Pergamon

0042-6989(94)00133-2

*Vision Res.* Vol. 35, No. 3, pp. 345–354, 1995

0042-6989/95 $7.00 + 0.00

# Stereopsis and Binocularity in the Squirrel Monkey

MARGARET S. LIVINGSTONE,*† SARITA NORI,* DAVID C. FREEMAN,* DAVID H. HUBEL*

*Received 30 March 1994; in revised form 13 June 1994*

**The squirrel monkey lacks anatomically demonstrable ocular dominance columns, and physiologically it has an ocular dominance distribution in V1 that is very different from that of macaques, with far fewer cells that strongly favor one eye over the other. We tested an alert squirrel monkey for physiological responses to stereoscopic stimuli by measuring evoked potentials in response to cytclopean patterns generated in dynamic random-dot stereograms. The monkey showed evoked responses both to changes in disparity and to shifts between correlation and uncorrelation between the two eyes. This result strongly suggests that the squirrel monkey can detect stereoscopic depth, which in turn casts some doubt on the assumption that ocular dominance columns bear an important relation to stereopsis.**

Stereopsis Ocular dominance columns Binocularity

## INTRODUCTION

Discovered almost 30 years ago, the function of ocular dominance columns (Hubel & Wiesel, 1965), and their relevance, if any, to stereopsis are still enigmas. It is tempting to think the two are related, because it would make sense that the regular shifts in eye inputs across a retinotopic map should be of some functional significance in generating stereoscopic interactions. Manipulations that disrupt ocular dominance columns also disrupt stereopsis (for references see Blakemore & Vital-Durand, 1981; Movshon & Van Sluyters, 1981; Boothe, Dobson & Teller, 1985), and during development stereopsis and ocular dominance column segregation appear and mature with similar time–courses (Atkinson & Braddick, 1976; Held, Birch & Gwiazda, 1980; Timney, 1981). Furthermore, several studies have suggested a difference in the disparity-tuning properties of cells with different ocular dominance: "near" and "far" cells mostly show strong eye preferences, whereas tuned excitatory cells generally have approximately equal inputs from the two eyes (Poggio & Fischer, 1977; Fischer & Krüger, 1979; Ferster, 1981; LeVay & Voigt, 1988; Poggio, Gonzales & Krause, 1988). This means that near and far cells should be centred on ocular dominance columns, and tuned excitatory cells should be close to their borders. So far such a relationship has not been demonstrated directly.

For squirrel monkeys the available anatomical methods have failed to reveal ocular dominance columns in V1 (Hubel, Wiesel & LeVay, 1975; Tigges, Tigges & Perachio, 1977; Hendrickson, Wilson & Ogren, 1978; Hendrickson & Wilson, 1979; Humphrey & Hendrickson, 1983), though hints of gentle swings in ocular dominance have been seen in long oblique microelectrode penetrations through V1 (Hubel & Wiesel, 1978). It would be surprising if these arboreal animals entirely lacked stereoscopic depth perception, though we know of no behavioral tests to indicate that they do have stereopsis. The narrow separation of their eyes must be a disadvantage for stereopsis, and perhaps for this reason it has been suggested that head-cocking behavior seen in small New World monkeys may be used instead of, or to supplement, depth information from stereopsis (Menzel, 1980).

Physiological studies of disparity in single cells of squirrel monkeys also do not clearly indicate whether or not squirrel monkeys have stereopsis. The thick stripes of V2, which in macaques are rich in disparity-tuned cells, are just as prominent in squirrel monkeys as in macaques, and in fact are more regular and better defined. We have recorded from many cells in V1 and V2 that fail to respond to stimulation of separate eyes and which show sharp disparity tuning; as in the macaque, these cells are most commonly found in layer 4B of V1 and in the thick stripes of V2. These cells would seem likely to play some part in stereopsis, but their tuning peaks have been at or very near zero disparity; cells tuned to near and far disparities, which are found in macaque monkey cortex and almost certainly subserve stereopsis, seem to be rare in squirrel monkeys (Hubel & Livingstone, 1987).

In light of these somewhat conflicting observations,

*Department of Neurobiology, 220 Longwood Avenue, Boston, MA 02115, U.S.A. [*Email* livings@warren.med.harvard.edu].
†To whom all correspondence should be addressed.

we wanted to test squirrel monkeys for stereopsis using dynamic random-dot stereograms (Julesz, 1971; Julesz, Breitmeyer & Kropfl, 1976a; Julesz, Petrig & Buttner, 1976b; Lehmann & Julesz, 1978). Difficulties in training these animals to fixate or indeed to take any sustained interest in such stimuli made us postpone attempts at a behavioral test, and we decided to look first for cortical evoked potentials in response to stereoscopic cues. Because evoked responses to correlation/uncorrelation shifts have been implicated as bearing on stereopsis (Tyler & Julesz, 1976; Julesz, Kropfl & Petrig, 1980; Miezin, Myerson, Julesz & Allman, 1981; Poggio, Motter, Squatritro & Trotter, 1985; Poggio *et al.*, 1988) we also looked for evoked potentials in response to shifts between correlation and uncorrelation. For comparison we recorded evoked responses to the same stimuli in two human subjects.

We used the technique of generating dynamic random-dot patterns to eliminate any possible monocular cues. In this technique, a pair of random-noise patterns is generated and then replaced by new random patterns at a rate of 14 Hz. At a very different rate (1 Hz) the relationship between the patterns in the two eyes is shifted, say from correlated to uncorrelated or from one disparity to another. There are thus no 1 Hz signals visible and none to the two eyes together to either eye alone unless the observer has the capacity to make rapid point-to-point comparisons between the two eyes.

While we consider as necessary for true stereopsis the ability to distinguish different horizontal disparities, including the sign of the disparity, one could imagine that other forms of binocular interaction might give differential responses to depth cues. So, for example, in the random-dot stereogram of Fig. 1(a) the background is at zero disparity (relative to the frames of the squares) and the central square is at +1 (pixel) disparity. True stereopsis should be able to distinguish this +1 disparity from −1 disparity [Fig. 1(b)] and from zero disparity [Fig. 1(c)]. An animal possessing only cells showing simple binocular summation but lacking a population of cells tuned to different disparities might still be able to distinguish non-zero disparities from zero disparity, since responses to non-corresponding contrasts in the two eyes should be different from responses to correlated regions (i.e. a binocular cell might well give an intermediate response when one eye sees a black check and the other eye sees a white check). With such binocular neurons the animal should be able to distinguish non-zero from zero disparity [or correlation from non-correlation—Fig. 1(d)] even if it cannot tell the disparity of the stimulus, or distinguish between different non-zero disparities, or even between non-zero disparities and non-correlation.

