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Research Note

Abolition of visual cortical direction selectivity affects visual behavior in cats

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Summary. We reared cats in an environment illuminated stroboscopically at 8 Hz, and studied their ability to detect and discriminate the direction of motion of sinusoidal gratings. Normal cats, like humans, could discriminate the direction of a grating's motion at contrasts that are just barely visible. Strobe-reared cats could detect the grating at contrasts similar to those required by normal cats, but required contrasts that were about 10 times threshold to identify the direction of motion. We subsequently studied the activity of single units in the striate cortex in these cats, and found that directional motion selectivity – normally a prominant feature of striate cortical neurons – was almost absent; other cortical receptive field properties were roughly normal. These results suggest that directionally selective neurons are involved in visual discriminations based on the direction of motion.

Key words: Motion sensitivity – Visual cortex – Directionally selective neurons – Strobe-reared cats – Behavior

Most cells in the cat's visual cortex are directionally selective: they respond vigorously to one direction of stimulus movement but weakly or not at all to the opposite direction (Hubel and Wiesel 1962; Orban et al. 1981). A number of psychophysical experiments have suggested that directionally selective mechanisms operate in human visual detection and discrimination (Sekuler and Ganz 1963; Levinson and Sekuler 1975; Sekuler et al. 1978). It is commonly assumed that directionally selective cortical neurons are the physiological substrate of perceptual phenomena associated with directional motion, but there has been no direct demonstration of the involvement of directionally selective neurons in perceptual performance. We have therefore studied visual performance and visual physiology in cats reared in an environment that markedly reduces cortical directional selectivity while leaving other cortical receptive field properties largely unaltered. Normal cats, like humans, could discriminate the direction of a grating's motion at contrasts that are just barely visible. Strobe-reared cats could detect the grating at contrasts similar to those required by normal cats, but required contrasts that were about 10 times threshold to identify the direction of motion. We subsequently studied the activity of single units in the striate cortex in these cats, and found that directional motion selectivity – normally a prominent feature of striate cortical neurons – was almost absent; other cortical receptive field properties were roughly normal. These results suggest that directionally selective neurons are involved in visual discriminations based on the direction of motion.

We reared cats in room illuminated by a 3 μs strobe flash delivered every 125 ms for 12 h each day; during the other 12 h the room was dark. Rearing of this sort has previously been shown to reduce the proportion of directionally selective cortical neurons while leaving most other receptive field properties qualitatively normal (Cynader and Chernenko 1976). At the age of eight months, the cats were removed to normal illumination and tested behaviorally. The details of our psychophysical procedures can be found elsewhere (Pasternak et al. 1983). During each 200 trial session, the cats viewed two displays through the response panels and a nose pressing response toward the correct stimulus was rewarded. Each display subtended 12 deg, and had a space- and time-averaged luminance of 75 cd/m^2, which was unaffected by the presentation of any stimulus. Incorrect responses were followed by a 10 s loud tone and no reward was delivered. We compared the ability of

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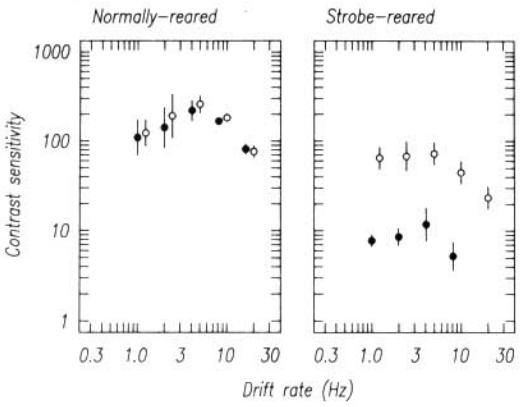

Fig. 1. Contrast sensitivity for normal (left) and strobe-reared cats (right) for the detection (open symbols) and direction discrimination (filled symbols) tasks. Each data point is a geometric group mean of 3–4 thresholds obtained for each cat, three strobe-reared and two normally-reared. The error bars indicate ±1 standard error of the mean; where the error bars are not apparent, they are smaller than the data points. Stimulus contrast is defined as (lmax–lmin)/(lmax+lmin), where lmax is the luminance of the brightest point in the stimulus and lmin is the luminance of the darkest point. The contrast thresholds were determined with a staircase procedure in which the correct response produced a 3 db decrease in stimulus contrast with probability of 0.3 and each incorrect response produced a 3 db increase in stimulus contrast. The thresholds were taken from the resulting psychometric function at stimulus values corresponding to 75% correct responding. At the highest drift rate (18 Hz), contrast sensitivity of strobe-reared cats could not be estimated, since even at the highest grating contrast (0.6) the cats could not discriminate directions above 75% correct. The drift rate of the grating is specified by its temporal frequency, the number of stimulus cycles that cross a point in the display in one second. The speed of motion is given by the drift rate divided by the spatial frequency: our test gratings thus moved at 4, 8, 16, 32 and 64 deg/s

