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SINGLE-UNIT RESPONSES TO NATURAL OBJECTS IN AREA 19 OF CATS WITH DIFFERENT EARLY VISUAL EXPERIENCES

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Abstract. Cats deprived of pattern vision with hoods and normal cats were used. During the first 3 months of life some hood-reared cats had visual experience with a three-dimensional cross or a ping-pong ball. Recording were performed in adult cats with a pretrigeminal brainstem transection. Unit responses to the cross and the ball were recorded in area 19 within the projection of area centralis. Stimulus-dominance of the exposed object was manifested weakly. Both exposed and control objects activated more units in the experienced hood-reared cats than in hood-reared and normal controls. Compared with previous finding, the present results indicated that early visual experience affects area 19 differently than areas 17 and 18.

INTRODUCTION

In a previous paper (4), single-unit responses to a three-dimensional cross and a ping-pong ball in hood-reared and normal cats were recorded in areas 17 and 18 within the projection of the area centralis (Fig. 1). During the first 3 months of life, some of the hood-reared cats were exposed to the cross or the ball for specific intervals in a play-box. The object that had been available in the play-box evoked stronger unit responses than were obtained when the control object was presented. In the present study, cats with the same visual experience were used to examine unit responses in area 19, also within the projection of the area centralis.

METHODS

The specific details of the methodology have been elaborated previously (4). The present experiment was performed on 8 normal cats (N8–N15), and 12 cats reared in hoods in the Laboratory. On the 8th day *postpartum*, these cats were hooded with double sheets of linen, which prevent pattern vision. Four hood-reared cats (H5–H8) had no visual experience. Eight hood-reared cats received training in a play-box from age 17 to 90 days. For 20 min daily each kitten was placed without mask in a box in which either two black, three-dimensional crosses (cats Hc4–Hc7) or two black ping-pong balls (cats Hb7–Hb10) were present. One of the crosses or balls was available on the floor, and the second was suspended from a thread. Observations made during this phase confirmed that all subjects played with the objects. After 3 months of such training, sessions were continued once a week until the acute phase of the experiment. The following groups of cats were litter mates: Cats Hc4, Hc5, Hc6, Hb7 and Hb8; cats Hc7 and Hb9; and cats Hb6 and H7. During the recording phase of the experiment, the hood-reared cats were approximately 10 months of age, with the exception of subjects H5 and H8 that were 7 months and 4 months, respectively.

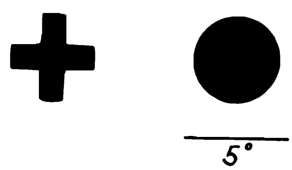

Fig. 1. The objects used in the previous (4) and the present study. The third arm of the three-dimensional cross is not seen on the photograph. Calibration refers to the acute experiment.

The pretrigeminal brainstem transection was made under ether anesthesia about 2 hr prior to recording (see 3). During this time the post-transectional coma passed, as shown by appearance of the ocular-following reflex, except in cat N15. Accordingly, this cat received 1 mg amphetamine intravenously, and the fixation reflex reappeared. A white tangent screen containing a middle window was situated 50 cm in front of the cat (Fig. 2). The visual stimulus consisted of either the cross or the ball moving donwnward across the window at a speed of 10 cm/sec. The left eye was occluded, and the vertical inclination of the visual axis of the right eye was monitored with a tensometric method (1, 4) (in the horizontal plane, the eyes of the pretrigeminal preparation are motionless). Unit activity was recorded extracellularly in the left area 19. We attempted