Besides this hypothetical mechanism, macaque monkeys possess, in V1, V2 and V3, cells that are exquisitely sensitive to correlation as opposed to non-correlation (Poggio *et al.*, 1985, 1988) though only about half of them are also disparity tuned. In some preliminary recordings in V1 of squirrel monkeys we have seen clear examples of cells responsive to correlation/uncorrelation shifts. These cells, too, should be able to distinguish zero from non-zero disparities without conveying any information on the sign or degree of disparity.

We therefore recorded evoked potentials in response to (1) shifts in dynamic random-dot stereograms from correlated to uncorrelated patterns in the two eyes, (2) shifts of a central square between zero disparity and various non-zero disparities, and (3) shifts of a central square between equal but opposite sign disparities. Since we see many cells in squirrel monkey V2 that respond to binocular but not to monocular stimulation (Hubel & Livingstone, 1987), we would be surprised not to find, at the very least, responses to shifts between uncorrelated and correlated patterns, but the squirrel monkey has been full of surprises for many investigators.

## METHODS

The experiments were carried out in one male squirrel monkey (*Saimiri sciureus*) and, for comparison, two human subjects, one male, one female, both of whom are authors.

The squirrel monkey was isometropic in both eyes. Several weeks before testing, under halothane anesthesia and using sterile techniques, we installed a head bolt, one 6 mm diameter gold-plated EEG electrode between the skull and the dura, over V1 on the occiput (just above the inion, and just to the right of the midline), and a scleral search coil in one eye. A stainless steel screw fixed in the skull at the top of the head, just to the right of the midline, was used as a reference electrode. The monkey was trained, using marshmallows and Tang™ as a reward, to sit quietly in a primate chair with his head fixed, for 1 hr periods. Evoked potentials were recorded from the implanted electrodes; the signals were amplified 100,000 times and filtered with a low frequency cut-off of 1 Hz and a high frequency cut-off of 100 Hz.

The human subjects are both myopic, with corrected-to-normal acuity and excellent stereopsis (Livingstone & Hubel, 1994). Evoked potentials were recorded using 10 mm diameter gold-plated EEG electrodes attached to the scalp with conductive paste. The recording electrode was placed at OZ (90% of the distance from nasion to inion) and the reference electrode on the left earlobe. A ground electrode was placed at CZ [50% of the distance from nasion to inion (Jasper, 1958)]. The signals were amplified 20,000 times and filtered with a low frequency cut-off of 1 Hz and a high frequency cut-off of 100 Hz.

Stimuli were generated on a Silicon Graphics Indigo XZ4000, a fast color workstation capable of stereo displays, refreshed at 120 Hz, together with Liquid Crystal Display goggles in which the left and right lenses alternately darken at 60 Hz. To generate random-dot stereograms, first a large table of random black and white values was created using the Iris system random number generator "drand48", then each display

used another random number to choose where in the table to start gathering values for the dots. The liquid crystal lenses were in goggles worn by the human subjects or were mounted on the primate chair 1 cm in front of the monkey's eyes. The monitor was positioned 0.5 m in front of the subject, and the random-dot stimulus covered an area of the visual field 30 × 30 deg. The random-dot pattern changed at a rate of 14 Hz, unless otherwise specified. This flicker of the random dots gave a strong signal on all the evoked potential records, but it was filtered out using a simple rolling average to eliminate specifically the response to the flicker. A rolling average of size $n$, in this case 71 msec, is created by replacing each entry in a list by the average of the entry and its $n - 1$ nearest neighbors. Each entry was thus replaced by the average of itself and 35 msec bins on either side. For some runs the background remained at zero disparity, and a central 18 × 18 deg

