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PATTERN EVOKED RESPONSE DEFICIENCY IN PATTERN DEPRIVED CATS[1]

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Depriving cats of patterned light has been shown to have profound effects on visually guided behavior. The animals are unable to learn pattern discriminations and lack visual placing, visual cliff discrimination and normal behavioral responses to impending collisions; these animals, however, are capable of light intensity discriminations (Riesen and Aarons 1959; Riesen 1965; Wiesel and Hubel 1965a, b).

Human visual evoked potentials have been shown to be altered when different patterned stimuli are presented (White and Eason 1966; John 1967; Harter and White 1968). The development of this pattern response has been found to correlate with age in a human infant (Harter and Suitt 1970). Alterations in this pattern evoked response have also been found in the amblyopic eye of children with amblyopia ex anopsia (Lombroso *et al.* 1969). Spehlmann (1965), studying the pattern evoked response in normal humans, has shown that the latency and amplitude of late positive waves can be altered by presentation of patterns containing different amounts of contour.

These findings suggest that a physiological correlate of defective pattern perception in the diffuse light reared cat might be found in its evoked response to patterned stimuli. We, therefore, undertook a study of slow wave evoked responses of pattern deprived cats and non-deprived litter mates to patterned visual stimuli containing varying amounts of contour to determine whether this physiological correlate exists.

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METHOD

Fourteen cats from four litters were reared by A.R. The litters were born in the lighted laboratory and moved into a totally darkened room one week after birth, before the eyes had opened. Daily exposures to light began on the 10th day after birth at which time each litter was divided into pattern deprived and control groups. Seven kittens were reared under each condition. Both groups were on a 21 h dark 3 h light schedule. Light exposure periods were divided into two 90 min intervals, and the kittens were away from their mothers during these times. During their hours in the light the control kittens were without visual restriction in a large area. The pattern deprived kittens were in the same area at the same time with fine percale hoods over their heads which diffused the light and thereby prevented pattern vision. When the cats reached the age of 6 months they were flown in light-tight boxes to Rochester, New York, where the physiological studies were performed. The experimenters did not know the rearing conditions of the cats until all the physiological measurements had been completed.

The cats were anesthetized with 65 mg/kg alpha chloralose given intravenously. The pupils were dilated and accommodation relaxed with cyclogyl (Schieffelin). The nictitating membrane of the right eye was retracted from the cornea and anchored to a head holder by suture threads and a contact lens was placed over the cornea to prevent drying. The animal was then positioned so that his area centralis was centered where visual stimuli were to be presented, using an ophthalmoscope to observe the optic disk and the measurements of Vakkur *et al.* (1963) to determine the relative location of the area centralis. The stimulus patterns were brought into focus on the area centralis using a Copeland Streak Retinoscope and trial lenses.

Experiments were performed in an electrically shielded sound-proof room. Body temperature was maintained between 35 and 38°C throughout each experiment. Seven different stimuli were used: 6 patterned cards and one blank white card. The patterns were all 50% black and 50% white and, therefore, reflected the same amount of light. A neutral density filter was placed in front of the eye when the blank white stimulus card was used, to reduce its brightness to the level of the other patterns. Three "low contour" patterns employed evenly spaced 3/4″ black and white stripes, arranged into either horizontal stripes, vertical stripes, or a grating pattern. Two "high contour" patterns consisted of alternate black and white 1/8″ stripes arranged in vertical stripe and curved stripe patterns. A checkerboard containing 1/4″ black and white checks was the third "high contour" pattern. The stimulus cards were 18″ × 24″ and were mounted on a black background 1 m in front of the eye. The stimulus cards were presented in a counterbalanced order. They were illuminated from outside the sound-proof room by a Slaughter model 163 stroboscope which was flashed every 3 sec by a PDP-5 computer. Forty visual evoked responses (VERs) were recorded and averaged by the computer for each stimulus pattern.

Small electrode holes were drilled through the outer table of the skull and into the diploë on the left side of the skull. The holes were drilled only part way through the cranium in order to prevent deterioration of, or damage to, the brain. Silver ball electrodes were inserted into the holes and electrode paste was used to maintain a good electrical connection. The head holder was used as ground.

