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THE SUPERIOR COLLICULUS AND MOVEMENTS OF THE HEAD AND EYES IN CATS

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SUMMARY

1. The superior colliculus has been studied in alert cats which were restrained and whose head and eye movements were monitored.

2. Microstimulation within the rostral part of the colliculus, which represents the central 25 deg of the visual field, evokes saccadic eye movements that carry the area centralis to that region of visual space previously occupied by the receptive fields of the cells that were stimulated ('foveation'). These saccades are not generally accompanied by a movement of the head.

3. At more caudal locations the visual receptive fields of collicular neurones lie at a greater eccentricity relative to the area centralis than the maximum possible deviation of the eyes from the central position in normal circumstances. At these sites electrical stimulation produces a combined movement of the head and eyes whose co-ordination is identical to that of natural gaze changes in response to novel stimuli. Prolonged stimulation results in the addition of further co-ordinated eye-head movements.

4. The addition of a movement of the head does not increase the area of visual space that may be foveated in a single gaze change. Movements of the head are compensated by the vestibulo-ocular reflex. The visual receptive fields of cells at more caudal locations cannot be foveated by a single gaze change.

5. A third class of response to electrical stimulation is also occasionally found in the caudal part of the colliculus. The head movement often begins before an accompanying eye movement and continues smoothly for the entire stimulation duration or until limited by the range of mobility.

6. Electrical microstimulation was never found to produce so-called 'goal-directed' eye movement, in which the eyes move, in a single saccade, to a fixed orbital position regardless of their starting position.

7. Ninety-nine cells were recorded from the superior colliculus and classified into four types based on their responses, or lack of responses, during or preceding eye and head movements. Type 1 cells did not show changes in activity prior to gaze changes Type 2 cells were inhibited prior to and during eye movements. Cells discharging before normal saccadic eye movements (type 3) were found only in the rostral part

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of the colliculus. Cells discharging before head movements (type 4) were found only in the caudal part.

8. These results are discussed with respect to the production of gaze changes in the cat.

INTRODUCTION

The optic tectum undoubtedly participates in the control of visual 'orienting' and localizing behaviour. Experimental evidence for this view comes from the use of lesions, electrical stimulation and, more recently, from the recording of single cell activity during natural orienting behaviour. Such studies indicate that in non-mammalian species the tectum is relatively more important in the organization of visual behaviour. Electrical stimulation of the tectum of fish evokes gross orienting movements of the body towards the opposite side (Akert, 1949; Feldman & Oslovsky, 1974). In the monkey, however, discrete movements of the eyes are the principal orienting movements evoked by brief electrical stimulation of the superior colliculus (Robinson, 1972; Schiller & Stryker, 1972). Amongst mammals, lesions of the superior colliculus cause gross impairments of orienting behaviour in hamsters (Schneider, 1967, 1969, 1970) whereas in monkeys (Wurtz & Goldberg, 1972*b*) and man (Heywood & Ratcliff, 1975) only subtle deficits of oculomotor behaviour result. Single-neurone recording of collicular cells of the monkey has failed to reveal cells concerned with any other aspect of orienting behaviour than eye movement (Robinson & Jarvis, 1974). In view of this phylogenetic variation it would be valuable to know the role of the cat's superior colliculus in orienting behaviour. Some workers have reported that electrical stimulation of the cat colliculus produces orienting movements of the whole body (Hess, Burzi & Bucher, 1946; Schaefer, 1970) but more recent studies have suggested that the cat's colliculus, like the monkey's, is concerned primarily with movements of the eyes alone (Stein, Goldberg & Clamann, 1976) although more complicated results have been described (Straschill & Rieger, 1973; Crommelinck, Guitton & Roucoux, 1977).

The retina projects directly to the superior colliculus and terminates in a retinotopic map that is similar in orientation for all species so far investigated (see Sprague, Berlucchi & Rizzolatti, 1973). In the monkey the eye movements elicited by discrete electrical stimulation of the colliculus carry the fovea fairly precisely to that point of visual space previously occupied by the visual receptive fields of cells in the vicinity of the micro-electrode tip (Robinson, 1972). This pattern of response is called 'foveation'. Thus the maps of sensory and motor function are neatly superimposed in the monkey colliculus. However, a large fraction of the cat's superior colliculus should, in principle, be unable, on stimulation, to produce such foveating eye movements because the oculomotor range of the cat is restricted to 25–30 deg from the central orbital position (Stryker & Blakemore, 1972; Blakemore & Donaghy, 1980). Thus, with the eyes starting at the position of rest, the part of the visual field more eccentric than about 30 deg cannot be foveated with a single eye movement. This part of the visual field is represented in the posterior part of the colliculus. It has been suggested that this part of the colliculus may use a different frame of reference to encode the targets of eye movement (Crommelinck *et al.* 1977).