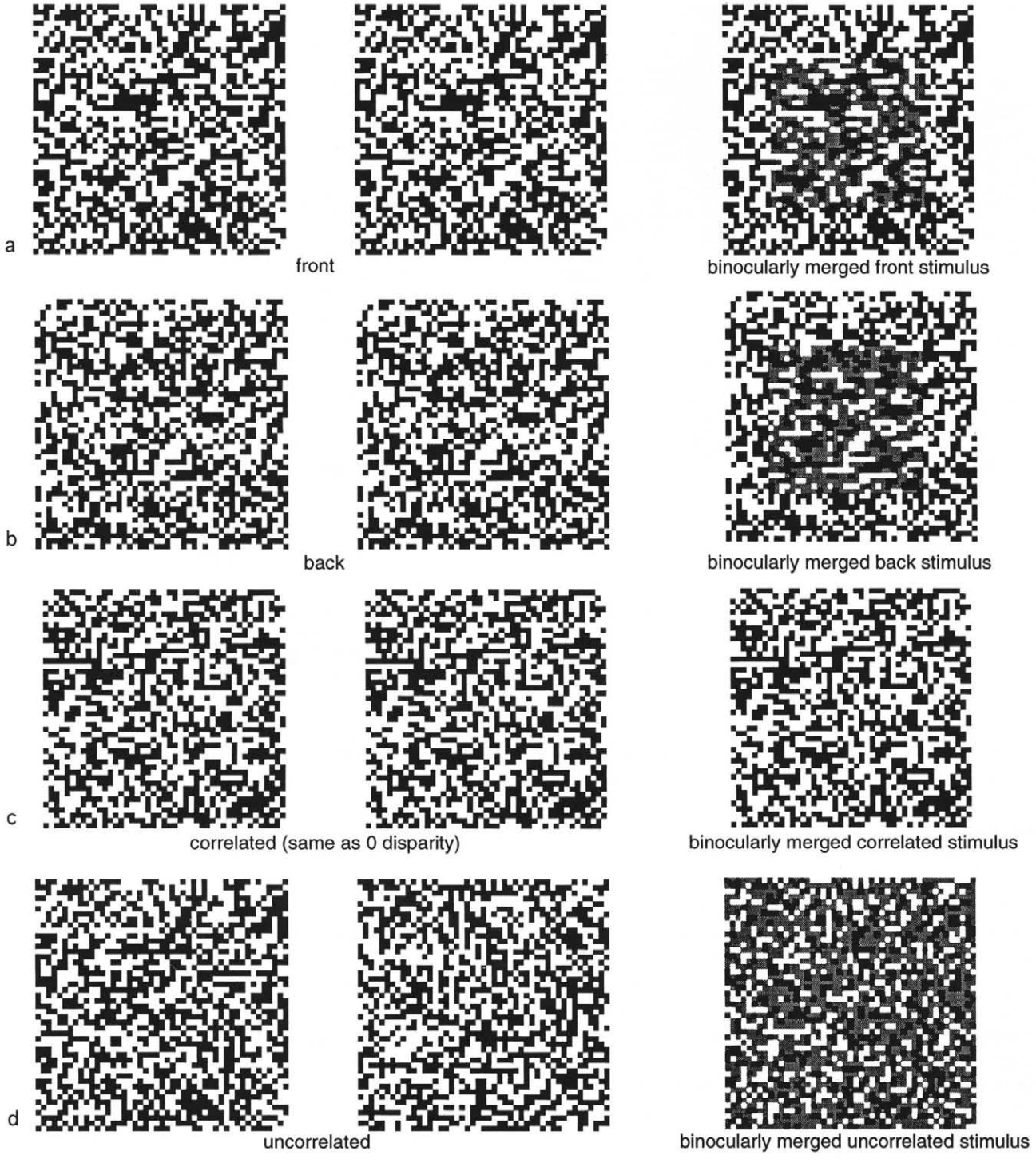


FIGURE 1. Left: single frames from dynamic random-dot stereograms, presented for crossed fusion. The single frames to the right show what we would predict the same stimuli would look like to a mechanism that additively combined the inputs from the two eyes.

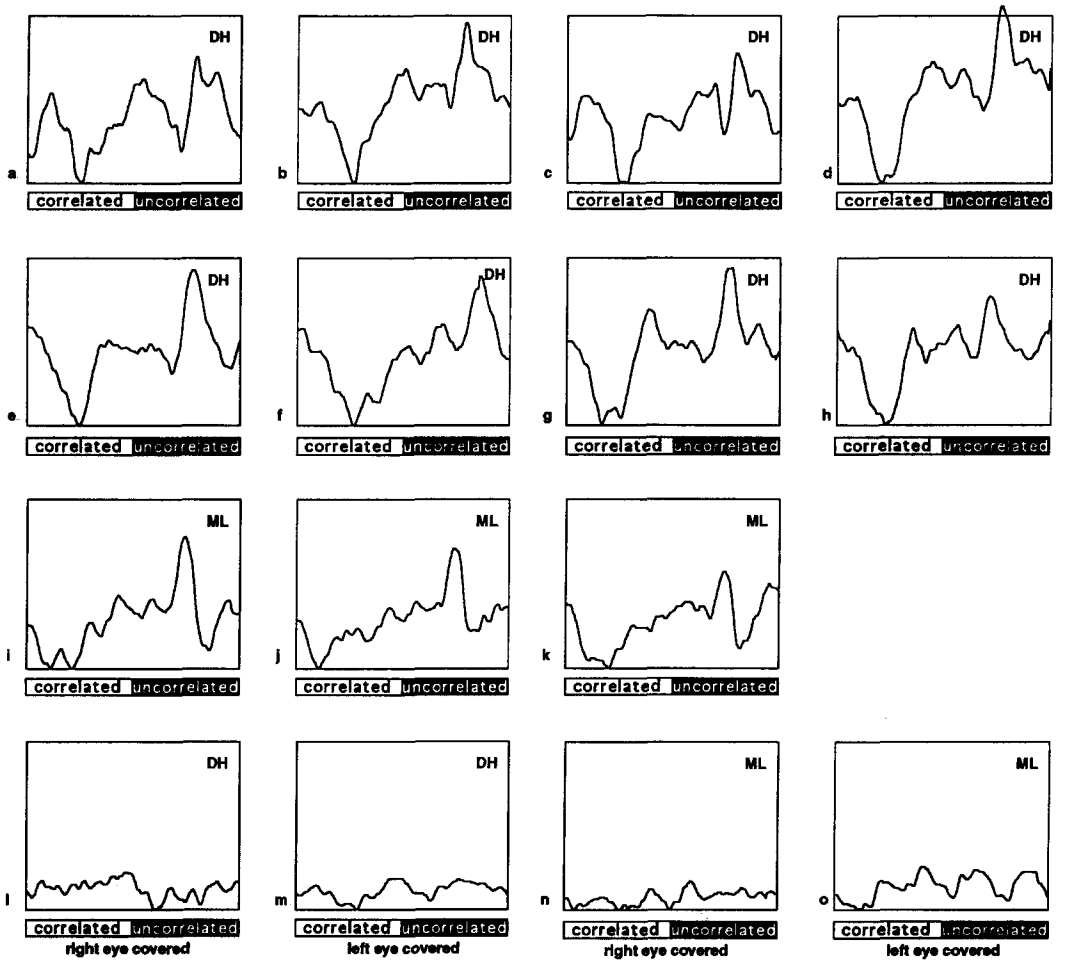


FIGURE 2. Responses of two human subjects to shifts between correlation and uncorrelation. Each panel represents the average of 200 1-sec stimulus intervals; duplicate stimuli were run on different days. The first three records for each subject (a)–(c) and (i)–(k) show responses to the exact same stimulus (45 × 45 checks, alternating between correlated and uncorrelated at 1 Hz, flicker rate 14 Hz). Records (d)–(h) show responses for subject DH to shifts between correlated and uncorrelated patterns with different size checks (total display size was always 30 × 30 deg) or different dynamic flicker rates: (d) 90 × 90 checks, flicker rate 20 Hz; (e, f, g) 90 × 90 checks, flicker rate 14 Hz; (h) 90 × 90 checks, flicker rate 26 Hz. Records (l) and (m), for subject DH, and records (n) and (o), for subject ML, are controls, showing responses to the exact same stimulus as the first three responses for each subject, but with one eye covered. Vertical scale = 4 $\mu$V; horizontal scale = 1 sec.

square alternated between positive and negative or zero disparities at a frequency of 1 Hz [Fig. 1(a, b, c)]. For others the entire random-dot display alternated between images that were correlated in the two eyes or uncorrelated [Fig. 1 (c, d)].

Luminances were measured with a Pritchard spot photometer. During testing the room was lit with dim overhead tungsten lights, so that the background reflectance of the monitor, with all phosphors set to zero, was $3 \times 10^{-3}$ cd/m$^2$. The stimuli were dynamic checked patterns of black (background) and white squares, the luminance of the white squares being 3 cd/m$^2$. The stereo goggles attenuated all luminances by 0.5 log units during the open phase and 1.8 log units during the closed phase, with equal time in each phase, alternating in counterphase for the two eyes at 60 Hz; the overall average attenuation to each eye was thus 0.8 log units. For one of our controls we inactivated the goggles, which left both lenses open continuously. To make the average luminance attenuation the same as when the goggles were active, we put 0.3 log unit neutral density filters over the goggles during this control.

For the human subjects several stimulus conditions were tested at a single sitting; for each stimulus condition 200 1-sec response intervals were averaged. For the monkey, during each daily session, 2000 1-sec responses were recorded and averaged for a single stimulus condition, with marshmallow and Tang$^{tm}$ rewards after each 400 sweeps. The human subjects tried to maintain fixation at or near the center of the display. The monkey's head was fixed and no attempt was made to control eye movements, but since the display covered 30 deg of visual field, it is likely that most of the time the monkey was looking at it.