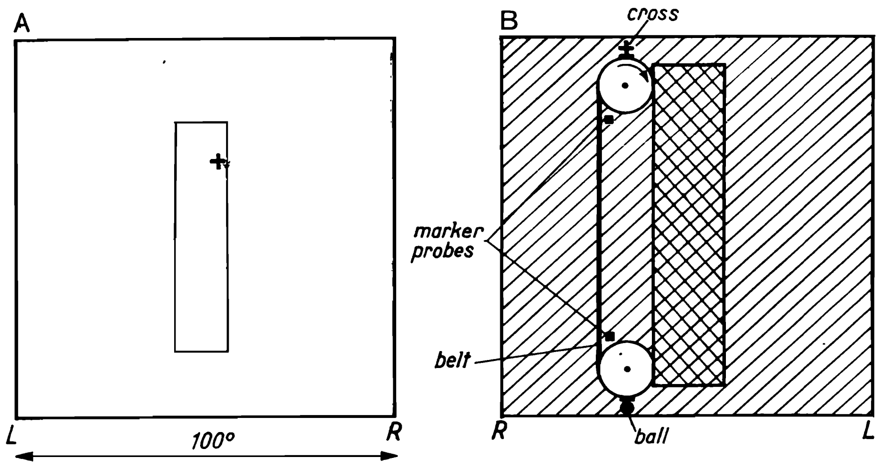

Fig. 2. The screen and the "generator" of the natural visual stimuli. *A:* The white screen as seen by the cat. In the "window" of the screen the black cross is at the beginning of its descent. *B*: Back of the screen. One can see that the cross and the ball are attached to the belt. Because of space limitations in the apparatus only half of the cross and half of the ball are used, but the lack of the rear halves of the objects can hardly be detected by a cat restrained in the stereotaxic apparatus. The objects are in the position of rest. When the cross enters the window, the lower marker probe is activated by the ball, and when the cross leaves the window, the upper marker is activated. Symbols: *L*, left; *R*, right.

to record from the region receiving a projection from the area centralis. Five penetrations were usually performed in both banks of the lateral sulcus at about AO level. In each pentration about 10 cells were collected. Upon isolation, the reactivity of a given unit was checked and the receptive field was approximated through the use of a light slit. Units that were unresponsive to the slit were stimulated with one or both objects attached to white sticks (the slit as well as the objects were moved by hand). When a cell was found to be reactive, the objects were presented automatically three times in alternation. The intertrial intervals averaged 20 sec, and after every penetration a duration of approximately 30 min elapsed. Unit responses were recorded on film.

RESULTS

The cross and the ball typically elicited clear ocular-following-reflexes during an entire recording session. The appearence of the object in the upper part of the window evoked a saccadic movement, and then the eye followed the object. After the disappearence of the object behind the lower margin of the window, the eye returned to the position of rest. In agreement with our earlier results (4), both objects evoked following-reflexes of the same amplitude and duration in each cat, and no impairment of the reflex was found in any of the group (Table I). This finding also held constant for the rate of habituation of the reflex.

TABLE I

Ocular-following reflex and its habituation. Symbols: Hc, hood-reared group with "cross" training Hb, hood-reared group with "ball" training; H, inexperienced hood-reared group; N, group of normal cats

Group	Mean size (deg) of the reflex in the first five trials				Mean size of the reflex in 11–13 trials expressed as percentage of the original size			
	Cross		Ball		Cross		Ball	
	mean	range	mean	range	mean	range	mean	range
Hc (n = 4)	19	11–26	21	11–28	79	53–100	73	60–81
Hb (n = 4)	17	10–22	17	11–24	64	18–140	64	33–;127
H (n = 4)	20	16–29	20	13–29	58	24–100	58	6–105
N (n = 8)	17	10–28	15	3–29	54	8–100	53	17–100

The density of isolated units appeared to be similar in all groups (Table II), and the considerable amount of individual differences were presumably attributable to differential electrode impedance. Conversely,

TABLE II

Density and reactivity of units

Group	Number of isolated units		Number of units in 1 mm of track		Percentage of units reactive to standard objects	
	mean	range	mean	range	mean	range
Hc	50	46–54	7	3–12	51	40–57
Hb	50	45–58	10	8–12	57	46–70
H	47	34–53	8	6–14	39	32–53
N	52	38–70	9	6–14	26	18–37

there were more reactive units to our standard stimuli in the hood-reared cats with play-box training than in either normal or hood-reared control subjects ($p < 0.05$, Duncan's test) (Table II). Moreover, in the experienced hood-reared cats the average responses tended to be stronger ($F = 5.49$, $df = 9/67$, $p < 0.01$) (Table III). Although the precise position of the receptive fields was not investigated, in the great majority of cells they were certainly within the area centralis.

