Creation of direction selectivity in adult strobe-reared cats

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Animals raised in a stroboscopically illuminated environment have deficits in several visual functions, including visuo-motor integration[1], discrimination learning[2] and spatial contrast sensitivity[3]. Moreover, recordings from the visual pathways of strobe-reared animals show severe functional abnormalities, including greatly reduced selectivity for orientation and for directional motion in neurones of the visual cortex and superior colliculus[4-9]. Subsequent normal visual experience improves cortical orientation selectivity, but does not alter the neural deficit in direction selectivity[6,7]. As the motion-analysing capacities of strobe-reared animals have not been studied, we examined the ability of strobe-reared cats to discriminate stationary from moving patterns. We report here that the cats detected motion in the direction for which they had originally been trained much better than motion in other directions. In recordings from striate cortex in these animals, orientation and direction-selective neurones were encountered with a frequency much higher than that seen in strobe-reared cats not trained in motion discrimination, and comparable with that in normal cats. Moreover, the distribution of the preferred directions of these neurones was sharply biased towards the direction first seen in training. We conclude that there exists an extended period of cortical plasticity in strobe-reared animals, which, in contrast to that previously reported[6], includes plasticity of direction selectivity.

We carried out behavioural tests on five cats; two were reared from birth to the age of at least 14 months in a room illuminated for 12 h each day with a stroboscopic flash of 3 μs duration at a rate of 0.67 Hz, and two were raised normally. One was raised in an environment intermittently illuminated with a flash of light 750 ms in duration at 0.67 Hz; the luminance of this flash was adjusted so that normal adult cats could resolve fine detail in this illumination as well as they could in the stroboscopic illumination. Behavioural testing began no less than 4 months after the animals were removed from their rearing environment.

The cats were trained to discriminate stationary from moving random-dot patterns using a forced-choice procedure based on that developed by Berkley[10]; our modification of this method has been described in detail elsewhere[11]. The animals were trained to indicate which stimulus moved by pressing with their noses on one of two transparent panels through which they viewed the stimuli. Each stimulus consisted of a sheet of 400 bright dots, each 0.5° in diameter, on a dark background; the sheet subtended 22° at a viewing distance of 30 cm. Most of the energy in the pattern was concentrated at spatial frequencies below 1c/deg, which are visible to strobe-reared cats[11].

During the initial training, the stimulus always moved to the right at 44° s⁻¹; after 12–30 days, with 200 trials per day, all cats satisfactorily discriminated between this stimulus and the stationary one. Strobe-reared cats were no slower in acquiring this discrimination than control cats. We next measured the lowest detectable speed using the method of constant stimuli. In each session five speeds were chosen to bracket threshold, and were presented randomly in blocks of five trials. Threshold was taken as the point at which resulting psychometric functions produced 75% correct performance.
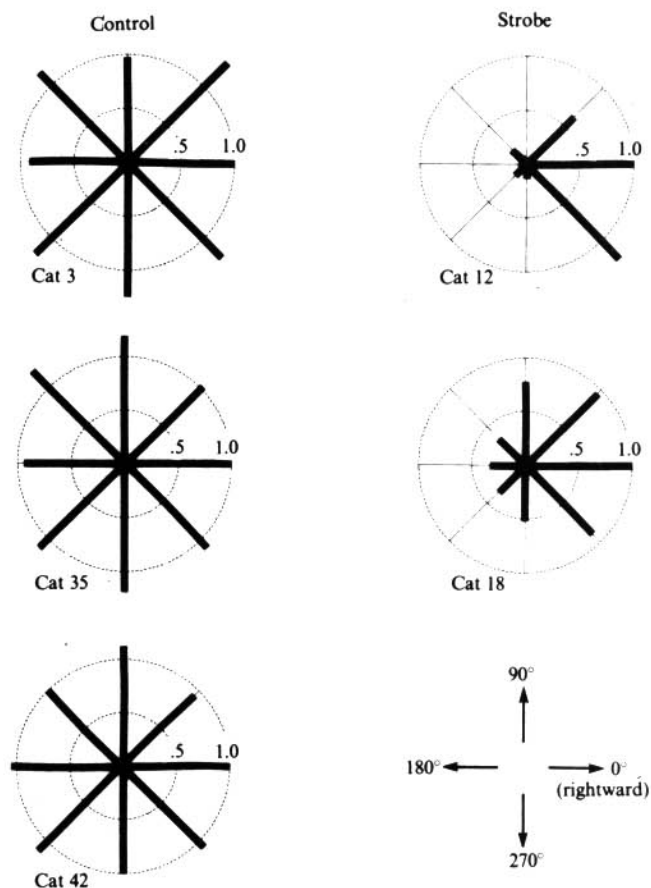