## RESULTS

### *Correlation/uncorrelation*

Figure 2 shows responses of the two human subjects to a dynamic random-dot pattern that alternated, at

1 Hz, between being identical for the two eyes (correlated) and being unrelated (uncorrelated) [cf. Fig. 1 (c, d)]. Each panel in Fig. 2 is the average of 200 responses. The first three rows show responses of the two subjects to correlation/uncorrelation shifts. In subject DH we tried varying the flicker rate and check size and found that the shape of the response did not change. The last row shows control records of responses to the same stimulus, but with one eye covered.

The binocularly viewed stimulus alternated in appearance between a clear, flat plane of flickering checks, for the correlated pattern, and disturbingly unclear, somewhat three-dimensional cloud of flickering checks, for the uncorrelated pattern. In contrast to the control, both subjects showed strong and consistent responses to the correlation/uncorrelation shifts; the responses were generally similar in shape, even for different sized checks or flicker rates.

Figure 3 shows the squirrel monkey's responses to the same stimulus used for the first three records for each human subject. Record (a) represents the average of 8000 responses, 2000 of which were obtained during each daily 1-h recording session. These daily responses are shown in (c), to give some idea of their consistency. In (a) and (c), both eyes were open. The control is shown in (b) and (d), in which one eye was covered. [Again (b) is the average of 8000 responses and (d) the averages of 2000 responses obtained on different days.] By comparison to the controls, it can be seen that the monkey shows large responses to the correlation/uncorrelation shifts. The waveform of the monkey's response is roughly inverted compared to the human subjects; this was a general finding for other stimulus conditions, including standard checkerboard contrast-reversal stimuli. We suspect this polarity inversion is related to differences in the position of the recording electrode with respect to the current generator of the response.

*Disparity*

To ask if the squirrel monkey possesses stereopsis, and not just the ability to distinguish between correlated and uncorrelated patterns, we looked at evoked responses to shifts between equal and opposite disparities. Figure 4 shows the responses of our two human subjects to shifts between positive and negative disparities. Both human subjects showed responses to the depth shifts that were clearly different from their control responses. Figure 5(a, c) shows the monkey's responses to the same stimulus; he also gave responses that were different from

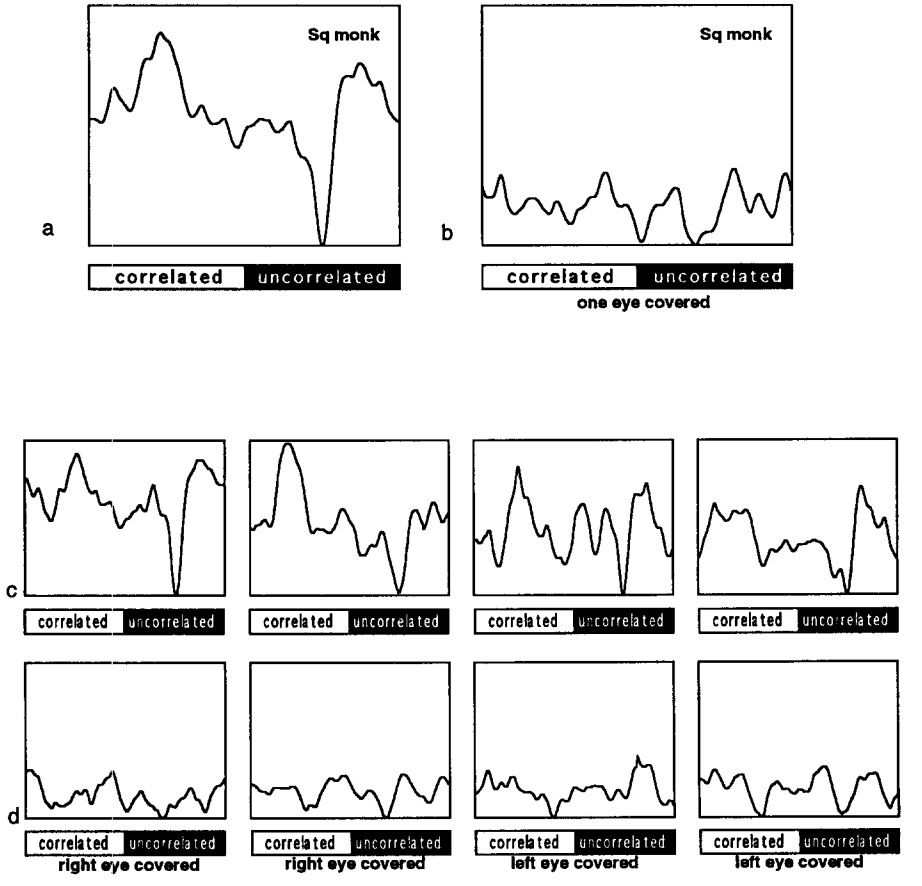


FIGURE 3. Responses of the squirrel monkey to the same stimulus used for records (a)–(c) and (k)–(m) in Fig. 2 (45 × 45 checks, alternating between correlated and uncorrelated at 1 Hz, flicker rate 14 Hz). (a) The average of 8000 respones to correlation/uncorrelation shifts. (b) The average of 8000 responses to the same stimulus with one eye covered. Rows (c) and (d) show the average of the 2000 responses from the daily sessions that were averaged to obtain records (a) and (b). Vertical scale = 5 $\mu$V for (a) and (b) and 7.5 $\mu$V for (c) and (d); horizontal scale = 1 sec.

