

MOTION MECHANISMS IN STROBE-REARED CATS: PSYCHOPHYSICAL AND ELECTROPHYSICAL MEASURES

Tatiana PASTERNAK * and William H. MERIGAN

University of Rochester, USA

J. Anthony MOVSHON

New York University, USA

Cats were reared from birth to at least 12 months of age in a visually static environment (illuminated 40/min by a 3 μ sec strobe flash). Single unit recordings from these animals revealed abnormalities in spatial and directional properties of cortical neurons. In an attempt to find psychophysical correlates of these neural deficits, spatial contrast sensitivity and motion detection thresholds were measured behaviorally. Both spatial vision and motion detection were greatly impaired. While spatial deficits failed to recover, motion thresholds improved greatly following extended training. These improvements in behavioral motion response were accompanied by the recovery of cortical directional selectivity. The recovery of motion thresholds and directional selectivity was direction specific: the distribution of the preferred directions of cortical neurons and motion thresholds were sharply biased towards the direction first seen in training. Thus, directional mechanisms of adult motion deprived cats may be modified if following deprivation the animals are trained to detect moving stimuli.

The studies described in this paper have examined the effects of motion deprivation on the development of vision, with particular emphasis of the neurophysiological and perceptual response to stimulus motion. Previous electrophysiological studies have shown reduced directional selectivity of neurons in the cortex and superior colliculus of cats and other animals reared in an environment intermittently illuminated by a low frequency strobe flash (Cynader *et al.* 1976; Flandrin *et al.* 1976; Chalupa and Rhoades 1978; Orban *et al.* 1978). Other properties of visual neurons, such as orientation selectivity and binocularity, are also greatly altered by this rearing. Although some recovery of orientation selectivity has been noted, directional selectivity appears to be resistant to reversal by subsequent exposure to normal light (Cynader *et al.* 1976; Cynader and Chernenko 1976).

Our own single unit recordings from such cats confirmed many of these

* Mailing address: T. Pasternak, Center for Visual Science, University of Rochester, Rochester, NY 14627, USA.

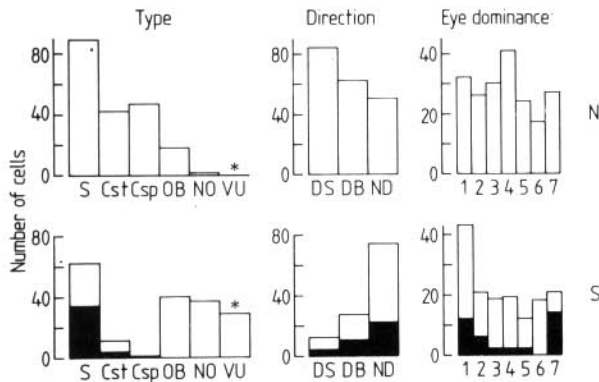


Fig. 1. Histograms illustrating numbers of cortical cells showing various receptive field properties. Data in the upper histograms are from normal (N) cats, and those in the bottom histograms from strobe-reared cats (S). Leftmost graphs show the numbers of cells in both groups of cats classified as simple (S), standard complex (Cst), special complex (Csp), orientation biased (OB), nonoriented (NO) and visual unresponsive (VU). The number of directionally selective (DS), directionally biased (DB) and nondirectional (ND) units is shown in the middle histograms. Ocular-dominance histograms for normal (top) and strobe-reared cats (bottom) are shown on the right. Black areas on the bottom histograms show the numbers of cells classified as "normal" in terms of spatial properties. Methods of procedure are described in detail in Movshon *et al.* (1978).

findings. In fig. 1, data obtained from 7 strobe-reared cats are compared to that of normal cats. The leftmost histograms show the distribution of cells recorded from area 17 as verified histologically. All receptive fields lay within 6 deg of area centralis. The units were classified according to a scheme similar to that of Gilbert (1977). It can be seen that strobe-reared cats have a higher number of visually unresponsive (VU), nonoriented (NO) or orientation biased (OB) cells. Of 62 cells that could be classified as simple (S) about half (blackened area) showed normal orientation selectivity, spatial tuning and resolution (max 3–4 c/deg) and contrast sensitivity (Movshon *et al.* 1978). We should note that all cells in this group showed the normal receptive field organization of the simple class, particularly, separated on and off zones, separated discharges to moving edges and roughly linear spatial summation. In contrast, very few truly complex cells were found. Of the 11 complex cells (Cst, CsP) only 4 appeared normal in terms of the above properties. Directionally selective (DS) cells shown in the center histograms were rarely encountered in strobe reared cats. The rightmost plots show ocular dominance in normal (top) and strobe reared (bottom). The data indicate a considerable reduction in the number of binocularly driven cells in strobe-reared cats.