In this study I have investigated the superior colliculus throughout the visual map. The anterior part of the colliculus appears to be involved only in eye movements, as in the monkey, but the posterior part is involved in head movements.

METHODS

Preparation and maintenance of the cats

Six docile cats were implanted with skull bolts by means of which their heads were attached to a lightweight metal superstructure (Blakemore & Donaghy, 1974) that could be fixed or allowed to rotate in the horizontal plane with the axis of rotation positioned close to the natural axis of head movements. Electro-oculographic (e.o.g.) electrodes (Bond & Ho, 1970) were implanted in the cartilage of the lateral border of each orbit and in the bony orbital ridges above and below the left eye, and Teflon-insulated silver wires were led under the skin to a small connector attached to the skull. For some cats the skull bolts were implanted through key-hole craniotomies in the skull, after Evarts (1968). Subsequently it was found adequate to imbed the heads of the bolts in dental acrylic cemented to the skull. A stainless steel cylindrical chamber was also implanted on the skull centred over the superior colliculus. Each cat was allowed a two-week recovery period and then trained to accept gentle restraint in a comfortable padded box with the head attached to the superstructure by means of the implanted bolts. All the cats rapidly came to tolerate, without any obvious discomfort, even quite long sessions in this condition. The preparation has been previously described (Blakemore & Donaghy, 1974, 1980; Harris, 1978).

Glass insulated microelectrodes (Levick, 1972; Merrill & Ainsworth, 1972) were used for single cell recording and electrical microstimulation of collicular cells. The electrodes were driven by a hydraulic micromanipulator that fitted on the implanted cylinder and which could be adjusted to allow different regions of the superior colliculus to be systematically explored in each animal.

Measurement of eye and head movements

Direct current electro-oculography was chosen as the method of recording eye movements. The main reasons were its complete independence from head movements, the rugged and stable nature of the implanted electrodes and the general convenience of the technique. E.o.g. signals were differentially amplified and stored on magnetic tape through an FM decoder of an 8 track tape recorder (SE Ltd. Model 8-4). Several independent calibration methods were employed, which gave stable and consistent measurements. A direct method of e.o.g. calibration was to note when the cat was looking at points of known eccentricities and plot the d.c. e.o.g. signal against the eccentricity. 1 cm diameter holes were cut in a translucent perspex hemisphere that was positioned in front of the cat. By looking through these holes and attracting the cat's attention it was possible to make several estimates of when the cat was looking in known directions. Some cats were trained for food reward to fixate light-emitting diodes fixed inside the hemisphere and this assisted calibrations.

Head movements were measured by monitoring the d.c. potential across a low-torque potentiometer attached to the vertical spindle of the head restraining frame. An independent calibration of the e.o.g. was made by turning the head through a known angle and noting the e.o.g. signal produced by the resulting compensatory eye movement under conditions in which the gain of the compensatory eye movements of the vestibulo-ocular reflex is known to be close to unity (Donaghy, 1980).

The range of cat's eye movement is restricted to about ± 25 deg from the position of rest (Stryker & Blakemore, 1972; Blakemore & Donaghy, 1980) and an approximate calibration can therefore be obtained by observing the over-all range e.o.g. signals in a large sample of spontaneous eye movements. All these methods agreed well and showed a good degree of consistency both across cats and between the horizontal and vertical vectors. The signal corresponding to the horizontal vector was twice that of the vertical presumably since the horizontal signal was obtained across both eyes whilst the vertical was across the left alone. A typical value of the calibration was 113 μV/deg (S.D. ± 6 μV) for the horizontal signal. Drift of the e.o.g. signal

due to change in the ambient illumination (Kris, 1958) was minimized by performing all experiments at a constant background light level wherever possible.

