Discharge Characteristics of Single Units in Superior Colliculus of the Alert Rhesus Monkey

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ACCUMULATING EVIDENCE suggests that the superior colliculus plays an important role in orientation and eye movement. Ablation studies have shown that destruction of superior colliculi interferes with spatial orientation and eye movement (25–29), although the evidence regarding the effects of such lesions in primates is conflicting (1, 7, 17, 18; and unpublished observations). Stimulation studies have disclosed that electrical or chemical stimulation of the superior colliculus elicits eye and head movement in several species (4, 11, 20, 22).

While most single-unit studies centered on the visual information-processing role of the mammalian superior colliculi (12–16, 30, 32, 33; M. Cynader and N. Berman, unpublished observations), a few studies have recently appeared that demonstrate eye-movement related unit activity (22, 31, 35).

The aim of the present study was to investigate the discharge characteristics of single units in the superior colliculus of the alert, unanesthetized monkey. We wished to assess both the visual receptive-field characteristics of units and the possible relation of unit discharges to eye movement. To carry out this plan one eye of each monkey was immobilized prior to the experiment by transection of the 3rd, 4th, and 6th cranial nerves. This made it possible to study in the monkey, whose head was restrained, receptive fields of units of the immobilized eye, and to relate the discharge characteristics of collicular units to the movement of the normal eye during both saccadic and smooth pursuit eye movements. M. Cynader and N. Berman (unpublished data) recently have shown that nearly all units in the monkey superior colliculus have binocular input with the receptive fields located in homologous retinal areas.

METHODS

Recordings were obtained from the superior colliculi of five alert monkeys (Macaca mulatta). One eye of each of these animals was immobilized.

Eye immobilization

The 3rd, 4th, and 6th cranial nerves were transected approximately 5 mm prior to entry of these nerves into the orbit through the superior orbital fissure. The animals were anesthetized with Nembutal and brain volume was reduced by infusion of mannitol (Osmitrol); 2 g/kg was infused over a period of 10–15 min. A bone flap was made under aseptic conditions over the temporal lobe, the dura was opened, and the temporal lobe was retracted gradually until the nerves were exposed. The oculomotor, trochlear, and abducens nerves were dissected from the dura with the aid of a dissecting microscope and transected. The 4th and 6th nerves were pulled out caudally, and a 3- to 5-mm section of the 3rd nerve was removed to impede possible regeneration. The dura was then sutured and the bone flap replaced, secured with stainless steel wire.

During the same operation, four stainless steel skull screws were implanted (8, 24), to be used subsequently to restrain the monkey's head. After recovery animals were returned to their cages for a period of 10–14 days.

This transection, in addition to immobilizing the eye, also 1) sever nerve input to the levator palpabrae causing a partial ptosis which becomes less and less pronounced over time, 2) paralyzes accommodation, and 3) dilates the pupil. The blink response persists. With proper care, the eye and particularly the cornea remain in excellent condition, provided that the ophthalmic branch of the 5th nerve has not been damaged. Ophthalmological examination of the monkeys used in this study did not reveal any

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defects in light transmission through the optic media. We have recorded unit discharges from the lateral geniculate nucleus and area 17 in such monkeys. The receptive fields of neurons in these structures mapped via the immobilized eyes are similar to those reported under standard recording conditions. Histological examination revealed no discernible damage resulting from retraction of the temporal lobe.

After transection of the 3rd, 4th, and 6th nerves, the eye remains immobilized 5–10 weeks. Subsequently, partial regeneration seems to occur as the eye begins to move again.

**Eye-movement electrodes**

Approximately 2 weeks after eye immobilization all animals were subjected to a second operation under general anesthesia. Eye-movement electrodes and recording wells were implanted.

The eye-movement electrodes we used for recording electrooculograms were a modified version of the d-c electrodes described by Bond and Ho (6). Small plastic cups (Delrin) measuring 2 mm in outside diameter and 4 mm in length, were prepared. One end of 25 µm silver wire, coated with Teflon, was inserted into the cup and was secured with epoxy glue. The cup was then filled from the other end with the silver, silver chloride, bentonite, and silver-epoxy mixture specified by Bond and Ho (6). Prior to implantation electrodes were tested for balance and stability and were sterilized in Zephiran.

Four electrodes, two for vertical and two for horizontal eye movement, were implanted into shafts drilled in the bone surrounding the orbit. The wires were led to a Sheats pedestal secured to the top of the skull.

Typically, 5–10 days after such an operation, the electrodes stabilize and remain reliable for several months. Examination of the tissue surrounding these electrodes has failed to show any adverse reaction even after 5 months. A resolution of 0.5° can be obtained with these electrodes if they are well placed. Considerable variation in the quality of the records can occur, however, among monkeys; if an electrode is in close proximity with muscle tissue, muscle artifacts will reduce resolution.

**Microelectrode placement techniques**

For localization of the superior colliculus with microelectrodes in the alert animal, a procedure similar to that of previous studies was employed (24). During the second operation, in addition to the eye-movement electrodes, one or two wells were implanted with stereotaxic guidance over the left or right colliculus, or both, through which the microelectrodes were subsequently lowered.

