VISUAL RESPONSES OF NEURONS IN THE CLARE–BISHOP AREA OF THE CAT

Krzysztof TURLEJSKI

Department of Neurophysiology, Nencki Institute of Experimental Biology
Warsaw, Poland

Abstract. Single unit responses in the Clare–Bishop area of the pretrigeminal cat were analyzed using stationary and moving visual stimuli. Of the units responding, 80% could be influenced by a 0.5 sec diffuse flash, most displaying inhibition or excitation to both “on” and “off”. In most units responses to stationary shapes were not very specific. Responses to moving stimuli were strong and directional preference was usually present. For the majority of cells the optimal speed of movement was in the range from 100 to 800 deg/sec, and some cells preserved their direction preferences when the speed was over 1,500 deg/sec. The direction preference could be reversed depending on the speed of movement, location in the receptive field or the shape of stimulus.

INTRODUCTION

The Clare–Bishop area is situated in the medial bank of the middle suprasylvian sulcus in the cat (17, 22, 26, 32, 42, 44). The subcortical input to this area comes from the thalamic lateral posterior nucleus (14,17), receiving strong afferent projection from the tectal and pretectal regions (3). A second input comes from the ipsilateral (8, 17, 21, 36) and contralateral (17, 21) visual cortex. Afferents from the LGN probably do not reach this area (17). Efferent fibers from the Clare–Bishop area terminate in the thalamic postero-lateral complex (17, 28, 29, 33) tectal and pretectal areas (28), visual cortex (17, 37), area 6αβ (17) and the anterior border of area 20 (17). Through the corpus callosum efferent fibers reach only the other Clare–Bishop area (17, 36).
Cells of the Clare–Bishop area react strongly to visual stimuli (15, 22, 45). Hubel and Wiesel (22) showed that the receptive fields are larger than in visual cortex, sometimes occupying a quadrant of visual field. Responses of the cells were described as of the “complex” or “lower order hypercomplex” type. Cells responded weakly to stationary, but strongly to moving stimuli, usually demonstrating a preferred direction.

Wright (45) reported somewhat different features. He found only small receptive fields (2–7 deg in diameter), and those units which he named “class III” gave strong “on–off” responses to a spot flash, without a preference to stimulus orientation or shape. Moving stimuli evoked “hypercomplex” responses from these cells. Other cells reacted only to the moving stimuli in a “complex” or “hypercomplex” manner, preferring velocities lower than 25 deg/sec.

Griisser (15) found that responses depended strongly on the direction and velocity of stimulus movement. Cells responded to movements as and orientation to the axis of movement also influenced the responses.

Because the association cortex was found to be involved in some visual functions (6, 7, 9, 23), and the Clare–Bishop area is one of the visually reactive parts of the cortex, further investigation of its responses to visual stimuli, seemed worthwhile. In the present paper the reactions to moving stimuli and changes of illumination were the main point of interest.

MATERIALS AND METHODS

The experiments were conducted on 13 adult cats, weighing 2–4 kg. Responses of 150 visually reactive units were analyzed.

Before an experiment the brain stem of the animal was transected pretrigeminally under ether anesthesia, according to the technique of Żernicki (47). Gallamine (Flaxedil–SPECIA) was administered intravenously (5–7 mg/hr x kg), and artificial respiration at the rate 16/min was applied. Eyelids were removed and the corneas were protected with contact lenses. Pupils were dilated with phenylephrine (neosynephrine hydrochloride 2.5%/ Winthrop). The positions of the optic disks in reference to the coordinates of the screen were measured with a reversible ophthalmoscope. Each hour 5–7 ml of physiological saline with 5%/ glucose was injected subcutaneously. The temperature of the cat was maintained between 37 and 38°C.

Craniotomy was made along the medial suprasylvian sulcus. The dura was removed and then an open chamber was fixed and filled with 2%/ agar. Action potentials were recorded with glass electrodes filled with 3 M KCl, with a resistance of 5–15 MΩ, as measured with 1 msec rectan-
gular pulses. The electrode was introduced at an angle 30° laterally from the vertical. It penetrated the cortex 1 mm medial to the suprasylvian sulcus. The AP coordinate was chosen according to the data described in the preceding paper (43).