Electrodes were placed over primary visual cortex, mid-suprasylvian gyrus and motor cortex. Electrode placements were verified visually when the brain was removed for a quantitative histological analysis of the brains which is now in progress.

RESULTS

The VER recorded over primary visual cortex had two consistent components, an early positive wave (P1) peaking 47.6 msec after stimulus presentation and a later positive wave (P2) peaking 111.2 msec after the stimulus. Average P1 amplitude was greater in the pattern deprived cats than in the normal controls ($P < 0.0262$-Mann-Whitney U test, 2-tailed). The latency of P1 was the same in both groups. Neither the latency nor the amplitude of the P1 wave appeared to change when patterns containing different amounts of contour were presented.

The amplitude of the later P2 wave in the pattern deprived cats did not differ from that of the control group. The P2 latency, however, was shorter in the pattern deprived cats than in the controls ($P < 0.0042$-Mann-Whitney U test, 2-tailed). In all control animals the average latency of the P2 wave after presentation of the high contour patterns consistently differed from its latency after low contour pattern presentation. The visual cortex P2 peaked later for the small patterns than for the large patterns in 5 out of 7 controls and earlier in the other two. In these two cats the small patterns appeared to produce a considerably shorter latency than that evoked by the blank stimulus as well. This appears to rule out small differences in sharpness of retinal focus which might obscure the contour in the small patterns and cause them to give VERs similar to the VERs evoked by the blank stimulus. In any single animal all electrode sites over primary visual cortex showed the same direction of latency change with changing amounts of contour. The average absolute difference between the latencies of small and large pattern evoked P2 waves was 13.3 msec in normally reared cats.

In contrast to the normally reared cats, none of the pattern deprived cats showed substantial difference ($P > 0.10$ Mann–Whitney U test, 2-tailed) between the average latencies of their P2 response to small patterns and to large patterns, the largest latency difference being only 4.27 msec. Two of the cats had no detectable difference in the latency of response to large and small patterns. The average absolute difference between the latency of small and large pattern evoked P2 waves was 1.8 msec in the pattern deprived animals.

This difference in latency of the P2 wave to high and low contour patterns was expressed by taking the average latencies to small patterns, subtracting the average latency to large patterns and dividing by the average P2 latency to both small and large patterns. The absolute value of this measure, the Contour Response (CR), was then used to rank the cats. The CR for P2 latency produced a complete separation of the deprived and control cats, all of the deprived cats showing a smaller CR than any of the normal cats (Table I). The difference between normal and deprived cats was, therefore, highly significant ($P < 0.00001$ U test, 1-tailed).

The suprasylvian VER had two principle components, an early positive wave (P1) peaking at 49.0 msec and a later positive wave (P2) peaking at 87 msec. The suprasylvian P1 wave showed no CR for latency or amplitude in either group.

The suprasylvian P2 wave had the same average latency and amplitude in both normal and pattern deprived groups. Although suprasylvian P2 *latency* in normals did not show the CR found in primary visual P2, the *amplitude* of the suprasylvian P2 did show a CR ($P < 0.0361$ U test, 1-tailed) in normally reared cats. No CR was observed in either the latency or amplitude of suprasylvian P2 in the deprived cats.

TABLE I

Contour Responses of latency of P2 component of evoked response to patterned stimuli recorded over primary visual cortex of normally reared cats and pattern deprived litter mates.

Contour response $= \frac{S-L}{1/2\,(S+L)} \times 100$ where S = latency to small patterns; L = latency to large patterns.

Litters	Normal		Pattern deprived	
	Cat	CR	Cat	CR
I	2D	9.0%	2C	3.8%
	2B	28.2%	2A	1.9%
	2E	21.4%		
II	1B	12.2%	1A	0%
			1C	2.5%
III	M	4.4%	K	2.5%
	O	4.2%	L	2.2%
IV	T	5.8%	S	0%

Neither of the waves that showed a CR in normal cats (suprasylvian P2 amplitude and primary visual P2 latency) appeared to be responding to the configuration of the individual patterns. All high contour patterns produced VERs of essentially the same amplitude and latency. VERs produced by the various low contour patterns also had the same amplitude and latency, although these amplitudes and latencies were different from those produced by high contour patterns.