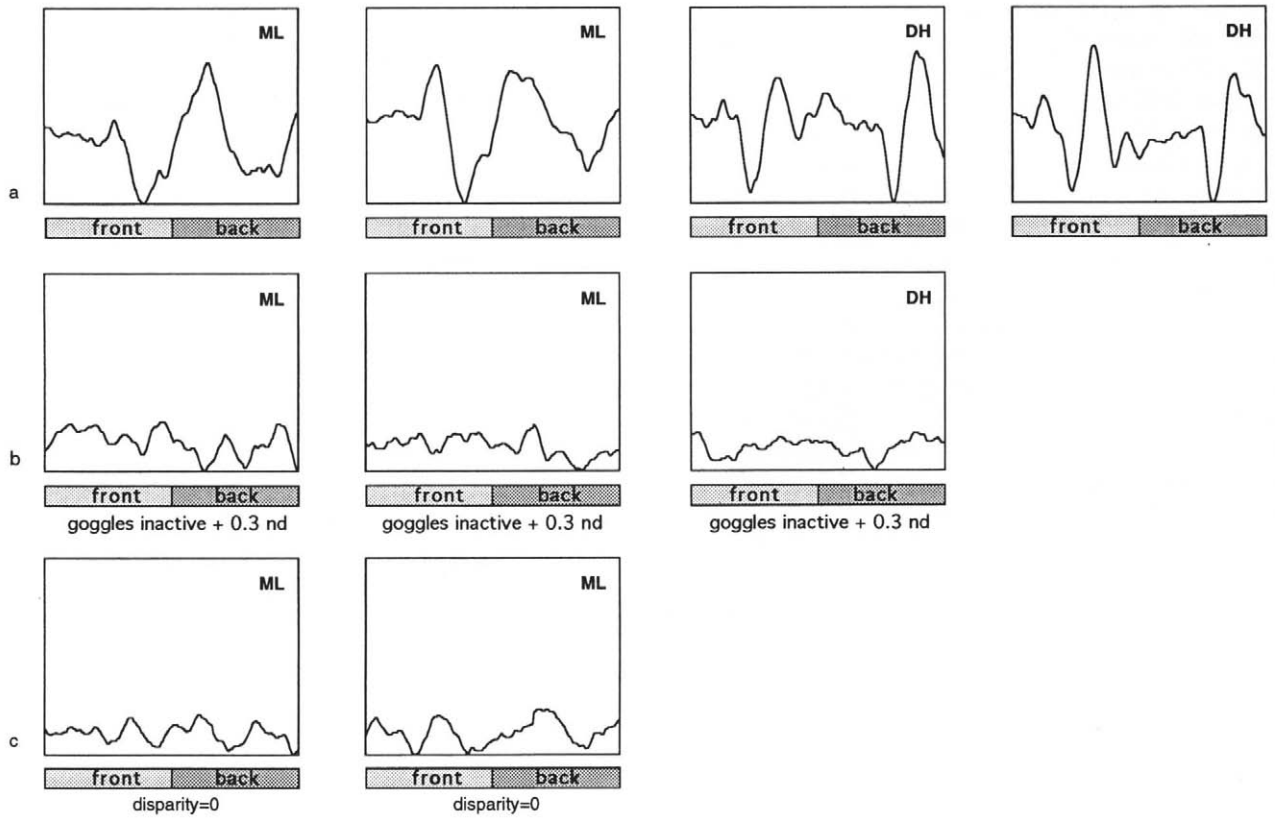


FIGURE 4. Responses of the two human subjects to disparity shifts between ±40 min arc disparity (front vs back). Each panel represents the average of 200 1-sec stimulus intervals; duplicate stimuli were run on different days. The controls are shown in (b) and (c): in (b) the stimulus was the same as in (a) (±40 min arc disparity), but the goggles were inactive, with a 0.3 n.d. filter over them; in (c) the disparity was set to 0, so there was no central square defined by disparity and no disparity shift. The stereogram was 45 × 45 checks, alternating between the disparities indicated at 1 Hz; random-dots flickering at 14 Hz. Vertical scale = 4 $\mu$V; horizontal scale = 1 sec.

the control and reproducible. We had hoped that clear responses to shifts from one non-zero disparity to another, such as front to back, would be evidence for true stereopsis, as opposed to some kind of correlation/uncorrelation response, since any non-zero disparity is just as uncorrelated as any other. The difficulty with this line of reasoning, however, is that we could not be sure that the animal was at all times fixating on the plane of the monitor. If he were fixating consistently on one of the two disparity planes, or fixating at random on one or the other, our supposedly pure stereoscopic stimulus would then be contaminated by shifts between correlation and uncorrelation. Since the responses of the two human subjects to front/back shifts were different from each other, and both were different from the monkey's, we cannot use the shape of the responses to determine that the monkey has the same kind of stereopsis as the humans. In principle, several possibilities remained for resolving this ambiguity: the monkey's responses to positive and negative disparity shifts might differ in shape; his response amplitudes might be graded with degree of disparity; and his responses to shifts in disparity might differ in shape from his responses to correlation/uncorrelation shifts. It turned out that only the second and third of these criteria were useful, as shown below; the first criterion was not, because shifts between zero and positive and between zero and negative disparities both evoked clear responses, which were not, however, clearly different from each other (not shown).

Figure 5(a, c) shows the monkey's responses to shifts between plus and minus 40 min arc disparity and Fig. 5(e, f) to shifts between plus and minus 20 min arc disparity. Two controls are shown: Fig. 5(g), plus vs minus 40 min arc disparity with goggles inactive and Fig. 5(h), "front" vs "back" but at 0 disparity. Each of the large records represents the average of 6000 responses, 2000 responses obtained during each daily 1 hr recording session. The two sets of smaller graphs [Fig. 5(b, d)] show the three sets of 2000 averaged responses that were averaged together to give the records Fig. 5(a, c). Compared to the controls both disparity shifts resulted in small, but reproducible, responses, and the responses to the 80 min arc disparity shifts were larger than the responses to the 40 min arc shifts.

In humans it has been found that for disparities close to perceptual threshold the size of the evoked response increases with disparity (Norcia, Sutter & Tyler, 1985). We repeated these tests in humans for larger disparities. Both the human and the monkey showed larger evoked potentials with increasing disparity. A comparison of response vs disparity for the monkey and one of the humans is shown in Fig. 6. While it hardly seems surprising to find an increase in responses with

increasing disparity close to threshold, we find it puzzling that there should be a continuing increase in response well beyond threshold, particularly since at early stages in the visual system most cells, including disparity-tuned cells, respond best to zero disparity (Poggio *et al.*, 1985, 1988; Hubel & Livingstone, 1987). Whatever the explanation, such a gradedness suggests that the squirrel monkey possesses true stereopsis, and it seems quite incompatible with the responses being due to correlation vs uncorrelation, since small disparities are just as uncorrelated as large disparities.

In further support of the idea that the monkey has true stereopsis and not just correlation/uncorrelation responses, the responses to shifts between back and front disparities were consistently different in shape from his responses to correlation/uncorrelation shifts. This rules out the possibility that the monkey was preferentially fixating on one disparity, either the front or the back plane, and usually giving the uncorrelation response to the other. The shape of the front vs back response also rules out the possibility that the monkey was randomly fixating on either the front or the back plane, and giving an uncorrelation response to the other plane, since then the response should be the same for front-to-back and back-to-front, and it is not [i.e. in Fig. 5 the first half of (a) and (c) is not identical to the second half]. The human subject DH, however, who can distinguish front from back, did show similar shaped responses for front-to-back and back-to-front whereas subject ML did not [Fig. 4]. Again we conclude that for the monkey these disparity-shift stimuli must be activating a mechanism distinct from that evoked by transitions from correlation to uncorrelation.