three of these cats to detect moving sinusoidal gratings with their ability to discriminate the direction of the gratings' motion. Control data were obtained from two normal cats. In the detection experiment the cats were presented with two side-by-side circular displays, one containing a vertical grating and the other a uniform field. The cats were rewarded for selecting the grating. In the discrimination experiment they viewed two identical vertical gratings moving in opposite directions and were rewarded for selecting the one moving rightward. We measured contrast sensitivity for detection and discrimination with 0.28 c/deg gratings drifting at 1.1, 2.2, 4.4, 9 and 18 Hz.

Figure 1 shows the results of this experiment. Normally-reared cats (left) had nearly equal sensitivity in the detection and the discrimination task at all temporal frequencies. Thus, normal cats could identify the direction of motion of a target that they could barely detect; in this respect, their performance was very similar to that of normal human observers tested under similar conditions (Watson et al. 1980; Lennie 1980; Thompson 1984). Strobe-reared cats (right) showed detection sensitivities for the moving patterns that were slightly depressed (by 0.2–0.4 log units; $p < 0.005$) compared to those of the normal cats. The best performance of a strobe-reared cat equalled that of a normal cat: either could detect contrasts less than 0.01 at the optimal drift rate. However, the strobe-reared cats' sensitivity for discriminating the direction of motion was reduced by a factor of ten or more at all stimulus speeds; at the highest drift rate, 18 Hz, the strobe-reared cats were unable to perform the discrimination task even at the highest contrast level (0.6).

After the completion of behavioral testing, we recorded single unit activity from area 17 of three cats that had been strobe-reared and given extensive behavioral training in the tasks similar to those described above. The methods for neurophysiological recordings are detailed elsewhere (Movshon et al. 1978a; Schumer and Movshon 1984). After surgery under halothane and sodium thiopental anesthesia, the cats were paralyzed with an infusion of gallamine triethiodide (10 mg/kg/h) or pancuronium bromide (0.15 mg/kg/h); anesthesia was maintained by infusion of sodium pentobarbitol (2 mg/kg/h) and artificial ventilation with a mixture of N_2O, O_2 and CO_2 (49 : 49 : 2). The visual cortex of the postlateral gyrus was exposed, and a tungsten microelectrode advanced down the medial bank of the cerebral hemisphere to record the activity of single units. Topical atropine sulfate and neosynephrine HCl produced mydriasis and cyclopegia, the eyes were covered with zero-power contact lenses containing 4 mm artificial pupils, and supplementary lenses were used to make the retinas conjugate with a screen 57 cm distant.

After mapping the visual receptive fields of a cortical unit on a tangent screen, we used a mirror to center the receptive field of the dominant eye on the face of an oscilloscope that subtended 9.5 deg and had a mean luminance of 40 cd/m^2. A PDP11 computer generated moving sinusoidal gratings on this CRT and collected neuronal action potentials. In the strobe-reared cats, we estimated orientation selectivity, spatial frequency selectivity and contrast sensitivity by adjusting the appropriate parameters of the grating stimulus while listening to the neuron's discharge relayed over an audiomonitor. We classified cells as simple or complex using the criteria described by Schumer and Movshon (1984). To assess directional selectivity, we measured responses using a grating of the optimal orientation and spatial frequency which moved in both directions over the

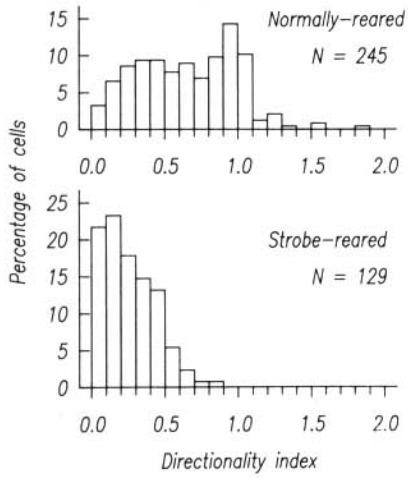

Fig. 2. The distributions of directionality index for normally-reared and strobe-reared cats (top and bottom, respectively). The directionality index is defined as $1 - (np/p$ where np is the response in the non-preferred direction and p is the response in the preferred direction. A cell without directional bias has a DI of 0, a cell meeting a 2 : 1 criterion for directionality has a DI of 0.5, and a cell yielding no response in one direction has a DI of 1.0. DI values greater than 1 occur when a cell's spontaneous discharge is suppressed by the stimulus moving in the non-preferred direction