Electrical stimulation and single unit recording

A microrelay switch built into the microdrive next to the preamplification stage (FET) of the recording probe allowed remote switching of the microelectrode between the recording preamplifier and the electrical stimulator. Great care was taken to measure accurately the current used for microstimulation by earthing the cat through the virtual earth of a current-to-voltage circuit. The voltage was then monitored over a convenient value of resistor. The stimulating current was kept just above the threshold for producing a motor effect except in experiments in which the influence of current strength itself was investigated. Threshold current was defined as that current that produced behavioural responses on more than 70% of trials. Threshold current in the intermediate and deeper layers of the colliculus was typically less than 15 μA and thresholds for all classes of response observed were often as low as 1–2 μA. A train of 0·3 msec pulses at 200 Hz of variable amplitude and over-all duration was used as the stimulating wave form. All stimulation was cathodal. For a sample of stimulation sites of each class the effect of increasing the stimulating current was investigated. No effect was found on the type of response evoked or any response parameters (with the exception of latency which occasionally decreased at high stimulation currents). These observations are consistent with all other reports (e.g. Robinson, 1972).

Single cell action potentials were amplified by conventional techniques, displayed on an oscilloscope and stored on analogue tape. Cells' responses could also be converted into pulses and histograms constructed by a PDP 11-10 computer synchronized with either eye or head movements. To do this movements above a particular velocity and of a certain direction could be converted to pulses that triggered the computer. A histogram of a cell's activity time-locked to these movements could thus be produced. An example of such a histogram is shown in Fig. 12*A*.

Histological reconstruction of the sites investigated

Reference points that could be related to the stereotaxic co-ordinates were obtained throughout the investigation of each animal from the regular, predictable and reliable retinotopic map over the surface of the colliculus. Visual receptive fields were plotted by projecting a small spot of light on to the Perspex hemisphere, whose inner surface was sand-blasted to form a projection surface. The position of the eyes was continuously monitored on a two-dimensional display on a storage oscilloscope. Whenever visual receptive fields were plotted the head was fixed and the animal's attention was repeatedly attracted to the central position. Eye position was constantly checked to be sure that it did not deviate by more than a few degrees from the anterior pole of the hemisphere whilst the visual receptive field was quickly mapped.

After the stimulation and recording experiments two of the cats were anaesthetized with a steroid anaesthetic (Althesin, Glaxo administered intravenously at 0·6 ml./kg.hr), paralysed with an I.V. infusion of Flaxedil (gallamine triethiodide 10 mg/kg.hr) and artificially ventilated whilst the temperature was maintained at 37·5 °C by a heating blanket and a rectal probe. Micro-electrode recordings were then made and a further retinotopic map was obtained with accurate reference to the area centralis, the projection of which was plotted on the hemisphere with a reversible ophthalmoscope. Electrolytic reference lesions were made at a number of points at the depths at which electrical stimulation had previously been effective. The animal was given an overdose of Nembutal (sodium pentobarbitone) and perfused through the heart with formol Ringer solution. The brain was then frozen and cut coronally at 40 μm and the lesions were subsequently identified in sections stained with cresyl violet. All other sites investigated could then be related to the position of the lesions.

RESULTS

Normal eye-head co-ordination in the cat

When a cat orients to a novel stimulus the eyes almost always start to move before the head. The mean latency for the head to follow the eyes is about 30 msec. The eye movement is therefore usually completed, and hence the new direction of

gaze achieved, before the head has completed its movement. The vestibulo-ocular reflex (VOR), however, almost precisely cancels the contributions that movement of the head would otherwise introduce into the gaze change. The compensatory VOR of the cat operates over the range of frequencies contained in natural head movements with a gain very close to unity (Donaghy, 1980), the eyes being counter-rotated by an amount equal to the head movement. The VOR is equally effective during saccadic eye movements (Blakemore & Donaghy, 1980) so that the original target of an eye movement is achieved and fixation maintained irrespective of head movement. During large shifts of gaze, a series of co-ordinated eye–head movements is executed in the same direction, with intervening brief periods of fixation, resulting in a staircase of gaze changes.

PART I

Electrical microstimulation of the superior colliculus

The effects of electrical microstimulation of the superior colliculus varied with the depth of the stimulating electrode. In the superficial layers, in agreement with previous observations (e.g. Straschill & Rieger, 1973), the minimum current necessary to elicit a behavioural response was found to be up to 100× higher than in the intermediate layers where the value was typically less than 10 μA. This was true throughout the colliculus. Electrical microstimulation with low currents of fifty-one sites within the colliculus evoked responses that were divided into three classes on the basis of the nature of head movement produced. The sudden lowering of the threshold current at the border of the superficial and intermediate layers occurred for all classes of response.