TABLE III

Percentage distributions of units according to the mean intensity of responses to both stimuli. Symbols: +, the response is weak; ++, the number of spikes is about doubled; +++, the number of spikes is about threefold; ++++, the number of spikes is at least about fourfold. In the inhibitory responses the number of spikes is respectively slight, two, three or at least four times decreased

Group	Intensity of response							
	+		++		+++		++++	
	mean	range	mean	range	mean	range	mean	range
Hc	34	25–41	25	13–33	33	18–42	8	6–12
Hb	24	20–33	34	26–36	32	22–40	10	4–18
H	50	23–63	32	27–38	12	7–26	6	0–18
N	56	44–71	20	8–25	17	0–31	7	0–21

Nearly all of the units responded to both objects, and in about 60% of the units, the intensity of the response was approximately equal (Table IV). The criterion for inequality of responses was that in two pairs of trials the response to one object was stronger and in one pair the responses were equal. In group Hc, the cross seemed to evoke a stronger average response than the control object (Table IV). In the remaining three

TABLE IV

Stimulus-dominance distributions (%) of units. Symbols: c, the response is evoked only by the cross; c > b, the response to the cross is stronger; c = b, the responses to both stimuli are equal; c < b, the response to the ball is stronger; b, the response is evoked only by the ball

Group	Stimulus-dominance							
	c	c > b		c = b		c < b		b
	mean	mean	range	mean	range	mean	range	mean
Hc	1	21	10–30	66	55–75	11	4–20	1
Hb	0	16	5–27	65	59–71	19	14–24	0
H	1	22	16–25	57	50–63	19	16–25	1
N	1	18	0–44	55	23–81	24	0–50	2

groups the mean percentages of units showing a stronger response to the cross were similar to those of units responding stronger to the ball.

Maintained activity was systematically recorded in reactive units only. Mean frequency seemed to be lower in cats with stimuli exposure in the play-box than in either hood-reared or normal controls (Table V). Possibly the units engaged during the play-box training had less frequently maintained activity.

TABLE V

Percentage distributions of reactive units according to the frequency of maintained activity

Group	Number of spikes per second								
	< 1		1–5		6–10		11–15		15 <
	mean	range	mean	range	mean	range	mean	range	mean
Hc	47	35–58	36	26–45	11	3–20	2	0–4	4
Hb	43	37–48	44	40–46	10	0–19	3	0–9	0
H	29	23–38	57	40–62	13	0–21	1	0–5	0
N	33	8–63	45	0–64	15	7–25	7	0–24	0

DISCUSSION

Our main finding is that in the experienced hood-reared cats both exposed and control objects were powerful stimuli for area 19 within the projection of the area centralis. These objects were less effective in the normal and hood-reared controls. Such results suggest the following conclusions concerning area 19: (i) In inexperienced hood-reared cats many cells are "uncommitted". (ii) During early experience many cells are engaged by the exposed object. (iii) The engagement is not very specific (area 19 seemed only to register the information that the kitten attended to a small object). This conclusion was unexpected since receptive fields of neurons in area 19 show a high level of complexity. (iv) In normal cats, many cells are engaged specifically by various stimuli and thus they were unresponsive to the standard stimuli employed. These conclusions obviously need further experimental confirmation with use of a greater variety of visual objects.

The comparison of the present results with previous data (4) shows that in hood-reared cats early visual experience affects the neurons in area 19 and in area 17/18 differently. In area 19 both visual objects (exposed and control) became evenly strong, whereas in area 17/18 the exposed object was stronger. These differences are in favor of a hypothesis (see 2) that area 19 and areas 17 and 18 process visual information in parallel rether than in a series. It should be noted that in addition to the input from areas 17 and 18, area 19 has major input from superior colliculus via the lateral nuclear complex of the thalamus.

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