The well consisted of a ball and socket joint with a 21 gauge stainless steel tube passing through its center. The tube was lowered into the brain stereotaxically, to a point 8–12 mm above the colliculus. The base of the ball and socket joint was then secured to the skull using small skull screws and dental cement. The tubes were lowered down true to the stereotaxic plane in the anterior-posterior direction and at a 10° angle in the mediolateral plane to minimize damage to midline structures.

The position of the 21-gauge tube during the experiment could be varied over 10° in any direction, using a calibration device which was attachable to the outer part of the ball and socket joint. This joint was adjusted with set screws. A coordinate system was devised for making the penetrations.

This method permitted the exploration of a 5- to 10-mm-diameter area at the depth corresponding to the location of the colliculus. Previously, we have tried a number of other methods; the one described has worked the most satisfactorily and produced the least damage to structures overlying the colliculus.

After recovery from surgery, animals were placed in a primate chair. Recordings began 3–4 days after the operation.

**Head immobilization**

During experimental sessions the head of the monkey was secured to the frame of the primate chair in a manner similar to that described by Evarts (8). The implanted skull screws served for this purpose.

**Light stimulation**

The animal, placed in a Faraday cage, faced a removable tangent screen (Polacoat LS 60) 5' inches from his eye. A variety of procedures were available for the mapping and stimulation of receptive fields. A small hand projector (Jules Scotometer) balanced on a gimbal secured to the cage was used to map out the receptive fields. Once this was accomplished the fields were stimulated using an optic bench. The light source was either a xenon-arc lamp (Hanovia 970c) or a tungsten ribbon filament. Stimulus size and shape were varied with apertures. The light was interrupted with a galvanometer shutter (Schwartz) which provided rise and fall times of about 1 msec. This shutter was driven with a timer permitting exposure durations of 5–1,000 msec (23). The light then passed through a mirror galvanometer and a
prism. The mirror galvanometer, driven with a waveform generator (Wavetek 012), enabled us to move stimuli at various rates and with various waveforms across the visual field. The prism was used to vary the orientation of this movement. Stimulus intensity was generally kept 1.0–2.5 log above unit-response threshold.

Eye-movement recordings

The eye-movement signals were amplified using d-c, chopper-stabilized, differential amplifiers, one for horizontal and one for vertical eye movement (Hewlett Packard, 8809A).

Eye-movement calibration was achieved by a method previously described (24). A perimeter was placed in front of the animal at a distance of 18 inches. This perimeter had 0.75° holes in it every 10° in the horizontal, vertical, and diagonal meridians. Each hole was covered with a rubber stopper. For calibration, rubber stoppers were removed one at a time and the experimenter looked at the animal through the hole. The exposure of an opening and the appearance of the experimenter’s eye or other objects, induced the monkey to look at this location with great consistency. The moment of looking was registered by pressing a switch. The signal thus obtained, along with the eye movement, was recorded on magnetic tape or on a strip-chart recorder (Visicorder 906c).

Unit recording procedures

Glass-coated platinum-iridium electrodes (34) were used for most of the penetrations, with 1.5- to 2μ tips, an exposed shaft of 20–30 μ, and capacitances of 15–35 pf (3). Electrodes were etched using 0.004-inch platinum-iridium (70–30%) wire. After the glass coating and testing, electrodes were placed into Teflon-coated, 50-gauge stainless steel tubes, and the junction was insulated with Insulex. These electrodes were lowered into the implanted 21-gauge tube. To facilitate this process the 21-gauge tubes were filed off one-half way across over a 4–5 mm distance at the exposed end prior to implantation. The microelectrode shaft could thus be laid against the inner surface of the tube prior to lowering. A low-power magnifying lens aided this procedure.

After the electrode was lowered to a point just short of its exit from the tube, a microdrive was attached to the ball and socket joint. The electrode was secured to the drive and lowered hydraulically during recording. The microdrive consisted of two cut-down syringes. The syringe at the head was housed in an aluminum frame fitting onto the ball and socket joint. The other syringe was attached to a micrometer. A Teflon tube connected the two syringes.

The signals from the microelectrode passed through a conventional head stage and were amplified using Grass a-c preamplifiers (P511).

The data gathered were recorded on magnetic tape using an FM tape recorder (Honeywell 8100) or were displayed on a strip chart recorder (Visicorder). For some conditions, histograms were obtained by means of a computer of average transients (10).

General procedure

After the head of the monkey was secured, the cables for eye-movement recording attached, and the microelectrode lowered, the monkey was positioned in the Faraday cage. Prior to each experimental run the immobilized eye was refracted and contact lenses were applied as necessary to obtain the proper focal length to the tangent screen. The optic disk and the fovea were mapped onto the tangent screen using a reversible ophthalmoscope. The electrode was then advanced with the microdrive until the colliculus was located.

Recordings from the first two monkeys centered primarily on the superficial layers of the colliculus. Subsequently, detailed analysis was devoted increasingly to the deeper layers.