These results support those of Cynader *et al.* (1976) in demonstrating reduced directional selectivity and binocularity in area 17 of the visual cortex of strobe reared cats. Our data also reveal that many cortical neurons in these cats have abnormal spatial resolution and contrast sensitivity.

In attempting to find psychophysical correlates of these profound changes in neuronal properties we tested several basic visual functions psychophysically; often examining more than one function in the same cat.

Spatial vision

We first quantified the spatial vision of cats reared in stroboscopic illumination by measuring their contrast sensitivity (Pasternak and Merigan 1979). This measure provides a broad description of pattern vision and, to the extent that certain assumptions are met, allows prediction of the visibility of untested stimuli. We felt that this initial study would provide crucial background information for subsequent experiments in which we would test motion perception of these cats using various spatial patterns.

Our behavioral procedures were based on those developed by Berkley (1970). Six cats were used: three strobe reared, two normal cats, and a control cat reared in a long duration (750 msec) flash of the same frequency as the strobe light. The latter condition permitted the perception of motion during rearing while providing a control for the periodicity and low time averaged luminance of the strobe environment. The effective luminances of the strobe and 750 msec illumination were equated by a behavioral test in which luminance thresholds for grating discrimination were determined in normal cats for each of the light sources. When the deprived cats were at least 12 months old, they were removed from stroboscopic illumination. Testing began after at least 2 months of adaptation to normal illumination. The cats were trained to discriminate between a vertical sinusoidal grating and a uniform field, each at a mean luminance of 16 cd/m². Procedural details are described in Pasternak and Merigan (1979, in press).

The contrast sensitivity functions for the three strobe reared cats show a great reduction in sensitivity at all spatial frequencies and a peak shifted toward lower spatial frequencies. Strobe cats also showed a reduction of acuity by 1–1.5 octaves. The lower part of fig. 2 shows log sensitivity loss for the three strobe reared cats, relative to the control cats. This plot clearly demonstrates increasing sensitivity loss with higher spatial frequencies. It is unlikely that optical factors can account for these losses. Refraction by slit lamp retinoscopy showed our strobe cats to be slightly myopic (–0.5 to –1.5 diopter), thus if their accommodative power was normal, they should have been able to focus at the distance of 30 cm (Bloom and Berkley 1977). These behavioral results have been confirmed electrophysically. Evoked potentials (EPs) have been recorded from one cat with extensive behavioral training. A comparison of EP and behavioral data obtained from this strobe cat is shown in fig. 3. The two types of measures are consistent in showing reductions of both contrast sensitivity and spatial resolution in the strobe-reared cat. These