The stimuli were presented binocularly. A tangent translucent screen, 50 cm in front of the cat, was scaled in rectangular coordinates with a nodal point at the midline, on the level of Horsley–Clarke horizontal zero. The luminance of the screen was $2 \times 10^{-2}$ cd/m² and that of the stimuli 2–4 cd/m². Scattered light from the stimuli increased the background luminance to $4 \times 10^{-2}$ cd/m² at a distance 2–3 deg from the stimulus. Light and dark spots, edges, slits and tongues of size 2–40 deg were projected from a distance of 1.5 m. Stimulus movement was generated by a revolving mirror driven by the solenoid from an EEG DC recorder connected to a trapezoid wave generator. The mirror reflected the stimulus from a slide projector onto the screen and the movement on the screen was variable from 1 to 3,000 deg/sec at displacement of up to 80 deg. With another mirror we were able to alter orientation of stimulus. A shutter, governed by rectangular pulses from a stimulator, controlled the projection of stationary stimuli. Time course of illumination onset and cessation was 7 msec. It was possible to illuminate a field of $60 \times 70$ deg².

The borders of visual receptive fields were established with hand-moved stimuli. Maintained activity and responses of the cell were tested with an ANOPS-2 on-line digital analyser. Its interval histogram (IH) and post-stimulus histogram (PSH) analyses have 512 bins of regulated width. The types of responses were described according to their first phases, and the strength of response (as well as latencies to stationary stimuli) were measured. The strength of response was determined by the maximal (for inhibition, minimal) rate of impulses, i.e., proportional to the maximal (minimal) number of impulses in a bin. If the rate of impulses in two responses differed by more than 25%, the responses were classified as of different strength.

RESULTS

About 45% of the units responded to the stimuli. The maintained activity of 69 reactive units was tested. In the standard illumination 38 cells had a mean frequency of between 0.1–10 imp/sec, and 14 had lower rates. The activity was frequently irregular, and in some cases a bimodal IH was obtained. The units generated “burst type” spikes superimposed on the slow, stochastic activity.
Fig. 1. Responses to diffuse flash. A: Examples of types of responses. In vertical columns, responses of the same type to “on” phase, and in horizontal rows— to “off” phase. E, excitation; I, inhibition; 0, lack of response. In lower row, at right, lack of response to diffuse flash. Every PSH is a sum of 32 responses. Time of analysis 3.3 sec. Light “on” lasted 0.5 sec from the beginning of analysis (see marker). The scale of bin content (length 5 imp/bin) at left of each histogram. B: Number of cells of the respective type.
Responses to stationary stimuli

About 80% of the reactive units responded to a diffuse flash. PSH analyses made for 95 units showed all the possible types of response (Fig. 1). The most frequent were the units responding with inhibition to “on” and “off”; many were of the “on–off” or “off” type. The latency of the response to “on” was usually 20–60 msec, but sometimes was over 100 msec, especially when inhibition occurred. Some cells changed their maintained activity for up to 3 sec after a diffuse flash. Changes of maintained activity were recorded too, if the background illumination was changed.

Thirty four units were tested with spot flash stimuli, 9 of them did not react. Most cells responded similarly to the stimulation of each part of the receptive field (Fig. 2). The type of response was usually the same as to the diffuse flash. This was also true of units whose maintained activity was depressed at both the “on” and the “off” phases. Some of the units were orientation selective or responded to the shape of the stimulus.

Responses to the moving stimuli

Ninety six units were tested with moving stimuli. Except for 12 units that were investigated for only a few minutes, all were reactive to the stimuli. The responses of 31 units to various directions of movement were tested. Twenty seven units showed direction sensitivity (Fig. 3). The null direction of 21 units was 180 deg from the preferred one. In half of the cases the sector of preferred reactions was narrower than 90 deg.

In two of four investigated fields portions of the field could have different preferred direction of movement than did the whole receptive field. For unit MA-7-5 the preferred directions were downward and towards the midline (Fig. 4), but in the parts of the receptive field where the responses were weaker the preferences could reverse or there was no preference (Fig. 4Aeh, Fig. 4Bf). Neither the direction sensitivity (Fig. 3) nor its changes (Fig. 4) were connected with differences of responses to the stationary stimuli in various parts of the receptive field. Homogenous responses to the stationary stimuli did not exclude specific responses to stimulus movement, and the units were direction sensitive (Fig. 5).