When a unit was sufficiently isolated to be discerned on the loudspeaker, we typically proceeded as follows: 1) The moving eye was occluded by placing a shaped ping-pong ball section in front of the eye. The occluder was painted black and was glued to a stalk which, in turn, was attached to the frame of the chair with a Flexibar. The receptive field of the unit driven through the immobilized eye was then mapped to determine its size, shape, and responsiveness. The field was subsequently stimulated either by flashing stimuli of various shapes and sizes onto the screen or by moving stimuli across the field with different waveforms. The optic bench, waveform generator, and the shutter timer were used for this purpose. Portions of the unit responses and eye movements were recorded and analyzed with stimulus-time histograms (10). The background illumination in most cases was kept in the photopic range. Stimuli were generally 1–5 log units above unit response threshold. 2) The immobilized eye was occluded and the moving eye was uncovered. Under this condition the relation of the unit to eye movement was studied. Eye movements were either spontaneous, with the monkey looking around in the room, or were elicited by presenting and moving objects around in the visual field. 3) Unit response was tested in the dark by closing the door of
the light-proof Faraday cage. Occasionally unit activity was also investigated with both eyes unoccluded.

Recordings were undertaken daily except for weekends, with typically one or two penetrations made per day. Care was taken to sterilize the electrodes and instruments used. In addition, once a week animals were injected with bicillin. Animals were released from the head holder after each experimental session.

After termination of the experiment, the animals were sacrificed and the brains were prepared for histology. Frozen section of 25 μ were cut in the area from which records had been obtained and every second or fourth section was stained with cresyl violet. The electrode tracks, some of which were marked with lesions, were reconstructed and related to the penetrations made during the experiment.

RESULTS

The results of this study identified two broad classes of units in the superior colliculus of the monkey; one class responded only to visual inputs while the other was associated both with eye movement and visual input. We recorded from the right colliculus of three monkeys and from both colliculi of two; in a total of 86 penetrations, we obtained 243 units in the superior colliculus, of which 78 were eye movement related. The majority of neurons related to eye movement also had visual receptive fields.

Units responding to visual stimulation

Units within 1.5 mm of entry into the superior colliculus responded almost exclusively to visual stimuli. In general these units were differentially sensitive to stimulus size, but not to stimulus shape, orientation, wavelength, and direction of movement. A distinction could be made between two classes of visual units. The first of these, which we termed “event detectors,” were broadly tuned in that they responded well to any stimulus of restricted size when such a stimulus was either flashed onto the receptive field or was moved across it at various rates. The second class of neurons, which we termed “jerk detectors,” differed from the event detectors in one notable respect: they responded poorly or not at all to smooth stimulus movement, but discharged vigorously to rapid, jerky stimulus displacements within the response field. All receptive fields were circular or slightly elliptical.

EVENT DETECTORS. Of the 165 visual units, 102 were classified as event detectors. These cells were most numerous in the superficial layers of the colliculus. The size of the receptive field area from which a response could be obtained in these units on presentation of visual forms varied from less than 0.5° near the fovea to 20° or larger in the periphery. In order to clarify the discharge characteristics of visual units in the superior colliculus, we made a distinction among the terms receptive field size, response field size, and optimal stimulus size. Receptive field size refers to the entire area which can influence the response of the unit. Response field size, by contrast, refers to the area within which stimuli can elicit spike activity in the unit. Optimal stimulus refers to the size of a stimulus which elicits the greatest number of spikes for a fixed mode of presentation. Typically, the response field is found in the center of the receptive field and is considerably smaller than this field. From the area outside the response field one generally fails to elicit spike activity in the superior colliculus; however, when this area is stimulated concurrently with the center of the field, the responses ordinarily elicited from the center are inhibited.

While the response fields of units in the superior colliculus varied considerably in size, the optical stimulus diameter seldom exceeded 5°, suggesting a considerable degree of size specificity. A typical example of an event detector demonstrating such specificity is shown in Fig. 1. The response field of this unit was 1°, as determined by mapping the area with small spots of light and moving stimuli; the field was located 3° from the center of the fovea. The receptive field was stimulated with disks of different diameters, all of them centered on the field. The data are shown in response histogram form. As can be seen, the largest response was obtained with a 0.3° spot. With larger spots less of a response was elicited; the 3.5° spot produced no discernible response at all. These observations suggest a center-surround organization which, however, is
different from that found in the lateral geniculate nucleus in several respects: the center of the receptive field of these superior colliculus units produces both an “on” and “off” response, even to very small stimuli; the responses are transient. These units, under photopic condition, are independent of sign of contrast; for a black stimulus on a light background one produces similar responses to those obtained to light stimuli on a dark background. In the surround area of the field one fails to produce a response to such stimuli as annuli or disks. This surround area does, however, have an inhibitory influence on the cell. The latency of these units ranged between 40 and 90 msec.