receptive field at 0.5, 1.5, 4 and 12 Hz; our estimate of directional selectivity used the drift rate yielding the largest response in the preferred direction. For simple cells, whose responses are modulated in synchrony with the passage of each bar of the grating over the receptive field, response was taken as the amplitude of the frequency component of the modulation of spike frequency that occurred at the stimulus frequency. For complex cells, which generally do not show strong modulated discharge to gratings, the response was taken as the mean firing rate less the spontaneous firing rate (for details see Movshon et al. 1978a, b). For each cortical unit, we noted ocular dominance, orientation selectivity, preferred spatial frequency, spatial resolution, contrast sensitivity, preferred temporal frequency, and directional selectivity. We studied 170 cells in the strobe-reared cats and compared that data with that from 280 cells from normally-reared cats. The receptive fields of all cells were within 10 deg of area centralis, and most were within 5 deg.

Figure 2 shows the distributions of cortical directional selectivity in the normally-reared and strobe-reared cats expressed as a directionality index. Directionality of cells in both, strobe-reared and normal cats did not appear to depend on the contrast levels at which responses were measured. Because ratio measures, such as our directionality index are best estimated when responses are large, we made all our measurements at high contrast (0.5). In normal cats, 64% of the cells (166/245) had DI values greater than 0.5, and thus would be termed "direction selective" if a 2 : 1 response criterion were employed. Only 9% of cells from the deprived cats (12/129) met this criterion for directional selectivity. Using a more stringent criterion of a 5 : 1 response ratio, 40% of the cells in normally-reared cats and 2% of the cells in strobe-reared cats were directionally selective. Complex cells seemed to suffer from the deprivation more than simple cells. In the strobe-reared group, no complex cell had a DI greater than 0.56 and almost all of the cells with a significant directional bias were simple. In normal cats, on the other hand, 49% of complex cells had DI values greater than 0.8, while only 29% of the simple cells met this 5 : 1 criterion.

Most other receptive field properties were roughly normal in strobe-reared cats. We found a normal proportion of orientation selective neurons (161/70: 93%). All preferred orientations were represented and there was the usual slight preponderance of vertical and horizontal orientation preferences. The range of effective stimulus orientations was similar to that seen in normal cats (mean for strobe-reared cats: 76 deg; mean for normal cats: 84 deg). Measurements of optimal temporal frequency and peak contrast sensitivity revealed no significant abnormality. In our sample of neurons from normal cats, there was no association between directional selectivity and contrast sensitivity. The sample from strobe-reared cats contained very few directionally selective cells. While these few cells seemed to have rather poor contrast sensitivity, the size of the sample prevented this from attaining statistical significance. One feature besides directional selectivity that was affected by strobe-rearing was spatial frequency response. Both the optimal spatial frequencies and spatial resolution limits of cells in strobe-reared cats were lower than seen in normally-reared cats. It should be noted that the spatial frequency used for behavioral testing, 0.28 cpd, was well outside the range of spatial frequencies affected by the deprivation. Examination of the ocular dominance distributions revealed a slight reduction in the numbers of binocularly driven units compared to normal, but this effect was minor.

Our physiological data from the cortex of 8 Hz strobe-reared cats thus confirm and extend the previous report by Cynader and Chernenko (1976) that directional selectivity is nearly abolished in these cats. Except for subtle decreases in spatial resolution and binocularity, we were unable to find abnormalities in other receptive field properties. We have shown that this loss of cortical directional selectivity is accompanied by greatly elevated psychophysical

contrast thresholds for identifying the direction of stimulus movement, and it seems reasonable to suppose that the profound and specific deficit in direction discrimination results from the loss of directionally selective neurons.

It is noteworthy that at high contrasts the ability of strobe-reared animals to discriminate direction is indistinguishable from that of normal cats (Pasternak and Leinen, in press). This suggests that the few directionally selective cells that remain in the primary visual cortex can support normal direction discrimination for clearly visible targets. The residual contrast sensitivity for direction discrimination at high contrasts could also be associated with the preservation of directional selectivity in visual areas outside striate cortex, but recordings from area 18 (Kennedy and Orban 1983), the lateral suprasylvian area (Spear et al. 1985) and the superior colliculus (Cynader, personal communication) of strobe-reared cats do not reveal any greater preservation of directional selectivity in those structures than in striate cortex. Thus, the residual contrast sensitivity of the strobe-reared cats for direction discrimination is likely to be determined by a very limited number of neurons encoding direction. The inability of these cats to make directional motion discriminations at low contrasts suggests that normal cats both detect and discriminate motion on the basis of signals from the directionally-selective neurons of the visual cortex. In the absence of this directional selectivity, moving grating patterns may still be *detected,* but the information needed to *discriminate* their direction of motion is no longer present.

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