Fig. 1 Polar diagrams showing the speed sensitivity of control and strobe-reared cats to motion in eight directions. Each bar plots the inverse of the speed required for 75% correct performance on a two-choice discrimination between a stationary and a moving random-dot field. The bars in each case are normalized so that sensitivity to rightward motion is given a value of 1. Data are shown for two normal cats (3 and 35), one cat raised in an intermittently illuminated environment (42, see text) and two cats raised in a stroboscopically illuminated environment (12 and 18). Their actual thresholds for rightward motion were 0.9, 1.2, 2.0, 2.0 and 4.4° s⁻¹, respectively. A repeated measures analysis of variance showed that none of the control animals was significantly better at motion discrimination in any particular direction ($P > 0.05$). However, both strobe cats were significantly more sensitive to motion within 45° of rightward than they were to other directions ($P < 0.05$).

The motion thresholds of the control cats improved over several months of testing from an initial value between 8 and 11° s⁻¹ to an asymptotic value between 0.9 and 1.5° s⁻¹. The initial thresholds of the strobe-reared cats were high in comparison (between 17 and 25° s⁻¹); after prolonged testing (~8 months during which the animals received ~18 h of exposure to moving dots) the thresholds stabilized near 3° s⁻¹, 2–3 times higher than those of control cats.

In all tests described above, rightward motion was used. We next examined the transfer of this training to other directions. On each day, the threshold for one direction was tested. Over several days, an irregular sequence of eight directions, evenly spaced around 360°, was presented. Figure 1 shows the sensitivity of each of the five cats to motion as a function of the direction tested. In each polar diagram, the length of bar represents the inverse of the speed threshold for a particular direction of motion; the values are normalized with respect to the cat's sensitivity to rightward motion, which is given a value of 1. The control cats had a similar sensitivity in all test directions, whereas the strobe-reared animals were much more sensitive to rightward motion than they were to motion in directions more than 45° from this, the initial direction of training. The high

thresholds for directions for which no training had been given remained stable over 7 months of further training, in which stimuli moved upwards, downwards and to the left, and did not improve as the initial high thresholds for rightward motion had done earlier. Note also that this deficit did not represent a simple failure to generalize from one direction to another, as the strobe-reared cats were capable of discriminating motion in all directions, yielding stable psychometric functions of normal slope; it was simply that when tested with rightward motion, they required only low stimulus speeds compared with those required for detection of motion in other directions.

The peculiar sensitivity of these strobe-reared cats to rightward motion led us to examine the orientation and direction selectivity of striate cortical units, using methods described elsewhere[12]. Control data were obtained from six other adult strobe-reared cats that had received comparable periods of normal visual experience but had not been trained to discriminate motion, and from seven normally reared adult cats. Animals were prepared for electrophysiology using barbiturate anaesthesia (Pentothal); they were then paralysed with Flaxedil and artificially ventilated with 80% N_2O in O_2 and CO_2. Their 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 cortical units were isolated using tungsten microelectrodes, and their activity amplified and displayed. We studied the properties of 88 and 87 units in the two strobe-reared animals, in each case drawing our samples equally from long medially directed penetrations in the two hemispheres. For comparison, we made recordings of 183 units from normal cats. All units were histologically verified to lie in area 17.