Event detectors respond vigorously to smooth stimulus movement, but are not directional, in apparent contrast to movement-sensitive cells in the cat superior colliculus (30, 32, 33). None of the units we obtained from the monkey in superficial gray and stratum opticum responded selectively to direction of movement. Figure 2 shows a typical example of responses to a 0.3° spot moving at a uniform rate of 6°/sec across the receptive field of a superior colliculus unit having a response field of 3°, centered 5° from the fovea. The stimulus was moved back and forth over a 24° distance with a triangular waveform. The first set of tracings shows the response to horizontal left-right movement; the second to vertical, up-down movement. The activity of the unit is shown along with a histogram which accumulated the responses over 30 sweeps. Similar responses were obtained with movements in opposing directions. Vertical sweeps produced slightly more activity due to the elliptical nature of the field. Following the exit of the stimulus from the response field a small degree of inhibition is evident. This inhibition is not readily attributable to the stimulation of the surround, since it was seen only when the stimulus left the field, regardless of the direction of stimulus movement. This unit responded over a broad range of stimulus-movement velocities; we found no evidence of “tuning” in this respect.

The cell shown in Fig. 2 had a high degree of spontaneous activity as well. Considerable variation was found among units in the rate of spontaneous activity. Some cells in the alert animal were very active without light stimulation while others under such conditions discharged only sporadically.

The third general consideration has to do with the question of shape specificity. None of the units we studied were shape or orientation specific. Similar responses could be elicited using squares, triangles, bars, or any of numerous other configurations. Similarly, the leading edge of a tongue brought into the field from any direction could have a variety of contours (concave, convex, serrated, etc.) without producing differential responses. The only critical factor was the size of the stimulus.

Finally, nearly all these units, as noted by others (M. Cynader and N. Berman, unpublished observations), appeared to be binocular. This was based on the observa-
tion that occlusion and exposure of the moving eye produced changes in discharge activity. Also, it was evident that when the moving eye was permitted to view the environment while the receptive field of the immobilized eye was repeatedly stimulated at high rates, the response became more erratic with bursts occurring after some of the saccades.

**Jerk Detectors.** In a region 0.9–1.5 mm down from the surface of the colliculus, we have found a population of 52 light-related units which differed from the event detectors in one notable way. These cells responded poorly or not at all to smoothly moving stimuli, whether the movement was within the response field or began outside the field and then entered it. A brief burst was occasionally obtained when the stimulus entered the field, but only for the first sweep. This unresponsiveness persisted at all velocities and directions of movement tested.

By contrast, these units responded well when stimuli of appropriate sizes were flashed onto the receptive field. An even better response could be elicited when such a stimulus was moved within the receptive field in a jerky manner, as was the case, for example, when the stimulus was displaced on the screen by driving the mirror galvanometer with a square wave. Thus, rapid displacements followed by a brief stationary period provided the optimal response.

A typical example of such a unit having a 4° response field located 7° from the fovea, is shown in Fig. 3. Two modes of presentation are shown: in the upper tracing the stimulus was moved within the receptive field with rapid displacements using a square wave; in the lower tracing the same stimulus was moved back and forth over the same distance at a smooth, constant rate using a ramp function. The unresponsiveness to smooth movement persisted with variations in velocity and in the area and direction over which the stimulus was moved.

In other respects these units were similar to event detectors. They also were size

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**Fig. 2.** Unit response to a 0.3° spot moved across the receptive field horizontally and vertically. Stimulus movement rate was 6°/sec. The spot was moved 24° in each direction. The histogram shows responses accumulated for 30 sweeps. Arrows show direction of spot movement. Discharges resulting from a single stimulus presentation are also shown.

**Fig. 3.** Discharge characteristics of a unit sensitive to a jerky stimulus displacement in the superior colliculus. Upper set of traces shows responses to a rapid displacement of a 1° disk (square wave); lower set shows responses to smooth movement. Response field of unit was 4°. Stimulus was moved within the field over a 3° area at 1.67 Hz.
specific, as indicated by Fig. 4, which shows stimulus-response histograms to different size stimuli. This unit, which had its receptive field located 18° from the fovea, had a response field of 13° in diameter, as assessed by flashing stimuli in various parts of the field. Yet it can be seen that the stimulus eliciting the optimal response was in the range of 1–3.5°. This observation highlights the fact, applicable to both event and jerk detectors, that the size of the response field and the size of the optimal stimulus are not identical.

Like the event detectors, these cells were independent of the sign of contrast, and were not selective regarding stimulus shape and orientation.

In addition to these two categories of cells we found a few units which habituated rapidly to all stimuli. They would respond for a few repeated stimulus presentations, but then would stop discharging. The most slowly habituating response for these cells was obtained when the central part of their field was illuminated with a small disk of light (1–5°) and a shadow was moved into this area by interruption of the beam behind the screen with such objects as pencils, fingers, etc. Too few such units were found to adequately assess their response characteristics other than the clear disposition to habituate.

