about half [59 out of 113 (52%)] were disparity-sensitive, of which 22 were in the tuned-zero category and the rest were either near or far neurons. These proportions are

in agreement with those described in studies with RDSs at a fixed target fixation distance, usually 1 m (2). However, because most neurons showed a modulation of their responsiveness, the percentage of disparity-selective units was actually higher when the neurons were tested at more than one viewing distance [37 out of 50 cells (74%)]. This proportion is also higher than that previously reported in studies that tested only one fixed fixation distance.

5. We tested cortical neurons by using RDSs of different dot densities and frequently found that cells were driven more efficiently by patterns of a particular dot density, usually between 10 and 30%. The pattern that elicited the optimal neural response was chosen to show the optimal effect of viewing distance. In the example of Fig. 3A, the cell was more sensitive to a dot density of 20% than to one of 10%, which explains the difference in the visual responsiveness at viewing distances of 40 and 80 cm but not the weak responses to both patterns at 20 cm.
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## TECHNICAL COMMENTS

### Siderophile Elements and the Earth's Formation

Siderophile (metal-seeking) element concentrations in the earth's upper mantle are indicators of how the earth accreted and differentiated. A long-standing problem in geology is that, although the earth has a large metallic core, mantle siderophile elements appear to be in much higher concentrations than can be explained by simple metal-silicate equilibrium (1). Murthy (2) suggests that the abundances of siderophile elements in the earth's mantle can be explained by equilibration at higher temperatures than those achieved in most laboratory experiments. Murthy (2) finds that metal/silicate partition coefficients ( $D$ ), measured in the laboratory at temperatures of 1200° to 1600°C, can account for high abundances of mantle siderophile elements if these coefficients are extrapolated to higher temper-

atures, 3000 to 4000 K. This method of extrapolation allows one to predict mantle siderophile element abundances that agree reasonably well with observed abundances, which argues for an extensive magma ocean early in the history of the earth. However, we believe that the extrapolation technique used by Murthy is incorrect.

First, Murthy's method of extrapolation (2) is made without reference to a governing chemical reaction. Such reference is important when dealing with metal/silicate partitioning because of the change in valence that accompanies the transfer of the siderophile element from metal to silicate (Fig. 1). Murthy's extrapolation equates the chemical potential of the siderophile element in the metal to that in the silicate with no account taken of

an oxidizing or reducing agent. This would require that the partitioning siderophile element does not undergo a change in valence during metal/silicate partitioning.

Second, Murthy's method implicitly assumes that the Gibbs free energy change for the partitioning reaction,  $\Delta G^0$ , is constant, independent of pressure and temperature. This assumption, however, is generally incorrect. One could argue that pressure effects may fortuitously cancel those of temperature and allow  $\Delta G^0$  to remain constant. However, the proper calculation cannot be performed because speciations and partial molar volumes of the relevant siderophile elements in silicate systems are unknown.

Third, Murthy's method does not seem to agree with most experimental evidence. For the great majority of siderophile elements, higher temperatures promote siderophile behavior and the values of  $D$  should increase, not decrease, as Murthy calculates. Nickel and, possibly, cobalt are exceptions to this rule, presumably because their stoichiometry