For class 1 sites, stimulation elicited an eye movement but motion of the head was very slight if it occurred at all. At class 2 stimulation sites a substantial head movement was evoked by threshold currents of 2–10 μA. The characteristics of this head movement and its co-ordination with the gaze changes were identical to the normal pattern of eye–head gaze changes. A third class of response was also occasionally encountered with low current stimulation from the posterior part of the colliculus. The head movement produced was unusual in form and usually started before movement of the eyes. This pattern of co-ordination is rare both as a result of stimulation of class 2 sites and in normal, visually triggered gaze changes in the cat, monkey or man.

Class 1

For twenty-five sites, all in the rostral part of the colliculus, electrical stimulation produced short latency saccadic eye movements at current intensities of less than 10 μA. The mean latency at a typical class 1 site was 64·4 msecs (S.D. $\pm$ 17·4 msec). The mean latencies for all class 1 sites fell within the range of 50–70 msec. Fig. 1 shows eye movements elicited from two class 1 sites. In Fig. 1*A* and *B* the movements are plotted on a representation of visual space and in Fig. 1*C* and *D* they are re-plotted with their starting points superimposed at the centre of the co-ordinate system. Also shown on Fig. 1*C* and *D* are the visual receptive fields of single cells recorded at the stimulation sites immediately before electrical stimulation. Clearly there was approximate 'foveation'. Electrical stimulation at a class 1 site evoked a saccadic eye movement that took the area centralis to that part of visual space previously occupied by the visual receptive field of cells in the stimulated region.

The area centralis was thus directed towards the position in space of a visual stimulus that would have excited cells in the electrically stimulated region. The rostral part of the cat's colliculus therefore behaves very similarly to the monkey colliculus (Schiller & Koerner, 1971; Robinson, 1972).

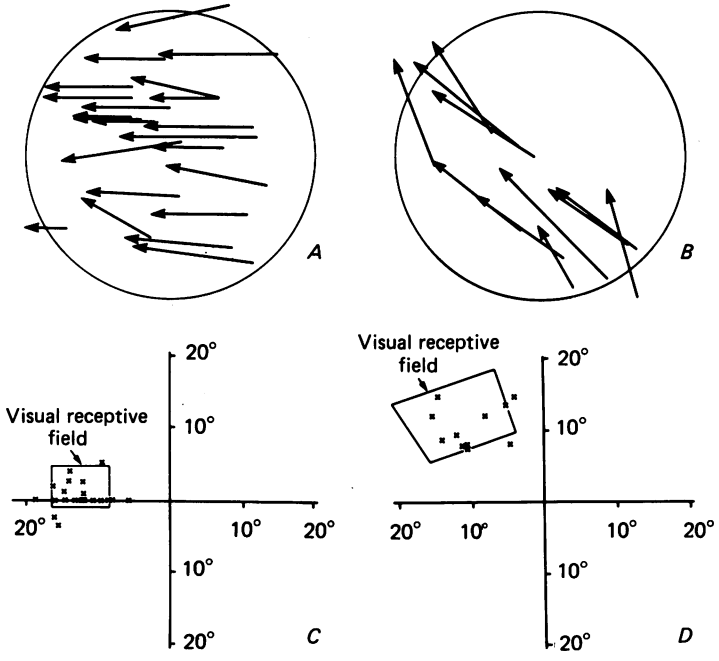

Fig. 1. The eye movements evoked from a number of starting positions are here plotted with respect to the orbit for two class 1 stimulation sites (*A* and *B*). Each arrow represents a saccade. The origin of the arrows represents the starting point of the eye movement and the arrow head represents the end point. The circle has a radius of 20 deg and is centred on the straight-ahead eye position. Below are the end points of the same eye movements plotted as crosses on retino-centric co-ordinates for each site (*C* and *D*). The centre of this co-ordinate system represents the starting positions of all eye movements. Also plotted are the visual receptive fields obtained from single cell recording in the stimulated areas, the centre of the co-ordinates being the projection of the area centralis.

Prolonged stimulation, as in the monkey, produced a staircase of saccades of similar amplitude and direction, each one resulting in foveation with respect to its own starting position (Fig. 2*A*). Towards the middle of the antero-posterior extent of the colliculus, where the individual saccadic eye movements elicited by a brief pulse train were quite large (> 10 deg), prolonged stimulation caused a staircase in which the first eye movement was often much larger than those that followed and was thus the only one that produced foveation (Fig. 2*B*). This may have been due to the saccade-initiating mechanisms becoming less efficient as the eye approached the limit of its normal oculomotor range.