Unit discharge and eye movement

It has generally been suggested that saccadic and smooth pursuit eye movements represent two distinct components of conjugate ocular motility. The function of saccadic eye movements is to acquire visual targets for foveal viewing, while smooth pursuit movements enable the organism to maintain targets on the fovea. These two kinds of eye movements frequently occur in close temporal proximity, particularly during tracking, when small corrective saccades appear superimposed on smooth pursuit movement which serve the function of centering the eye on moving targets. The following describes the response characteristics of single units in the superior colliculus in relation to saccadic and smooth pursuit eye movements.

The units described so far, the event and jerk detectors, did not seem to have persistent relations to eye movement. In the light, with the moving eye unoccluded, they occasionally discharged after a saccade, but this activity was by no means consistent. Such discharges would be expected in visually related units; with each saccade a new set of visual patterns impinges on the retina, some of which may fall into the receptive field of such units, thereby eliciting a burst of spikes.

In contrast to these units we found a
population of 78 cells, usually 1.5-2.5 mm down from the surface of the superior colliculus, which showed a clear-cut relationship to eye movement. All of these units discharged prior to saccades and their burst activity was specific in terms of the size and the direction of the saccade but was independent of the position of the eye in orbit. The onset of the burst preceded appropriate saccades 70-500 msec. Units in the right colliculus responded in association with leftward saccades including left-up and left-down: the converse was the case for the left colliculus. The majority of units related to eye movement also had visual receptive fields; these fields were typically located in that area of the visual field to which the eye moved after discharge-associated saccades. Those units which had their receptive fields near the center of the fovea responded in association with both small saccades and some smooth pursuit eye movements.

**UNIT ACTIVITY ASSOCIATED WITH SACCADIC EYE MOVEMENT.** A typical example of a unit related to saccadic eye movement recorded from the right superior colliculus is shown in Fig. 5. The trace in lines A and B show that this unit initiated its discharge prior to the saccade. The response is specific in terms of both saccade size and direction. Line C shows that a variety of saccades, including those in the same direction as the discharge-associated saccades but of a larger size, are not associated with unit activity.

The last segment in this figure shows that this unit could be driven through the immobilized eye, using a small spot of light which was moved back and forth within the receptive field with a square wave driving the mirror galvanometer. A clear response is obtained, but with less activity than that elicited prior to saccades. We found that 90% of the eye movement-related cells could be driven by visual stimuli; the response was typically erratic and quite weak. No reliable response could be elicited with stimuli driven by a triangular or sinusoidal waveform. Response latency to light varied from 50 to 90 msec.

The center of the visual response field of the unit shown in Fig. 6 was located 3.5° left and 3.2° up from the fovea and had a circular receptive field of approximately 5° in diameter. Saccade associated responses were obtained with left and up saccades not exceeding 7° in length. The best response occurred with 3-4° left and up saccades. Such responses occurred irrespective of the initial position of the eye in the orbit. Thus 3° left and up saccades were preceded by similar bursts when position of the eye in the orbit prior to the saccade was down, up, left, or right.

These findings suggest that 1) the discharge characteristics of eye movement units in the colliculus are specific with respect to the size and direction of saccades, and 2) that the receptive fields of these units lie in that area of the visual field to which the eye moves as a result of a discharge-associated saccade.

To further assess unit specificity in relation to eye movement, two kinds of quantitative analyses were carried out. In the first, the relation of unit discharge activity was studied in terms of the position of the eye in the orbit. This analysis failed to yield consistent data supporting our initial observation that these units are not directly concerned with coding the position of the eye relative to the head.

The second analysis stems from the hypothesis that the colliculus is part of the eye-centering system which enables the organism to acquire visual targets for foveal viewing. This system is involved in the coding of retinal points relative to the fovea, and is fundamental in eliciting eye movements specific to target locations regardless of the position of the eye in orbit. Unit activity was therefore analyzed quantitatively with respect to saccade direction and size. These two dimensions of each saccade were assessed in relation to the discharge activity of the unit. We found that all eye-movement neurons showed such specificity, the degree of which, however, varied considerably.

Records of a unit showing a high degree of saccade size and direction specificity are shown in Fig. 6. The direction and size of each saccade was plotted relative to the 0 point in the center of the figure which represents the fixation prior to the occurrence of the saccade. The open circles rep-
Fig. 5. Discharge characteristics of a unit related to eye movement. A, B, and C: unit discharge and eye movement in the light, moving eye unoccluded. D: response to a 0.25° light spot moved back and forth within the receptive field of the immobilized eye with a square wave; moving eye occluded. Stimulus marker displaced up and down represents onset and offset of light.

resent saccades not associated with unit activity. Black disks represent saccades preceded by a burst of spikes. The plot shows that this unit responded specifically in association with small left and slightly upward saccades. The area spread is about 4°. Larger saccades in the same direction as well as saccades in other directions are not associated with unit activity. Such a response, it should be clear, is obtained regardless of the initial position of the eye in the orbit.