Receptive fields were mapped on a tangent screen using bars, edges and spots of light, and classified according to the scheme of Hubel and Wiesel[13] as modified by Blakemore and Van Sluyters[14]. No quantitative response measures were used but we paid careful attention to the orientation and direction selectivity of each neurone. Cells were classified as orientation selective (OS), orientation biased (OB), or not oriented (NO) using criteria described elsewhere[14]. Cells were direction selective (DS) if they responded markedly better to one of the two directions of motion of an optimally oriented stimulus, direction biased (DB) if they responded discriminably better to one direction than the other, and not directional (ND) if there was no difference in the responses to the two directions.

The data from the two cats trained to discriminate motion were generally similar to those from normal cats, and differed markedly from those of other strobe-reared animals studied by
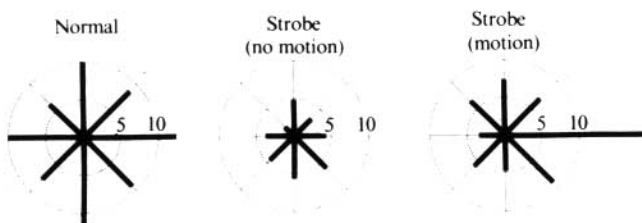
us and others[4-7,15]. Table 1 lists the proportions of OS and OB neurones in the three groups of cats, and the proportions of those in each of the three classes of direction sensitivity. While strobe-reared cats given a period of normal visual experience showed abnormally low proportions of orientation- and direction-sensitive neurones (62% and 35% respectively), both motion-trained animals had roughly normal proportions of selective cells: in our sample, 93% of neurones were classified as OS or OB; of these 65% were either DS or DB. By comparison, 99% of neurones 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

Table 1 Proportion of orientation- and direction-sensitive neurones

Experimental group	Cells	All cells		OS and OB cells		
		%OS	%OB	%DS	%DB	%ND
Normal cats	192	90	9	42	32	26
Strobe cats (not motion-trained)	183	40	22	12	23	65
Strobe cats (motion-trained)	175	91	2	32	33	35

distribution of direction selectivity. This is shown in Fig. 2, which gives the direction preferences of cortical units from the three groups of cats. In the two motion-trained cats, 59 units had preferred orientations within 22.5° of vertical: of these 40 (68%) showed a direction preference, with 34 of the 40 (85%) preferring movement to the right and only six (15%) preferring movement to the left. In these cats, 89 cells were both direction selective and preferred orientations within 67.5° of vertical; 62 of these (70%) preferred the direction having a rightward component; only 27 (30%) preferred motion with a leftward component. By comparison, among the 70 direction-sensitive cells preferring orientations within 67.5° of horizontal, 36 (51%) preferred motion with an upward component and 34 (49%) preferred motion with a downward component. Neither the direction-sensitive neurones from normal cats nor the few such neurones from strobe-reared cats not motion-trained showed any significant anisotropy in the distributions of their preferred directions.

Thus in two adult strobe-reared cats trained extensively to discriminate motion, we found both recovery of motion detection performance and recovery of cortical direction selectivity. This confirms previous suggestions[6,16,17] 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. 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.