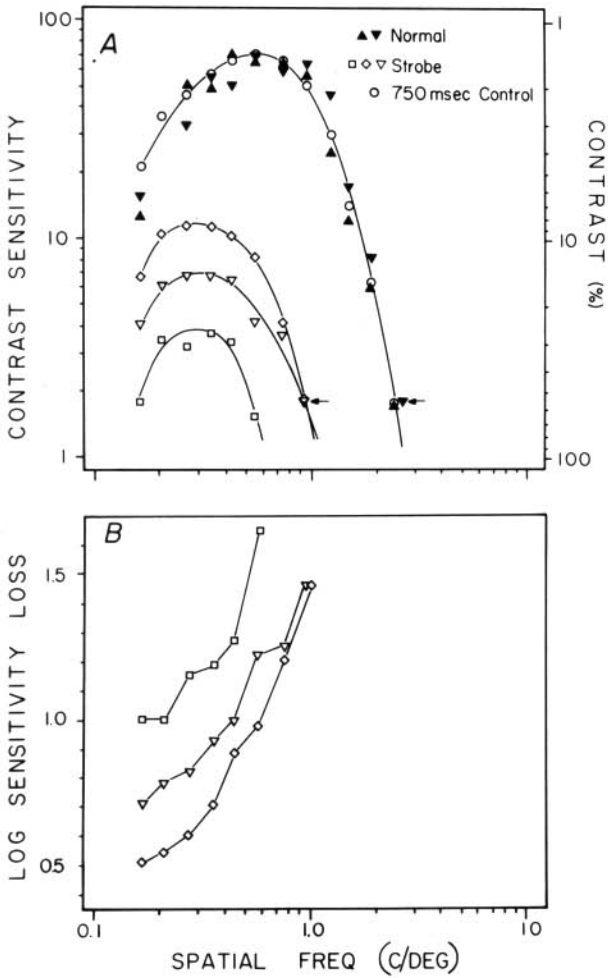


Fig. 2 (a) Contrast sensitivity (reciprocal of threshold contrast which is shown on the right ordinate) as a function of spatial frequency. ○, 750-ms Control cat; □, ◇, ▽, three strobe-reared cats. Individual curves were fitted by eye. ▲, ▼, the two normal cats. Points indicated by the arrows are acuity measurements obtained by presenting a range of spatial frequencies at 55% contrast. Each point represents the reciprocal of the contrast value corresponding to 75% correct performance at that frequency and is based on at least 400 trials. Luminance, 16 cd m⁻²; viewing distance, 30 cm; field size, 20×16 deg. (b) Sensitivity loss for the three strobe-reared cats compared to the 750-ms control cat as a function of spatial frequency. The same symbol is used for each cat as in a. Each point represents the ratio of sensitivity of the 750-ms control cat to the sensitivity of the strobe-reared cat expressed in log units. 0.0 corresponds to no loss, 1.0 to a 10-fold reduction in sensitivity (from Pasternak and Merigan 1979).

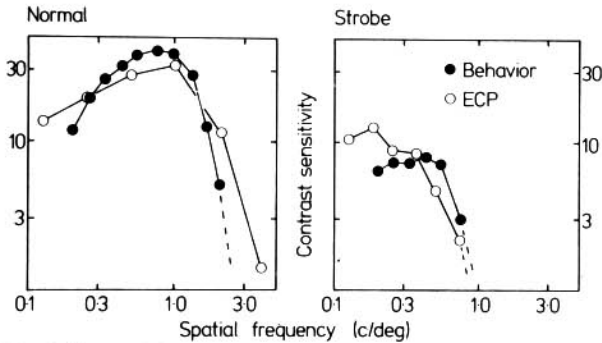


Fig. 3. Comparison of spatial contrast sensitivity (SCS) measures obtained with behavioral and electrophysiological (evoked potentials, ECP) techniques. Plots on the left show typical behavioral and electrophysiological results for normal cats. Plots on the right show the two types of measures obtained from the same strobe-reared cat. Stimuli for behavior: standing sine-wave gratings, luminance = 16 cd/m². Stimuli for physiology: sine-wave gratings sinusoidally counter-phase modulated at 8 Hz; luminance: 6 cd/m². During ECP recordings the cats were paralyzed, and maintained with N₂O/O₂/CO₂ (78:20:2). Potentials were recorded from screws mounted in the skull in the vicinity of the cortical projection of area centralis. ECP contrast thresholds were determined by extrapolating to zero a function relating EP amplitude and stimulus contrast (Campbell *et al.* 1973)

results demonstrated the necessity of using high contrast stimuli containing spatial frequencies below 1 c/d in subsequent experiments that examined the motion sensitivity of strobe-reared cats.

Motion thresholds

As a first step in describing the motion perception of strobe-reared cats we determined the range of velocities at which motion was detectable (Pasternak *et al.* in press). In these studies we wished to minimize orientation cues to the direction of motion. Thus, we chose isotropic dot patterns (fig. 4) rather than gratings because no single orientation is dominant in such patterns. Also Fourier analysis showed a predominance of low spatial frequencies (< 1c/d) in such patterns, which was appropriate for the impaired vision of the strobe-reared cats described above. Detailed procedures used in our motion studies are described elsewhere (Pasternak and Merigan 1980).