The location of visual receptive fields of eye-movement units relative to the fovea corresponded closely to the response area plotted in terms of saccade direction and size in degrees. Twenty units were plotted in this fashion in detail. For these units the two areas were always in the same quadrant; in 85% of the cases the two fields
There are several sources of experimental error which may lead to a lack of correspondence between the location of the visual receptive field from the fovea and the saccade size and direction producing anticipatory unit discharges. These include the accuracy of visual-field mapping which is difficult because the visually evoked response is generally weak, the accuracy of mapping retinal landmarks onto the tangent screen, and the accuracy of eye-movement calibration.

The smallest fields were found for units which had their visual response areas close to the fovea. Saccade response fields as small as 3° were found in units whose receptive fields were within 1–3° of the center of the fovea. The assessment of such small saccades is near the limits of our present system. Areas of 0.5° or less would probably have been missed.

Figures 7, 8, and 9 show the saccade-associated response characteristics of another unit related to eye movement in the superior colliculus. In Fig. 7, a cumulative histogram was obtained from 30 saccade-associated unit responses. These data, having a bin width of 20 msec, show that the response of this unit begins about 200 msec prior to the onset of the saccade, reaches a peak at 20–40 msec before the saccade, and then rapidly declines after its completion. The insert shows the unit response to one such saccade.

Figure 8 shows the plot of this same unit, which had one of the largest response areas we have found. The saccade response field takes up more than a 15° area. An assessment of the relationship between saccade size and direction and the number of associated discharges was also made for this unit. To do this we analyzed unit activity for 254 saccades for horizontal and 248 saccades for vertical eye movement. The data were pooled in 2° steps for each of these directions over a range of 13° in the area of the response field. This then represents, for the horizontal analysis, a strip from down 3° to up 10° (Fig. 8) and for the vertical analysis a strip from left 2° to left 15°. These data are displayed in Fig. 9. The optimal response is seen at approximately 10° diagonally left and up. Smaller as well as larger saccades are associated with bursts of fewer spikes.

Of the 78 units related to eye movement only 8 showed eye movement-related activity both in light and dark. A typical example of such a unit is shown in Fig. 10. The upper set of traces was recorded in the dark, the lower set in light. The anticipatory response is sharper and clearer in the light. This unit did not appear to have a visual receptive field.
SMOOTH PURSUIT MOVEMENT. We have found that those units related to eye movement which have their receptive fields more than about 5° from the fovea did not respond during smooth pursuit movement. By contrast units whose receptive fields were located near the center of the fovea responded in association with both very small saccades and smooth pursuit movement.

A typical example of such a unit is shown in Fig. 11. The response field of this unit, as shown in section A, was very close to the center of the fovea. To define the field, a 0.25° spot was moved back and forth horizontally, vertically, and diagonally using 0.5° displacements. The center of this area, when stimulated in this fashion via the immobilized eye, produced a small but consistent burst. Weaker responses were obtained near the edges of this area. Sections B and C show the response to small (1–2°) saccades going left and up. Larger saccades, even in the same direction, were not preceded by a burst, as shown in section D.

The responses of this unit during smooth pursuit, as elicited by moving objects of interest in front of the monkey are shown in sections E-K. Only certain planes of pursuit produced discharges. In section E, a left-down pursuit is followed by right-up motion. The unit is relatively inactive. By contrast, diagonal pursuit going left-up and right-down is generally associated with unit activity. Discharges are greatest when the pursuit is uneven and when a corrective saccade occurs in the left-up direction. After such corrective saccades activity typically ceases. In section F the corrective saccade is in the direction of pursuit move-
ment, while in sections H and I the corrective saccade is in the direction opposite to the tracking movement. In section K it occurs just prior to the change in the direction of the stimulus movement.

These findings suggest that the activity of this unit increases when a target, which is being pursued, is no longer in the center of the fovea but enters the receptive field of the unit. The ensuing firing thus appears to result in a recentering of the eye on the target. Recentering may occur either by increasing or decreasing the rate of pursuit movement or by corrective saccades.

Topography and cytoarchitecture

All brains were sectioned and the penetrations were reconstructed. The histology suggests that event detectors are situated primarily in superficial gray and stratum opticum; jerk detectors appear mostly in griseum intermedium, and eye movement-related cells in album intermedium and griseum profundum.

The general topography we found supports earlier findings (30, 32, 33; M. Cynader, and N. Berman, unpublished observations). The left colliculus receives inputs from the right visual field and vice versa, with the vertical meridian representing the division between colliculi. The distinction applies also to eye movement-related units. Such units in the left colliculus are associated with saccadic eye movement to the right; the right colliculus is associated with movements to the left. Moving lateromedially in the superior colliculus results in receptive-field displacement in the visual field from down to up. Going from the posterior part of the colliculus anteriorly yields receptive fields going from lateral to medial in the visual field. The foveal and perifoveal regions are represented in the anterior region of the colliculus.

The response fields in the anterior region of the superior colliculus tend to be small, while recordings in areas representing increasingly greater distances from the fovea yield larger and larger fields. Figure 12
Fig. 11. Response characteristics of a single unit during saccadic and smooth pursuit movement in the superior colliculus. A: receptive field location relative to the fovea as mapped through the immobilized eye. B-D: unit responses during saccadic eye movement, immobilized eye occluded. E-K: unit responses during smooth pursuit. The burst-associated saccades are 0.5-2° in size.

shows the relationship of the diameter of the response field size and retinal location relative to the fovea. Two types of units are shown, the event and jerk detectors. The latter are shown as black disks.