Responses to various speeds of movement were investigated in 24 units. The units usually preserved their direction preference throughout a broad range of speeds. For example, unit MA-3-8 (Fig. 6) responded only to upward movements when the speed changed from 100 to 1,600
deg/sec. Outside this range it did not react. Direction preference proofs that the responses depended on the movement of stimulus, and not the change of illumination. When stimulus moved with the speed 1,500 deg/sec, it passed receptive field of the cell in 4 msec. Then, either the differentiating processes could act in such a short period, or subthreshold influences were exerted from broad area outside the receptive field. In most of the investigated units the intensity of response was maximal when the movement velocity was in the range from 100 deg/sec to 800 deg/sec (Fig. 7).

Fig. 3. Direction of movement preference. Unit MA-4-10. A: Every PSH is a sum of 64 responses. Time of analysis 3.3 sec. Light rectangle 2 X 5 deg entered receptive field (broken lines) with its shorter border from various directions. Speed of movement about 100 deg/sec. Histograms show responses to two opposite directions of movement (according to arrows). Two periods of movement (slopes of the marker) are separated by periods when stimulus remained at the end of its traverse (flat parts of marker). B: Strength of responses to movements in various directions, as measured by maximal frequency of impulses. Strength proportional to length of arrow (scale under the vectogram). For three ipsilateral directions no response is seen.

Fig. 2. Responses to spot flash in various parts of receptive field. Unit MA-12-13. All parts of the field responded similarly, and only the strength of response varied. Every PSH is a sum of 16 responses. Time of analysis 3.3 sec. Stimulus (light rectangle 2 X 5 deg) was shone at points where the histograms are centered. Light lasted 0.5 sec from the start of the analysis (see marker). The most distant parts of field were off the screen. Responses of those parts, when investigated by hand-moved stimuli, were of the same type.
Fig. 4. Differences in direction preference of various receptive field parts. Ceil MA-7-5. A: Vertical and horizontal movements. PSH's are sum of 32 responses. Calibration of 10 imp/bin in g is common for all the histograms except d and j, which are calibrated separately. Time of analysis 1.64 sec. Stimulus: $2 \times 10$ deg light rectangle entering receptive field (broken lines) with its longer border. Phases of movement shown in c. Numbers under histograms, movement velocity. When stimulus moved in excitatory part of receptive field, directions downward (i, j) and to midline (d) were preferred. The preference could reverse in the distal part of receptive field (e, f) or diminish considerably (h). Shift of stimulus position producing the changes was small (h, j) compared to size of receptive field and stimulus. Because a tangential screen was used, the speed of movement was variable, but this was not crucial for responses (compare a, d and j). B: Oblique movements. The calibration in c also refers to a, b and f, that in e — also to d. In the upper row of histograms the strength of response is much lower than in c. In lower row both the changes of strength of response and preferred direction on the border of the field are shown (f).
Fig. 5. Direction preference of unit MA-12-13 which responded preferentially to fast, downward movement. When tested with spot flash, its field gave homogenous responses (Fig. 2). Every PSH is a sum of 16 responses. Time of analysis: upper PSH, 13.2 sec; second PSH, 6.6 sec; lower PSHs, 1.64 sec. Light 2 × 5 deg rectangle moved across central part of receptive field. Arrows under histograms show beginning of movement in a direction, and numbers the velocity.

In six units the relation of responses to the speed of movement was more complex. The units changed their direction preferences when the speed of movement was changed. For example, the unit MA-15-6 preferred horizontal movement from the vertical midline to the contralateral side when the speed of movement was 50 deg/sec (Fig. 8), but as the speed increased, the preference disappeared and at 200 deg/sec it reversed. Still faster movements inhibited the spontaneous activity of the unit. The unit changed its preference, because the optimal speeds for the movements left and right were different. In other units the strength of response to movements in one direction was constant and to the opposite movement the response changed (increased or decreased) with the change of speed, and this caused the change of preferred direction. Direction sensitivity changes in one unit could depend on more than one variable. For example, unit MA-4-10 changed its preferred direction
Fig. 6. Responses to various speeds of movement. Unit MA-3-8. Horizontal movements did not evoke a clear response of the unit. When the stimulus moved in the vertical orientation, unit preferred the upward direction, if the stimulus velocity was between 50 deg/sec and about 1,500 deg/sec. Outside the range, the responses ceased. Two phases of excitation can be seen; their dependence on speed of movement was different. Downward movement inhibited spontaneous activity. A: PSH of responses to various speeds of movement. Every PSH is a sum of 32 responses. The scale of the number of impulses per bin as in g. Time of analysis: a, 13.2 sec; other histograms, 1.64 sec. Stimulus 5 X 2 deg light rectangle. Under each histogram — the averaged shape of potential controlling the stimulus movements. Directions are indicated with arrows and the speed of movement with the numbers under histograms. For technical reasons the opposite velocities were not equal. B: The receptive field (broken line) and the way of stimulus movement in relation to the coordinates of the screen. C: Maximal frequency of impulses in the first (I) and the second (II) phase of response to the various speeds of upward movement. D: The duration of the responses phase I and II. E: The duration of the maintained activity inhibition by the downward movement.
Fig. 7. Distribution of movement velocities producing maximal responses of cells. White bars, numbers of cells responding maximally when the movement velocity (indicated below) was applied. Black bars, numbers of cells ceasing to react directionally when the velocity exceeded that value. Total number 27 cells.