Briefly, the cats were trained to discriminate moving from stationary random dot patterns. They responded to the moving stimulus by pressing with their noses on one of two circular, transparent response panels through which the stimuli were visible. Responses during the first 2 sec of stimulus presentation were ineffective: this set a lower limit on viewing time. Each stimulus consisted of a sheet of approx. 400 bright dots 0.47 deg in diameter on a dark

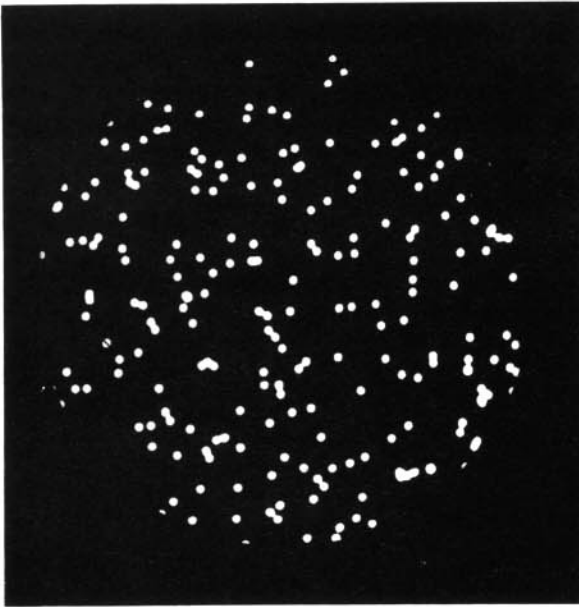


Fig. 4. An example of isotopic dot patterns used in motion discrimination studies.

background. The stimuli were rear projected on a circular screen 22 deg in diameter, at a viewing distance of 30 cm.

The velocity of the moving target during initial training was 44 deg/sec. All cats reached criterion performance (4 consecutive days $\geq 80\%$ correct) within 12 to 30 sessions of 200 trials and the rate of acquisition was not related to rearing conditions. Thus, strobe reared cats show no impairment in learning to discriminate moving from stationary stimuli even though they never saw motion during development.

We next measured minimal detectable velocity using the method of constant stimuli. In each session 5 velocities, chosen to bracket the threshold, were presented in random order within each block of 5 trials. The threshold was defined from the resulting psychometric function as the velocity corresponding to 75% correct responding. Fig. 5 shows the improvement of thresholds over the course of testing. The performance of normal cats and of the 750 msec control cat improved abruptly in the first 4–8 weeks of testing with thresholds stabilizing between 0.9 and 1.5 deg/sec. Some further reductions in thresholds were seen with continued testing, but these were slight. The thresholds of strobe reared cats, on the other hand, were initially quite high 17–25 deg/sec compared with those of the control animals. After some 30 weeks of testing these thresholds decreased to 2.5–3 deg/sec (2 to 3 times those of control cats), and with further testing remained elevated.

The above data were obtained with rightward motion. Since directional

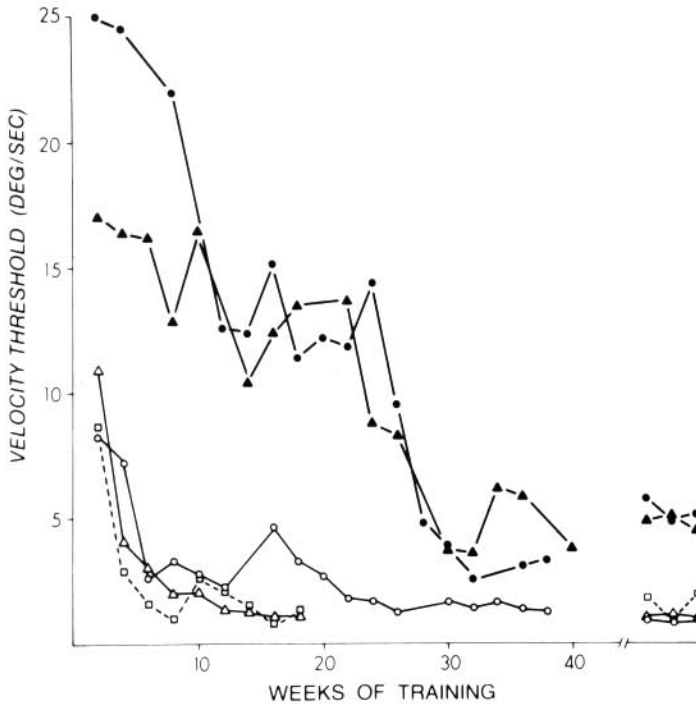


Fig. 5. Low velocity thresholds obtained during the course of testing. The performance of normal cats is shown by open symbols connected by a solid line and that of the 750 msec control cat is shown by open squares connected by an interrupted line. The thresholds of strobe-reared cats are shown by filled symbols. Each data point represents a threshold obtained in a single session. The thresholds are plotted at two-week intervals.

selectivity is impaired in strobe reared cats, we were interested in observing whether the substantial improvements in motion sensitivity would transfer to other directions of motion. Therefore, low velocity thresholds were measured for the following directions of motion: 0 (rightward), 45, 90, 135, 180, 225, 270, and 315 degrees. The threshold for a single direction of motion was tested in each session and the sequence of directions was irregular.