The direction of our penetrations was close to the coronal stereotaxic plane. Since the surface of superior colliculus is at a considerable angle to this approach, our penetrations were actually in a ventroposterior direction in the colliculus. Thus there was a tendency for receptive fields to become displaced laterally as the microelectrode advanced. This was less pronounced in the anterior part of the colliculus where a relatively large portion of this structure represents the foveal and perifoveal areas.

Units discharging in association with eye movement were most abundant in the anterior portion of the colliculus. The location of the receptive fields of these units was generally close to the receptive fields of visual units located earlier during the same penetration. Thus when visual receptive fields of event and jerk detectors were close to the fovea, so were the visual fields of eye-movement units.

Discussion

The results of this study identified two broad classes of units in the monkey superior colliculus. The superficial layers of this structure contained the first class, cells responsive only to visual inputs. Two types were predominant, which we termed event detectors and jerk detectors. Nearly all units of either type appeared to have binocular inputs. Event detectors responded well to any stimulus of restricted size, and were sensitive to stimulus movement, whether smooth or abrupt, without being directionally specific. The jerk detectors, equally devoid of directional specificity, were unresponsive to smoothly moving stimuli, but responded well to flashes and
to any rapid stimulus displacements within their receptive field.

In the lower layers of the colliculus, cells related to eye movement predominated. These cells discharged in relation to particular saccades characterized by a specific direction and extent of rapid eye movement. In addition, most of these cells also had visual receptive fields. For any given saccade-sensitive unit this receptive field was located in that area of the visual field to which the animal moved its eye during the saccade. Units whose visual response fields were close to the center of the fovea responded in association with both small saccades and some smooth pursuit movement. Discharges appeared most pronounced when the eye movement was along a line drawn between the location of the fovea and the center of the receptive field as assessed via the immobilized eye. Movement in either direction along this line produced discharges, especially when the pursuit was uneven or when corrective saccades occurred in the direction which brought the target into the fovea.

The characteristics of visual cells we observed in the superior colliculus of the alert animal correspond closely to those reported by M. Cynader and N. Berman (unpublished data) in the paralyzed monkey anesthetized with N₂O. Under this condition as well, a distinction could be made between two classes of units in the upper layers of the colliculus: those which responded to any stimulus presentation, including smooth movement, and those which preferred flashes and rapid stimulus displacement. In the lower layers of the colliculus where we found eye movement-related units, M. Cynader and N. Berman (unpublished observations) encountered cells which responded erratically to visual inputs, preferred jerky movement and suddenly appearing stimuli, and tended to habituate on repeated stimulus presentation. It is likely that some of these cells were the same as our eye movement-related units. Nearly all the cells encountered by these investigators, including those in the lower layers of the colliculus, were binocular, with receptive fields located in homologous retinal areas.

The responses of visual units in the monkey colliculus differ from those of the cat in two respects: first, in the cat a high percentage of units appears to be directionally selective (30, 31; M. Cynader, and N. Berman, unpublished data), which is not the case in the monkey. Second, the distinction between the two most common types of visual units in the monkey, event detectors and jerk detectors, has not been made for the cat, although the phenomenon of habituation in the lower layers appears to be as common in the cat as it is in the monkey. It must be noted, however, that not all previous reporters have identified units in the monkey which we called jerk detectors. Humphrey (12) and Kadoya and Massopust (13) reported that all the units they studied in the rhesus and squirrel monkeys, respectively, responded well to smooth stimulus movement.

Units related to eye movement have been reported for the cat recently by Straschill and Hoffman (31) who found in the superior colliculus of the encephale isolé preparation that some units respond in association with saccades, and others in association with slow eye movements. Eye
movement-related activity in the superior colliculus units of the alert monkey was reported recently by Wurtz and Goldberg (35) whose results are in many respects similar to ours. They also found units which discharged prior to saccades, although they did not find any visual receptive fields for the units they studied and noted only directional specificity of saccade-associated discharge.

The findings reported here indicate that in the monkey colliculus units related to eye movement are specific in terms of both the direction and the size of the saccade, and that the visual receptive fields of these units lie in the target area to which the eye moved as a result of the saccade. We should stress that such discharges were obtained during spontaneous eye movement in an unchanging, visually textured environment. Furthermore, our observations indicate that stimulation of the receptive fields of these units by visual stimuli is insufficient to elicit a rapid eye movement; such stimulation produces only weak responses and does not generally elicit saccades in the moving eye. It would seem then that the activity of these units must be gated by inputs from other structures mediating pattern discrimination and attention.