Only a very slight jerk of the head (maximum 1 or 2 deg) or no measureable head movement at all was elicited from class 1 sites with a stimulation duration sufficient to produce only a single saccadic eye movement. For all class 1 sites a movement of

the head did, however, occur when the eyes approached the edge of their range of mobility. Such a head movement (Fig. 2*C*) therefore had a latency which varied with the initial eye position and which was often extremely long (720 msec in the example illustrated in Fig. 2*C*). This pattern of head movement is similar to that previously reported from the monkey colliculus (Stryker & Schiller, 1975). Fig. 9 shows that class 1 responses were only evoked from sites within the central 25 deg of the collicular retinotopic map.

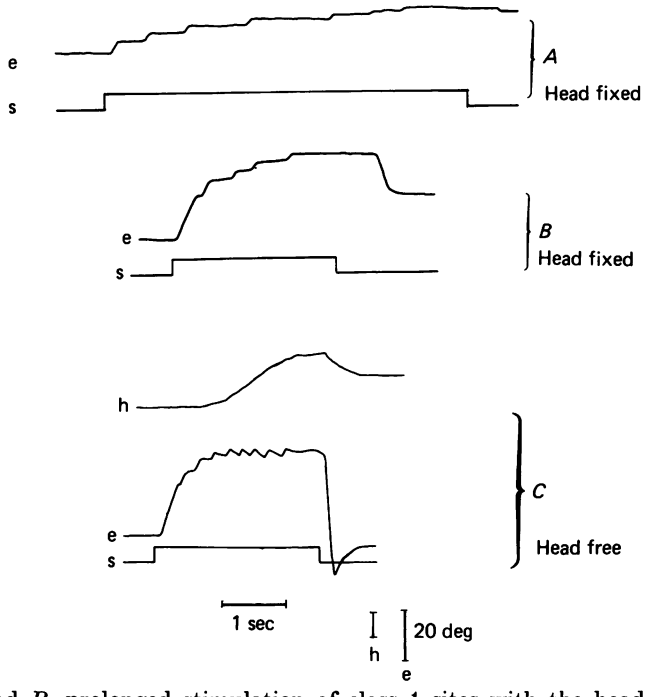

Fig. 2. *A* and *B*, prolonged stimulation of class 1 sites with the head fixed evokes staircases of eye movements. *C*: if the head is free to move it does so only when the eyes are deviated very eccentrically and stimulation is prolonged. Note that when stimulation ceases, both the eyes and head return sharply to a central position. The record shown in *C* was obtained from the same site as for *B*. Up represents movement to the left. e = horizontal eye movement. h = horizontal head movement. s = stimulating pulse train duration. The amplitude calibration for head (h) and eye (e) is shown below.

Class 2

The only way in which head movements may be electrically evoked from the monkey colliculus is by prolonged electrical stimulation (Stryker & Schiller, 1975). By contrast, brief stimulation of sites outside the rostral half of the cat's colliculus that evoked a gaze change with low threshold current, invariably produced a large head movement of short latency. This pattern of response was classified as class 2.

From twenty stimulation sites, representing positions in the visual field more eccentric than about 25 deg, co-ordinated eye–head movements were evoked that appeared identical to normal eye–head gaze changes. Fig. 3 shows histograms of the relative latencies of the eye and head components evoked from a typical class 2 site. The mean latency from the onset of stimulation to the start of the eye movement

for this example was 51·3 msec (S.D. ± 14·8 msec). The range of mean latencies of eye movement was from 50 to 70 msec for all class 2 sites (the same as that for class 1 eye movements). The mean latency of head movement was 76·7 msec (S.D. ± 17·7 msec) and the head lag relative to the eye was 25·4 msec (S.E. ± 2·2 msec). The average eye–head lag for natural gaze changes was found to be 30·3 msec (S.E. ± 3 msec). The relative lag of the head movement for stimulation of class 2 sites was therefore within the range for normal co-ordinated gaze changes.