Fig. 6 shows sensitivity to motion as a function of direction. Both the normal cats and the 750 msec control cat (left side of figure) have similar sensitivity to motion in all directions, *i.e.*, detection is independent of the direction of motion. Thresholds ranged from 1.0 to 2.0 deg/sec. Strobe reared cats, on the other hand, show a very pronounced reduction in sensitivity for directions more than 45 degrees from the original training direction (0 deg). Unlike normal animals, strobe-reared cats showed no immediate transfer of the discrimination to directions more than 90 degrees from the training direction

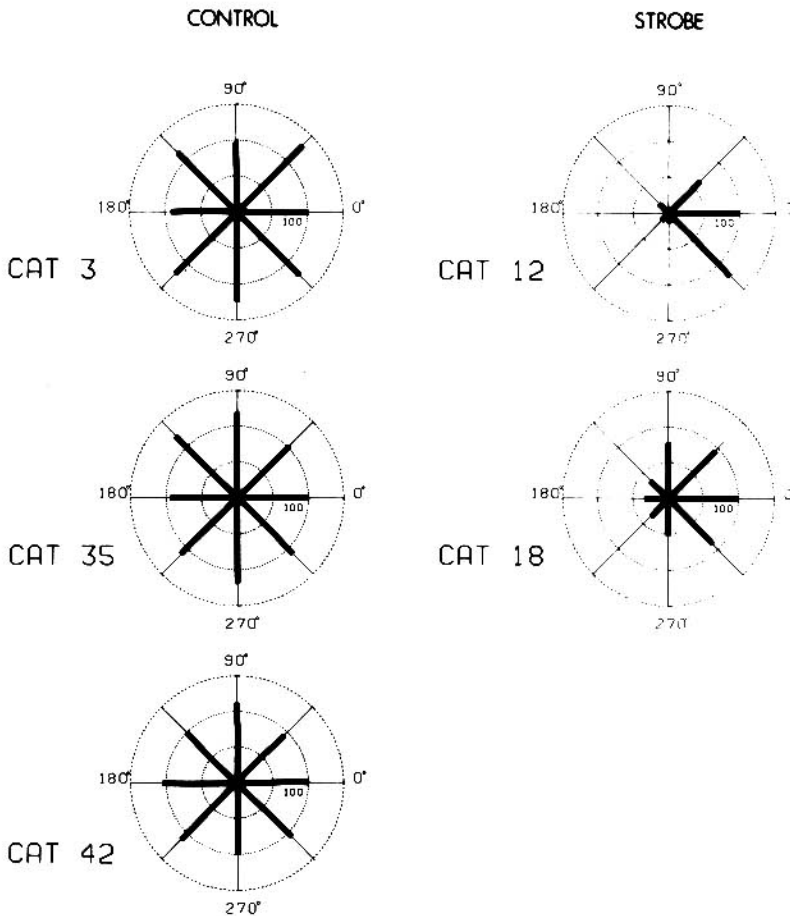


Fig. 6. Velocity thresholds as a function of direction. Velocity thresholds were measured for 8 directions of motion. Sensitivity, which is the reciprocal of velocity threshold, is represented by the distance that the heavy lines extend out from the origin. The scores are normalized to emphasize relative sensitivity to different directions. Sensitivity to the original training direction was set to 100.

even at the highest velocities. Additional training (usually 2–3 sessions) was necessary to re-establish discrimination at these directions. However, once performance recovered the cats responded reliably to high velocity stimuli, and we were able to obtain stable thresholds at these directions. For cat 18, the threshold elevation was greatest near 180 deg while for cat 12 great deficits were found at all directions more than 45 deg from rightward motion. The thresholds shown in fig. 6 represent data which satisfied a stability criterion of less than $\pm 20\%$ deviation from the mean of 3 determinations. Both strobe

animals received extensive subsequent training (> 7 mo.) with stimuli moving leftward, upward and downward. When retested following this training, they showed the same sensitivity profile seen in fig. 6. It is unlikely that a simple learning deficit (*e.g.* failure to generalize) could account for this asymmetry since strobe reared cats eventually responded to the novel directions and showed stable psychometric functions of normal slope, yet thresholds remained elevated. Thus, the results shown in fig. 6 appear to reflect differences in the visibility of rightward and leftward motion in strobe-reared cats.