The motor cortex VER consisted of a single positive wave peaking at 88.6 msec. The amplitude of this wave was significantly smaller in pattern deprived cats than in normals ($P < 0.049$ U test, 1-tailed). The latency was the same in both groups. Neither group showed a CR in either the latency or amplitude.

DISCUSSION

The lack of VER latency and amplitude response to contour in pattern deprived cats provides a striking parallel to the lack of behavioral responsiveness to contour in these animals. Thus, CR appears to be a promising tool which might provide a quantifiable physiological correlate of both normal perceptual development and changes in perceptual abilities resulting from enriched or impoverished environments.

Previous visual evoked response studies on binocularly pattern deprived cats (Scherrer and Fourment 1964; Baxter 1966) have not employed patterned stimuli and have not controlled peripheral variables, such as pupil size, focus and orientation of the retina towards the stimulus as we have. These earlier studies are, therefore, not directly comparable to this one.

The findings that diffuse light rearing causes a diminution of the motor cortex VERs confirms similar findings of Glass (1971) on monocularly deprived cats and extends them to the binocular condition. The effect is not nearly as strong after our binocular deprivation as it was after Glass' monocular deprivation. The difference is probably due to the imbalance caused by Glass' having one half of the visual system functional. Monocular deprivation has also been shown to produce more severe abnormalities in unit firing than binocular deprivation (Wiesel and Hubel 1965a).

The diminution of motor cortex VERs indicates that the physiological connections that exist in a normal animal between visual and motor systems (Buser *et al.* 1968) are susceptible to environmental influences. The susceptibility of visuo-motor coordination and placing responses to deprivation of sight of limbs has been clearly shown (Hein and Held 1967). Our pattern deprivation condition similarly prevents reafference stimulation from the limbs. This factor suggests that the lack of visuo-motor coordination rather than the total lack of pattern vision might be responsible for the diminution of the motor cortex VER. Physiological investigation of the motor cortex of cats deprived of limb vision might clarify this issue.

Our finding of visual CRs in normal anesthetized animals now makes it possible to experiment on the physiological processes underlying both the human pattern evoked response and the CR. One phenomenon meriting further investigation is the difference in the manifestation of the CR in the suprasylvian and primary visual cortical areas, the CR primarily affecting amplitude in the former and latency in the latter. The differing behavior of the late wave in these two areas seems to indicate that there is an overriding modulation, specific to each area, of any common subcortical (Rose and Lindsley 1968; Creutzfeldt *et al.* 1969) or retinal (Bignall and Rutledge 1964) influences generating the P2 wave. Another problem of interest is the relation of unit firing to the CR Receptive field studies do not appear to explain either the presence of the CR in normals or their absence in pattern deprived animals. Studies of unit evoked responses to patterned stimuli in conjunction with slow potential studies in the visual system would be helpful in answering these questions.

SUMMARY

Normally reared cats showed a change in the latency of VERs (visual evoked responses) recorded over primary visual cortex and a change in the amplitude of VERs recorded over the suprasylvian association cortex when patterns containing different amounts of contour were presented. Pattern deprived cats did not show this contour response. A reduction in the amplitude of motor cortex VERs and an increase in the amplitude of the early visual cortex response were also observed in the pattern deprived cats.

RESUME

IMPERFECTION DU PATTERN DE LA REPONSE EVOQUEE CHEZ DES CHATS PRIVES DE PATTERN

Chez les chats élevés normalement, s'observe une modification de la latence de la réponse évoquée visuelle (VER) enregistrée sur le cortex visuel primaire et une modification de l'amplitude des VERs enregistrées sur le cortex associatif supra-sylvien lorsque des patterns contenant différentes quantités de contour sont présentés. Les chats élevés en condition de privation de pattern ne montrent pas cette réponse de contour. Une réduction de l'amplitude de la VER sur le cortex moteur et une augmentation de l'amplitude de la réponse corticale visuelle précoce sont également observées chez les chats privés de pattern.

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