when either the speed of movement or stimulus was changed (Fig. 9 and 10). The changes were not caused by the variability of responses, because the same unit responded after long periods in a very similar way to the same stimulating situation.

DISCUSSION

More than 50% of the units in the Clare–Bishop area did not react to visual stimuli. It is possible that vision is not the only modality influencing this area. Non-visual cells have also been found in the other parts of the cat's association cortex (10–12). However, it is possible that the pretrigeminal transection influenced the number of reactive units, because this lesion can depress the spontaneous activity of units in the suprasylvian gyrus without a change in EEG activity (5).

Most of the units responded to a diffuse flash, in contrast to the observations of Hubel and Wiesel (22) and Wright (45). However, most units in the visual cortex of unanesthetized cats are also reactive to this stimulus (31, 34). It seems that these responses are frequent in the waking brain.

In agreement with Hubel and Wiesel (22), Wright (45) and Grüsser (15), the strongest and most specific responses were evoked by moving stimuli. Data were insufficient to classify the units according to Hubel and Wiesel' criteria (19–21). Most of the units showed direction preferences. Consistently with Wright's (45) data, the preferred sector was usually broad and the null direction in most cases was 180 deg from the preferred one.
Fig. 8. Dependence of the direction preference on the speed of movement. Cell MA-15-6. Preferred direction is opposite for horizontal movements faster and slower than 100 deg/sec. When stimulus moved vertically (way of movement shown in Figure) unit preferred downward movement in the full range of effective speeds (2-160 deg.). Responses were optimal at 40 deg/sec. A: Receptive field broken line) and directions of movement in relation to coordinates of screen. Stimulus was $2 \times 5$ deg slit of light. B: PSHs of responses to horizontal movements. Every PSH is a sum of 32 responses. Time of analysis: a-d, 13.2 sec; e, 3.3 sec; f-i, 1.64 sec. Calibration in impulses per bin at right of histograms. Under each histogram — the averaged shape of potential controlling the stimulus movement. Movement velocities are indicated by numbers and arrows under histograms. In a, b, and c speeds of opposite movements were different: C: Duration of responses for movements left and right. D: Maximal impulse frequency of responses. Line with dots indicates level of maintained activity.
Fig. 9. Dependence of the direction preference on speed of movement. Cell MA-4-10. Full characteristic of unit's direction preferences shown in Fig. 3. A: Position of receptive field and direction of movement of 6 deg spot stimulus. B: PSH of responses. Each PSHs is the sum of 64 responses. Scale for impulses per bin common for all histograms. Time of analysis: a-c, 13.2 sec; d, 6.6 sec; e, 3.3 sec; f-g, 1.64 sec. C: Duration of responses. Two phases of the response to upward movement shown independently. D: Maximal impulse frequency in the response. Upward direction preferred when movements were slower than 50 deg/sec, then the preference reserved. For velocities faster than 100 deg/sec maximal frequencies for opposite movements were very similar.
Fig. 10. Dependence of preferred direction on the stimulus shape. Unit MA-4-10. Strength of reaction and direction preference can be changed with change of stimulus shape. Each PSH is the sum of 64 responses. Scale for impulses per bin in c is common to all the histograms. Time of analysis 3.3 sec. Velocity of movement 90 deg/sec. Point of each stimulus, marked with asterisk, moved vertically in the directions showed in the Figure. The stimuli were light inside the contours, and their shapes are shown under histograms. There is great difference in the responses to the stimuli elongated horizontally and vertically (b and f, c and g), and this is not caused by the size of stimuli (compare a, b and c).
Specific responses to very fast movement and changes of the preferred direction have not been previously described in this area. The significance of the directional reactions to very fast movements is not clear. In the natural environment, an object can cross visual field with the velocity 1,000 deg/sec if it moves 7 m/sec, 30 cm in front of cat, or if cat runs with this speed by an object. Till now it is not possible to say how the reactions are developed. Explanation of mechanisms must take into account the preferred direction changes with the change of velocity, shape of stimulus or stimulated part of the receptive field. The changes were found also in colliculus superior (41) so they are probably a more common property of visual reactions.