The peculiar sensitivity to rightward motion led us to examine the orientation and direction selectivity of striate cortical units of these two cats. The methods of recording have been described in detail elsewhere (Movshon 1976). Animals were prepared for electrophysiology under barbiturate anesthesia (Pentothol); they were then paralyzed with Flaxedil and artificially ventilated with 80% nitrous oxide in oxygen and carbon dioxide. The corneas were covered with contact lenses containing 4 mm artificial pupils, and supplementary lenses were used to focus the eyes on a screen 72 cm distant. Single units in visual cortex were isolated with tungsten microelectrodes (Levick), and their activity was conventionally amplified and displayed. We studied the properties of 86 and 87 units in the two animals, drawing our samples equally from the two hemispheres. We made long electrode penetrations angled medially down the bank of the postlateral gyrus in order to sample widely from each hemisphere.

Receptive fields were mapped with stationary and flashing bars, edges and spots and were classified according to the scheme of Hubel and Wiesel (1962) as modified by Blakemore and Van Sluyters (1975). We carefully attended to two properties of each neuron: orientation selectivity and direction selectivity. Cells were classified as orientation selective (OS) if they gave no response to a line or edge presented at right angles to the optimum orientation, as orientation biased (OB) if they gave some response at right angles to the optimum, and as non oriented (NB) if we could discern no preference. Similarly, cells were direction selective if they gave a markedly better response to one direction of motion of an optimally-oriented stimulus than to its opposite, direction biased (DB) if they responded discriminably better to one direction than the other, and not directional (ND) if we detected no difference in the responses to the two directions.

While strobe-reared cats, given a period of normal visual experience, showed abnormally low proportions of orientation- and direction-sensitive neurons (62% and 35%, respectively), both motion-trained animals had roughly normal proportions of selective cells: in our samples, 93% of neurons were classified as OS or OB; of these, 69% were either DS or DB. By comparison, 99% of neurons in normal cats were orientation sensitive, and 74% of these were DS or DB.

While cells preferring all orientations were direction selective in the motion-

trained cats there was a marked bias in the distribution of direction selectivity for units having preferred orientations within 22.5 deg of vertical: of these 40 of 59 (68%) showed a direction preference, with 34 of the 40 (85%) preferring movement to the right and only 6 (15%) preferring movement to the left. Excluding only cells preferring near-horizontal orientations, 62 of 89 cells (70%) preferred the direction having a rightward component; only 27 (30%) preferred motion with a leftward component. By comparison, excluding only cells preferring near-vertical orientations, 36 of 70 (51%) preferred motion with an upward component and 34 (49%) preferred motion with a downward component. Neither the few direction-sensitive neurons in our other strobe-reared cats nor similar neurons from normal cats showed any significant anisotropy in the distributions of their preferred directions. The recovery of normal properties did not appear to be confined to any particular class of cortical cells; simple, standard complex and special complex cells were all present in roughly normal numbers.

Thus in two adult strobe-reared cats trained extensively on a discrimination task involving motion, we found both recovery of motion detection performance and recovery of cortical direction selectivity. This confirms previous suggestions that in strobe- and dark-reared cats it is possible to demonstrate a period of cortical plasticity that extends beyond the traditional "sensitive period" for cortical development (Cynader *et al.* 1976; Cynader and Mitchell 1980; Timney *et al.* 1980). Our results are unusual in that they suggest that this extended plasticity, which does not normally include direction selectivity, may do so if animals are preferentially exposed to moving stimuli.