Also interesting is our finding of a bias towards the initially trained direction in both the psychophysical motion sensitivity and the directional preferences of cortical neurones in these cats. Cortical direction selectivity can be biased in young kittens exposed to a restricted range of directions of motion[18-20], but these changes have only been shown to occur during a restricted period in early life that ends well before the period of sensitivity to the effects of monocular occlusion[21,22]. Our data show that a qualitatively and quantitatively similar effect may be seen in adult strobe-reared cats exposed to a motion-biased environment. The magnitude of the effects is similar to those reported elsewhere for young animals, which is surprising in view of the fact that our animals received 4 months of normal vision before training and received 12 h per day of concurrent unbiased visual stimulation. In our experiments the cats were required to attend to the moving stimuli to obtain behavioural reward, which may have rendered those stimuli in some way more potent modifiers of cortical function.

| Normal | Strobe (no motion) | Strobe (motion) |

Fig. 2 Polar histograms showing the distributions of direction preference for cortical neurones showing direction sensitivity in three groups of cats: normal; strobe-reared but not motion-trained; and strobe-reared and trained in motion discrimination (cats 12 and 18 from Fig. 1). The histograms show the percentage of the total population of cortical neurones in each group that preferred directions in the ranges indicated. The results are based on totals of 192 cells from seven normal cats, 183 from six strobe-reared cats not trained in motion discrimination, and 175 cells from two strobe-reared cats trained in motion discrimination using rightward motion. The distributions of direction preference were similar in the two motion-trained cats: 21% of all cells in cat 18 and 17.5% in cat 12 preferred rightward motion, whereas only 5% of cells in cat 18 and 2% in cat 12 responded preferentially to leftward motion.

1. Hein, A., Gower, B. C. & Diamond, R. M. *J. comp. physiol. Psychol.* **73,** 188–192 (1970).
2. Chalupa, L. M. & Rhoades, R. W. *Expl Neurol.* **61,** 442–454 (1978).
3. Pasternak, T. & Merigan, W. H. *Nature* **280,** 313–314 (1979).
4. Cynader, M., Berman, N. & Hein, A. *Proc. natn. Acad. Sci. U.S.A.* **70,** 1353–1354 (1973).
5. Olson, C. & Pettigrew, J. D. *Brain Res.* **70,** 189–204 (1974).
6. Cynader, M., Berman, N. & Hein, A. *Expl Brain Res.* **25,** 139–156 (1976).
7. Cynader, M. & Chernenko, G. *Science* **193,** 504–505 (1976).
8. Orban, G., Kennedy, M., Maes, H. & Amblard, B. *Archs ital. Biol.* **116,** 413–419 (1978).
9. Flandrin, J. H., Kennedy, H. & Amblard, B. *Brain Res.* **101,** 576–581 (1976).
10. Berkley, M. A. in *Animal Psychophysics* (ed. Stebbins, W.) 231–247 (Appleton-Century-Crofts, New York, 1970).
11. Pasternak, T. & Merigan, W. H. *J. comp. physiol. Psychol.* **94,** 943–952 (1980).
12. Movshon, J. A. *J. Physiol., Lond.* **261,** 125–174 (1976).
13. Hubel, D. H. & Wiesel, T. N. *J. Physiol., Lond.* **160,** 106–154 (1962).
14. Blakemore, C. & van Sluyters, R. C. *J. Physiol., Lond.* **248,** 663–716 (1975).
15. Pasternak, T. & Movshon, J. A. *Invest. ophthalmol. vis. Sci. Suppl.* 225 (1980).
16. Cynader, M. & Mitchell, D. E. *J. Neurophysiol.* **43,** 1026–1040 (1980).
17. Timney, B., Mitchell, D. E. & Cynader, M. *J. Neurophysiol.* **43,** 1041–1054 (1980).
18. Cynader, M., Berman, N. & Hein, A. *Expl Brain Res.* **22,** 267–280 (1975).
19. Tretter, F., Cynader, M. & Singer, W. *Brain Res.* **84,** 143–149 (1975).
20. Daw, N. W. & Wyatt, H. J. *J. Physiol., Lond.* **257,** 155–170 (1976).
21. Berman, N. & Daw, N. W. *J. Physiol., Lond.* **265,** 249–259 (1977).
22. Daw, N. W., Berman, N. & Ariel, M. *Science* **199,** 565–567 (1978).