Visual responses of units in the Clare-Bishop area (15, 22, 45) and in other parts of the suprasylvian association cortex (10-12) seem to be similar. The main difference is that only the contralateral part of the visual field is represented in the Clare-Bishop area (22, 32, 43), whereas in other parts of the suprasylvian cortex the projection is bilateral (10, 12). Another difference is that many cells in the suprasylvian gyrus do not show direction specificity (11). However, this may depend on using different methods and evaluations (single responses and mean frequency as opposite to the PSH and maximal frequency). Other response properties such as the large size of receptive fields, specific responses to stimulus movement, “off” or “on-off” responses to diffuse flash and unclear responses to the orientation and shape of stimuli are very similar in all parts of the association cortex (10-12, 22, 45). Therefore these areas of cortex may be relatively functionally homogenous.

Although efferent fibers of the visual cortex strongly influence the Clare-Bishop area (8), the unit responses in both areas are different (18-22, 45). The main differences are in receptive field size, reactions to shape and orientation of stimuli and in the responses to fast movements (22). There are also some similarities between the visual and association cortices (e.g., the movement direction sensitivity, 10, 11, 18), and the similarities are still more frequent when the unanesthetized animals are investigated. For example, Sanseverino et al. (35) found direction sensitive responses to fast movements (330 deg/sec) in area 18 of the cat, and similar results were reported by Noda et al. (30, 31). The preferred direction could change with the change of stimulating situation (25). According to Ribaupierre et al. (34), many units in the visual cortex respond to a diffuse flash.

The unit responses in the lateral posterior nucleus are more similar to those in the Clare-Bishop area than in the visual cortex. Godfraind et al. (13) found that in all the nuclei of the posterior complex the retinotopy is unprecise and receptive fields are very large, as in the Clare-
Bishop area (22). Most cells responded specifically to stimulus movement, and the spot flash evoked "on-off" responses. Some units showing strong direction preferences, could change it when the stimulus-background contrast was changed (13).

The main visual input to the posterior complex comes from the superior colliculus. Receptive field sizes and responses in this structure are also similar to those found in the Clare–Bishop area (16, 27, 40, 41). There are also some differences, e.g., more clear retinotopy in the superior colliculus (4).

Thus, along the pathway superior colliculus–posterior complex–association cortex one can find some general functional similarities: cells react strongly to the dynamic aspects of the visual stimuli (movement, appearance and disappearance) and, on the contrary, responses to the static feature (shape and the position in the visual field) are less precise and less frequent.

In monkey's brain there is a cortical region functionally similar to the cat's Clare–Bishop area. The middle temporal visual area, receiving afferents from area 17 (1, 2, 38, 39, 46) and pulvinar (24) was found in the anterior temporal sulcus of various monkey species. Zeki (46) reported that cells in the area had broad receptive fields and gave specific responses to the direction of movement, but not to the shape of stimuli. Zeki (46) concludes that the area analyses visual object movements and he stresses its strong similarity to the Clare–Bishop area.

I thank to Dr. Bella Harutiunian, Dr. R. Tarnecki and Professor B. Zernicki for help in various stages of the paper.

This investigation was supported by Project 09.4.1. of the Polish Academy of Sciences and by Foreign Research Agreement 05.275.2 of the U.S. Department of Health, Education and Welfare under PL 480.

REFERENCES


37. SHOUMURA, K. and ITOH, K. 1972. Intercortical projections from the lateral wall of the suprasylvian gyrus, the Clare–Bishop area, of the cat. Brain Res. 39: 536-539.


Received 26 October 1974

Krzysztof TURLEJSKI, Department of Neurophysiology, Nencki Institute of Experimental Biology, Pasteura 3, 02-093 Warszawa, Poland.