Cortical directional selectivity can be biased to a narrow range of directions by exclusive exposure of young kittens to a single direction of motion (Berman and Daw 1977; Daw and Wyatt 1976; Cynader *et al.* 1975; Tretter *et al.* 1975). This change can occur only during a well defined critical period early in life (Berman and Daw 1977). Our results show that under appropriate conditions a similar effect can be induced in adult strobe-reared cats. It is important to note that unlike orientation selectivity, the directional selectivity of deprived animal shows no recovery if the animal is simply returned to normal illumination (Cynader *et al.* 1976; Cynader and Chernenko 1976). Furthermore, no recovery in cortical directional selectivity was seen in strobe reared cats which were tested for over two years with stationary gratings. Thus, the effects obtained in the present study appear to be a specific result of motion detection testing.

The precise correlation between our results and the original training direction is somewhat surprising given that the cats had concurrent exposure (12h/day) to a normal laboratory environment. It is unclear which aspects of behavioral training were crucial for producing this unusual effect. One possibility is that a threshold amount of stimulation is required and this threshold was exceeded only for the original training direction. It is also possible that training stimuli were prepotent over other environmental stimuli in modifying neural

mechanisms simply because they were behaviorally important.

Thus, in our initial studies of motion perception in cats with greatly reduced cortical directional selectivity we found that: (1) the detection of slow motion in such cats is greatly impaired; (2) the recovery of motion thresholds appears to be accompanied by the recovery of directional selectivity; (3) the recovery of motion thresholds and directional selectivity is specific to the direction first seen in training.

References

- Berkley, M.A., 1970. 'Visual discrimination in the cat'. In: W.C. Stebbings, (ed.), *Animal psychophysics: the design and conduct of sensory experiments*. New York: Appleton-Century-Crofts. pp. 23–247.
- Berman, N. and N.W. Daw, 1977. Comparison of the critical periods for monocular and directional deprivation in cats. *Journal of Physiology* 265, 249–259.
- Blakemore, C. and R.C. Van Sluyters, 1975. Innate and environmental factors in the development of the kitten's visual cortex. *Journal of Physiology* 248, 663–716.
- Bloom, M. and M.A. Berkley, 1977. Visual acuity and the near point of accommodation in cats. *Vision Research* 17, 723–750.
- Campbell, F.W., L. Maffei and M. Piccolino, 1973. The contrast sensitivity of the cat. *Journal of Physiology* 229, 719–731.
- Chalupa, L.M. and R.W. Rhoades, 1978. Modification of visual response properties in the superior colliculus of the golden hamster following stroboscopic rearing. *Journal of Physiology* 274, 571–592.
- Cynader, M. and B. Chernenko, 1976. Abolition of direction selectivity in visual cortex. *Science* 193, 504.
- Cynader, M. and D. Mitchell, 1980. Prolonged sensitivity to monocular deprivation in dark-reared cats. *Journal of Neurophysiology* 43, 1026–1040.
- Cynader, M., N. Berman and A. Hein, 1975. Cats raised in a one-directional world: effects on receptor fields in visual cortex and superior colliculus. *Experimental Brain Research* 22, 267–280.
- Cynader, M., N. Berman and A. Hein, 1976. Recovery of function in cat visual cortex following prolonged visual deprivation. *Experimental Brain Research* 25, 139–156.
- Daw, N.W. and M.J. Wyatt, 1976. Kittens reared in an unidirectional environment: evidence for a critical period. *Journal of Physiology* 257, 155–170.
- Flandrin, J.M., H. Kennedy and B. Amblard, 1976. Effects of stroboscopic rearing on the binocularity and directionality of cat superior colliculus neurons. *Brain Research* 101, 576–581.
- Gilbert, C.D., 1977. Laminar differences in receptive field properties of cells in cat primary visual cortex. *Journal of Physiology* 268, 391–421.
- Hubel, D.H. and T.N. Wiesel, 1962. Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *Journal of Physiology* 160, 106–154.
- Movshon, J.A., 1976. Reversal of the physiological effects of monocular deprivation in the kitten's cortex. *Journal of Physiology* 261, 125–174.
- Movshon, J.A., I.D. Thompson and D.J. Tolhurst, 1978. Spatial and temporal contrast sensitivity of neurons in areas 17 and 18 of the cat's visual cortex. *Journal of Physiology* 283, 101–120.
- Orban, G.A., M. Kennedy, M. Maes and B. Amblard, 1978. Cats reared in stroboscopic illumination: velocity characteristics of area 18 neurons. *Archives Italian Biology* 116, 413–419.
- Pasternak, T. and W.H. Merigan, 1979. Abnormal visual resolution of cats reared in stroboscopic illumination. *Nature* 280, 313–314.