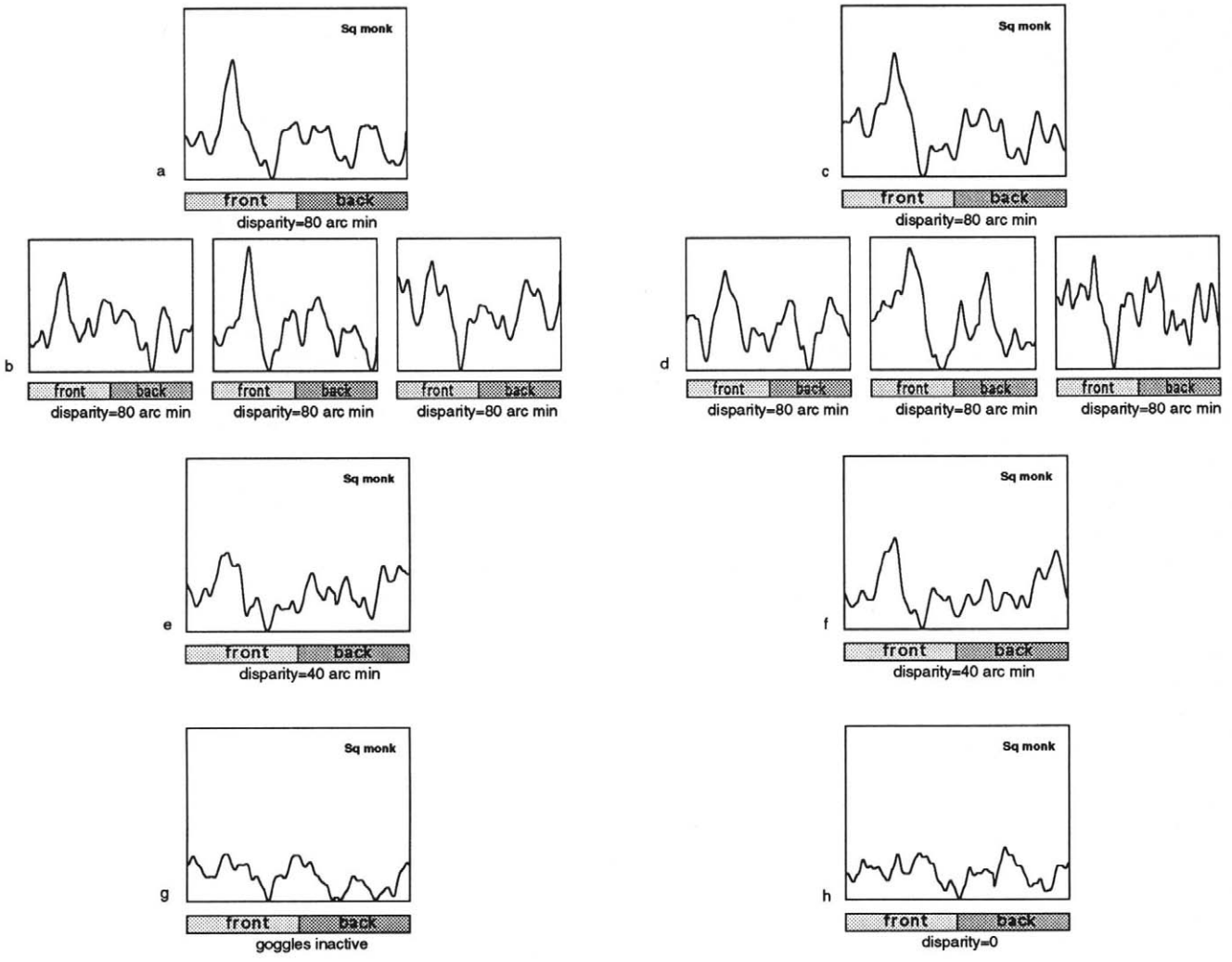


FIGURE 5. Responses of the squirrel monkey to different disparity shifts. In (a)–(d) "front" indicates +40 min arc disparity; "back" indicates −40 min arc disparity. In (e) and (f) "front" indicates +20 min arc disparity; "back" indicates −20 min arc disparity. (g) and (h) are controls, with (g) showing the average response to shifts between ±40 min arc disparity, but with the goggles inactive (so both lenses are open all the time) and a 0.3 log unit neutral density filter taped over the goggles; in (h) the disparity shift was set to 0. Each large panel represents the average of 6000 responses obtained over three daily sessions, and the sets of three smaller panels in (b) and (d) show the averages for the daily 2000 responses averaged to obtain records (a) and (c). All stimuli were 90 × 90 checks flickering at 14 Hz; disparity shifts at 1 Hz. Vertical scale = 4 μV; horizontal scale = 1 sec.

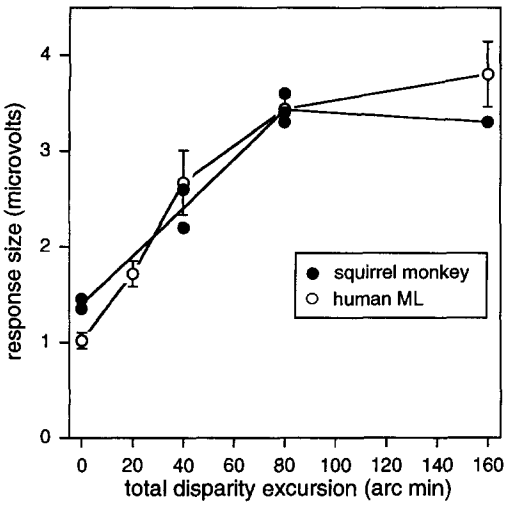


FIGURE 6. Comparison of the responses of the squirrel monkey with the human subject ML to different disparity shifts. The disparity shifts are given as the total disparity excursion of the central square (e.g. 40 min arc on the abscissa corresponds to shifts between ±20 min arc). The response size was taken as the distance between the most negative point and the most positive point of a given average. Each point for ML represents the mean voltage excursion for averages of 200 trials each ± SEM, and for the squirrel monkey, each point represents the voltage excursion for the average of 6000 trials. For ML the stimuli were 180 × 180 checks flickering at 14 Hz, and for the monkey the stimlui were 90 × 90 checks flickering at 14 Hz.