These observations support the hypothesis that the superior colliculus, in general, and the units related to eye movement, in particular, are involved in the mechanism of foveation involving both target acquisition by saccades and target maintenance during smooth pursuit (2, 11). Two of the basic functions of the oculomotor system are to enable the organism to move his fovea to targets of interest or relevance in the visual world and to maintain such targets on the fovea during movement. Thus when an object of interest appears in the visual field at some distance from the fovea, the location of this object relative to the fovea is coded and appropriate signals are sent to the oculomotor complex resulting in a saccadic eye movement, which brings the fovea to the target. If the target or the organism is in motion, smooth pursuit performs the function of keeping the target in foveal view.

The cells in the superior colliculus appear well suited to carry out part of these tasks. The event and jerk detectors, which are sensitive to stimuli of restricted size regardless of their shape, are thus equipped to code where in the visual field a stimulus has appeared. The jerk detectors, which are perhaps intermediaries between event detectors and eye movement-related cells, show specialized sensitivity for sudden appearances, thus filtering out conceivably conflicting signals which might arise when stimuli traverse the visual field during normal head and body movements. These units in turn probably feed into the eye movement-related units which must receive additional inputs from areas involved in visual pattern analysis and attention. Thus when a stimulus appears which attracts the attention of the animal, signals converge on the appropriate eye movement-related units; a discharge results which eventually activates units in the oculomotor complex resulting either in a saccadic eye movement or in smooth pursuit.

The mechanism of foveation, as also suggested by stimulation data (20, 21; and unpublished data), is coded in terms of retinal loci relative to the fovea. It would seem then that this system is not directly concerned with the location of the eye in orbit. Yet it is evident that the eye musculature and the final common path are coded in terms of the relative position of the eye in orbit. Recent studies suggest (9, 19, 24) that appropriate muscle contraction for the various positions of the eye are brought about by neuronal discharges in the oculomotor complex which increase or decrease their rate of firing in a linear fashion with changes in angular deviation of the eye in the orbit. These same units discharge in high-frequency bursts to elicit saccadic displacements. The hypothesis advanced here suggests that the visual origin of saccades initiated by these bursts in the neurons of the oculomotor complex are mediated in part by the superior colliculus.

Unit activity related to eye movement has recently also been found in the frontal eye fields of the alert rhesus monkey (5). The discharge characteristics of units in this area, however, are quite different from those reported here for the superior colliculus. In the frontal eye fields two classes
of units related to eye movement have been discerned. One class has been found to discharge, not before, but during or after saccades; some degree of specificity was found in terms of saccade direction, but not in terms of saccade size. The second class of units appeared to respond in association with the position of the eye in orbit. The difference in the activity of units in these structures suggests that the frontal eye fields and the superior colliculi are engaged in distinctly separate types of tasks in regulation and registration of eye movement-related activity.

Ablation and stimulation studies provide additional support for the hypothesis that the superior colliculus is involved in foveation. We (unpublished data) have shown that ablation of the superior colliculus in the primate results in the persistent inability of animals to accurately acquire targets in the visual world by saccadic eye movements even though the animal learns to orient appropriately and reach for objects accurately. Stimulation studies show that when the frontal eye fields, visual cortex, or the superior colliculus are stimulated electrically (100–300 Hz), saccades are elicited, the direction and size of which are independent of the position of the eye in the orbit (20, 21; and unpublished observations). This saccade size and direction is almost exclusively a function of the brain site stimulated. Prolonged stimulation of these structures results in a staircase of saccades with intervening periods of fixation. Part of this activity appears to be mediated by the colliculus; ablation of this structure eliminates saccades elicited by electrical stimulation of visual cortex. Paradoxically, frontal eye field stimulation remains effective even after superior colliculus ablation (unpublished observations).

SUMMARY

1. Single unit activity was studied in the superior colliculus of the alert rhesus monkey. One eye of each animal was immobilized prior to the experiment by transection of the 3rd, 4th, and 6th cranial nerves. Eye-movement electrodes were implanted around the orbit of the moving eye. During recordings the head was restrained, permitting the study of both the receptive fields of collicular units via the immobilized eye and their relation to eye movement as assessed by EOG records of the moving eye.

2. In the superficial layers of the superior colliculus units responded only to visual stimuli. These units were not specific regarding stimulus shape or direction of stimulus movement. They were selective, however, in terms of stimulus size. Two types of such units were discerned; one class responded well both to smoothly moving and stationary, flashing stimuli. The other class failed to respond to smooth movement and discharged most vigorously to rapid, jery stimulus displacements.

3. In the lower layers of the superior colliculus units associated with eye movement were found. These units fired in sharp bursts prior to saccades. Discharge was specific in terms of both the direction and the size of rapid eye movements and was independent of the initial position of the eye in the orbit. Most of these units had receptive fields which were located in that area of the visual field to which the fovea was directed as a result of a discharge-associated saccade. Some of these units discharged prior to saccades both in the light and dark.

4. Those units related to eye movement which had their visual receptive fields near the center of the fovea discharged both prior to small saccades and during smooth pursuit. These units appear to participate in the correction of retinal-target errors during tracking.

5. The results suggest that the monkey superior colliculus plays an important role in the foveal acquisition and maintenance of visual targets.

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