## DISCUSSION

Although many previous studies have seemed to equate the ability to respond to correlation/uncorrelation shifts with stereopsis (Tyler & Julesz, 1976; Julesz *et al.*, 1980; Miezin *et al.*, 1981; Poggio *et al.*, 1985, 1988), we thought that an animal might be able to distinguish between identical and dissimilar patterns in the two eyes, simply by virtue of having neurons with inputs from both eyes. If such binocular cells simply combined the inputs from the two eyes (instead of coding for positional differences between the two eyes) an uncorrelated pattern would appear to have some checks of an intermediate value (gray, for example). In physiological recordings from several squirrel monkeys (Hubel & Livingstone, 1987, and unpublished observations) we found both disparity-tuned cells and cells that were not sharply tuned for disparity yet responded more strongly to both eyes than to either eye alone. Most of the binocular neurons we have recorded from in squirrel monkey V1, especially in layer 2/3, have fallen into the second category. These binocular-but-not-disparity-tuned cells usually respond well to either eye alone but better to both eyes (usually slightly less than additive); and the region over which the response to both eyes is better than to either alone is about the same size as the receptive field, suggesting that the responses from the two eyes simply summate. Other cells in squirrel monkey V1, especially cells in layer 4B, are clearly disparity tuned, falling into Poggio and Fischer's Tuned Excitatory and Tuned Inhibitory categories. For the Tuned Excitatory cells, the range over which the response is critically dependent on disparity is much narrower than the receptive-field size, the cells respond poorly to either eye alone, and the response at the best disparity is much larger than the sum of the responses to the two eyes alone. Tuned Inhibitory cells show response decrements that are likewise critically dependent on interocular disparity. Both the Tuned Excitatory and Tuned Inhibitory cells peak at zero disparity or too close to zero to be resolved by our methods. (Even if non-zero, the disparities are small relative to the widths of the tuning peaks, so it seems unlikely that departures from zero are significant.) We see the same three kinds of cells also in V2 in squirrel monkeys (Hubel & Livingstone, 1987). "Near" and "Far" cells, such as those described for the macaque, are very rare in squirrel monkey V1 and V2.

Thus we find, in the squirrel monkey, cells that are differentially selective for zero versus non-zero disparity and cells that show binocular interactions but do not seem to be selective for disparity. If squirrel monkeys indeed lack the richer assortment of cells that one finds in macaques, they may be inferior to macaques and humans in their stereoscopic capabilities. The results presented here, however, suggest that the squirrel monkey has true stereopsis and not just correlation/uncorrelation detectors. It is of course possible that squirrel monkeys will turn out to have cells tuned to near and far disparities in visual areas beyond V2.

Our perception, as well as evoked potential and single unit studies, all suggest that correlation/uncorrelation shifts can indeed be a powerful stimulus, though the biological function and the relation to stereopsis are at present not clear. The recordings of Poggio *et al.* (1988) show that in the macaque the population of cells responding to stereopsis is not identical to that responding to disparity cues; in fact, more than a third of the cells that show responses to correlation/uncorrelation shifts are not disparity selective, and almost half the cells that are selective for disparity are not responsive to correlation/uncorrelation shifts. Similarly, evoked potential studies in humans suggest that only part of the response to correlation/uncorrelation shifts can be accounted for by disparity-selective mechanisms (Livingstone, unpublished results).

Like the human, the squirrel monkey showed reproducible evoked-potential responses to shifts between correlation and uncorrelation, and responses to disparity reversals that were different in waveform from the correlation/uncorrelation responses and were graded with depth. This suggests that the squirrel monkey does indeed have stereopsis, despite its seemingly important differences from old-world primates in binocular organization. The squirrel monkey [and to varying degrees other new-world primates (see Florence & Kaas, 1992 for references)] differs from old-world primates in that (1) it lacks any anatomical evidence for ocular dominance columns, (2) its ocular dominance distribution in V1 is much more binocular (i.e. most of the cells receive input from both eyes rather than being driven primarily by one or the other) (Hubel & Wiesel, 1978; Hubel & Livingstone, 1987), (3) its lateral geniculate

nucleus lacks obvious partitioning between the parvocellular layers (Le Gros Clark, 1941), and (4) in squirrel monkey V2, unlike V2 in the macaque, cells tuned to near or far disparities are very rare (Hubel & Livingstone, 1987). Though the regularity of ocular dominance columns would seem to provide an excellent means of comparing the inputs from the two eyes in an orderly fashion, the squirrel monkey seems to be able to encode disparity information without their benefit, or at least with only a poorly developed version of them.

We can think of several possible explanations for this seeming paradox. (1) Ocular dominance columns are essential for stereopsis in most primates and other animals with binocular overlap, and the squirrel monkey has some quite different and unique mechanism for detecting stereopsis. This monkey may discriminate depth, for example, by combining information about eye vergence with information about correlation and uncorrelation in the two eyes. (2) Despite the evidence presented in this paper, the squirrel monkey may not have stereopsis. (3) The distinct and stripe-like character of ocular dominance columns may not be necessary for stereopsis, though grouping of cells with similar eye preference would seem likely to facilitate the connections involved. Ocular dominance stripes probably arise from a tendency for cells with common firing patterns to strengthen common connections by an activity-dependent Hebbian mechanism. This kind of mechanism may serve in some animals solely to refine the retinotopic map, and in others also to segregate eye inputs (Hebb, 1949; von der Malsburg & Willshaw, 1976; Swindale, 1980; Miller, Keller & Stryker, 1989). Thus under this third possibility there would be two extremes: ocular dominance segregation might facilitate, but not be necessary for, the connections underlying stereopsis; alternatively ocular dominance columns could be thought of as an epiphenomenon, not serving any purpose, arising from a mapping mechanism. The idea that ocular dominance stripes, despite their orderliness and prominence, arise from some mechanism not involved in stereopsis, or binocularity in any sense, is supported by the finding of Law and Constantine-Paton (1981) that distinct ocular dominance columns can be produced in a frog, which normally does not have stereopsis, or even overlapping vision from the two eyes, by artificially implanting an extra eye on one side of a tadpole. Of course, it remains a mystery why this sort of mechanism would fail to segregate out ocular dominance columns in squirrel monkeys.

## REFERENCES


Atkinson, J. & Braddick, O. (1976). Stereoscopic discrimination in infants. *Perception, 5*, 29–38.

Blakemore, C. & Vital-Durand, F. (1981) Postnatal development of the monkey's visual system. In Elliott, K. & Whelan, J. (Eds), *The fetus and independent life, Ciba Foundation Symposium* (Vol. 86, pp. 152–171). London: Pitman.

Boothe, R., Dobson, V. & Teller, D. Y. (1985). Postnatal development of vision in human and nonhuman primates. *Annual Review of Neuroscience 8*, 495–545.

Ferster, D. (1981). A comparison of binocular depth mechanisms in areas 17 and 18 of the cat visual cortex. *Journal of Physiology, 311*, 623–655.

Fischer, B. & Krüger, J. (1979). Disparity tuning and binocularity of single neurons in the cat visual cortex. *Experimental Brain Research, 64*, 1–8.

Florence, S. L. & Kaas, J. H. (1992). Ocular dominance columns in area 17 of Old World macaque and talapoin monkeys: Complete reconstructions and quantitative analyses. *Visual Neuroscience, 8*, 449–462.

Hebb, D. O. (1949). *The organization of behavior*. New York: Wiley.

Held, R., Birch, E. E. & Gwiazda, J. (1980). Stereoacuity of human infants. *Proceedings of the National Academy of Science, 77*, 5572–5574.

Hendrickson, A. E. & Wilson, J. R. (1979). A difference in (14C)deoxyglucose patterns in striate cortex between Macaca and Saimiri monkeys following monocular stimulation. *Brain Research 170*, 353–358.

Hendrickson, A. E., Wilson, J. R. & Ogren, M. P. (1978). The neuroanatomical organization of pathways between the dorsal lateral geniculate nucleus and visual cortex in old world and new world primates. *Journal of Comparative Neurology, 182*, 123–136.

Hubel, D. H. & Livingstone, M. S. (1987). Segregation of form, color, and stereopsis in primate area 18. *Journal of Neuroscience, 7*, 3378–3415.

Hubel, D. H. & Wiesel, T. N. (1965). Binocular interaction in striate cortex of kittens reared with artificial squint. *Journal of Neurophysiology 28*, 1041–1059.

Hubel, D. H. & Wiesel, T. N. (1978). Distribution of inputs from the two eyes to striate cortex of squirrel monkeys. *Society of Neuroscience Abstracts, 4*, 632.

Hubel, D. H., Wiesel, T. N. & LeVay, S. (1975). Functional architecture of area 17 in normal and monocularly deprived macaque monkeys. *Cold Spring Harbor Symposium on Quantum Biology, 40*, 581–589.

Humphrey, A. L. & Hendrickson, A. E. (1983). Background and stimulus-induced patterns of high metabolic activity in the visual cortex (Area 17) of the squirrel and macaque monkey. *Journal of Neuroscience, 3*, 345–358.

Jasper, H. H. (1958). The ten twenty electrode system of the International Federation. *Electroencephalography and Clinical Neurophysiology, 10*, 371–375.

Julez, B. (1971). *Foundations of cyclopean perception*. Chicago, Ill.: University of Chicago Press.

Julesz, B., Breitmeyer, B. & Kropfl, W. (1976a). Binocular-disparity-dependent upper–lower hemifield isotropy as revealed by dynamic random-dot stereograms. *Perception, 5*, 129–141.

Julesz, B., Petrig, B. & Buttner, U. (1976b). Fast determination of stereopsis in rhesus monkey using dynamic random-dot stereograms (abstract). *Journal of the Optical Society of America, 66*, 1090.

Julesz, B., Kropfl, W. & Petrig, B. (1980). Large evoked potentials to dynamic random-dot correlograms and stereograms permit quick determination of stereopsis. *Proceedings of the National Academy of Science, 77*, 2348–2351.

Law, M. I. & Constantine-Paton, M. (1981). Anatomy and physiology of experimentally produced striped tecta. *Journal of Neuroscience, 1* 741–759.

Le Gros Clark, W. E. (1941). The lateral geniculate body in platyrrhine monkeys. *Journal of Anatomy, 76*, 131–140.

Lehmann, D. & Julesz, B. (1978). Lateralized cortical potentials evoked in humans by dynamic random-dot stereograms. *Vision Research, 18*, 1265–1271.

LeVay, S. & Voigt, T. (1988). Ocular dominance and disparity coding in cat visual cortex. *Visual Neuroscience, 1*, 395–414.

Livingstone, M. S. & Hubel, D. H. (1994). Stereopsis and positional acuity under dark adaption. *Vision Research, 34*, 799–802.

von der Malsburg, C. & Willshaw, D. J. (1976). A mechanism for producing continuous neural mappings: Ocularity dominance stripes and ordered retino-tectal projections. *Experimental Brain Research (Suppl.) 1*, 463–469.

Menzel, C. R. (1980). Head-cocking and visual perception in primates. *Animal Behaviour, 28*, 151–159.

Miezin, F. M., Myerson, J., Julesz, B. & Allman, J. M. (1981). Evoked potentials to dynamic random-dot correlograms in monkey and man: A test for cyclopean perception. *Vision Research, 21*, 177–179.

Miller, K. D., Keller, J. B. & Stryker, M. P. (1989). Ocular dominance column development: Analysis and stimulation. *Science, 245*, 605–615.

Movshon, J. A. & Van Sluyters, R. C. (1981). Visual neural development. *Annual Review of Psychology, 32*, 477–522.

Norcia, A. M., Sutter, E. E. & Tyler, C. W. (1985). Electrophysiological evidence for the existence of coarse and fine disparity mechanisms in human. *Vision Research, 25*, 1603–1611.

Poggio, G. F. & Fischer, B. (1977). Binocular interaction and depth sensitivity in striate and prestriate cortex of behaving Rhesus monkey. *Journal of Neurophysiology, 40*, 1392–1405.

Poggio, G. F., Gonzales, F. & Krause, F. (1988). Stereoscopic mechanisms in monkey visual cortex: Binocular correlation and disparity selectivity. *Journal of Neuroscience, 8*, 4531–4550.

Poggio, G. F., Motter, B. C., Squatrito, S. & Trotter, Y. (1985). Responses of neurons in visual cortex (V1 and V2) of the alert macaque to dynamic random-dot stereograms. *Vision Research, 25*, 397–406.

Swindale, N. V. (1980). A model for the formation of ocular dominance stripes. *Proceedings of the Royal Society of London B, 208*, 243–264.

Tigges, J., Tigges, M. & Perachio, A. A. (1977). Complementary laminar termination of afferents to area 17 originating in area 18 and in the lateral geniculate nucleus in squirrel monkey. *Journal of Comparative Neurology, 176*, 87–100.

Timney, B. (1981). Development of binocular depth perception in kittens. *Investigative Ophthalmology and Visual Science, 21*, 493–496.

Tyler, C. W. & Julesz, B. (1976). The neural transfer characteristics (Neuronotropy) for a binocular stochastic stimulation. *Biological Cybernetics, 23*, 33–37.

Wiesel, T. N. (1982). Postnatal development of the visual cortex and the influence of environment. *Nature, 299*, 583–591.

---

*Acknowledgements*—We are very grateful to Richard Andersen for helping us with the headpost implantation surgery and to Patrick Cavanagh and Ken Nakayama for constructive criticism on the manuscript. This research was funded by NIH grants EY00605 and EY10203, Office of Naval Research grant N00014 88 K 0200, and by the McKnight Foundation.