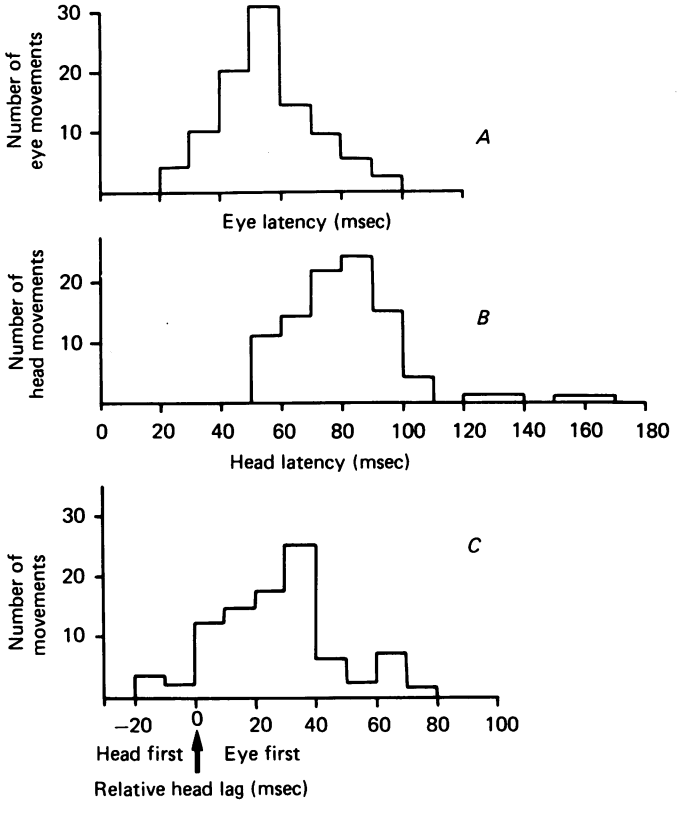

Fig. 3. *A*, the distribution of latency of eye movements, relative to the onset of electrical stimulation, for a typical class 2 site. *B*, latency of evoked head movements for the same site. *C*, relative latency between eye and head for the co-ordinated movements elicited from this site.

A brief stimulation pulse train (up to 200 msec long), sufficient to produce a single saccadic eye movement alone from a class 1 site, elicited a co-ordinated eye–head movement at a class 2 site, and thus a single gaze step equal in size to the saccadic component of the eye movement (since the head movement component in turn elicited perfect vestibulo-ocular compensation: Blakemore & Donaghy, 1980). Class 2 sites lay in the collicular representation of the peripheral field and so the evoked movement was rarely sufficient to achieve foveation because of the limited range of ocular motility. The movement was however, of the approximate *direction* necessary for the visual axis to reach the previous projection in space of the visual receptive

fields of neurones at the stimulation site. For all class 2 sites it was possible, with a brief stimulation pulse-train, to evoke a single eye–head movement. The elementary response of a class 2 site was therefore not the complete series of multiple eye–head movements that would be necessary to achieve foveation.

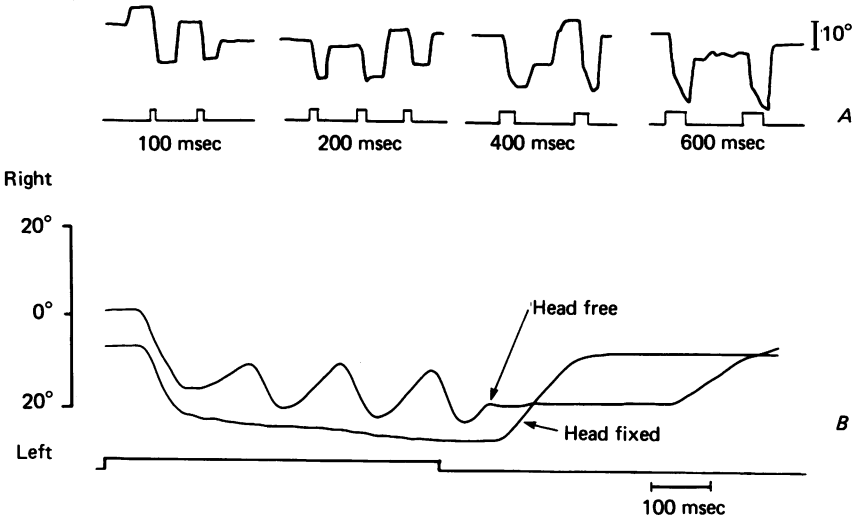

Fig. 4. *A*, examples of horizontal eye movements (upper traces) evoked by stimulation at a class 2 site with the head fixed. Each record shows the response to two or three stimulating pulse trains. The stimulation duration varies between 100 and 600 msec, as shown by the event marker below the eye movement trace. Rightward movement gives upward deflexion; amplitude calibration on right. Note that for pulse trains of 400 and 600 msec, but not for 100 or 200 msec, the initial leftward saccade is followed by a slow drift in the same direction. *B*, records of eye movements evoked by a 560 msec pulse train at the same site as for *A*, with the head free and head fixed. Note the expanded time-base (calibration below).

Prolonged electrical stimulation of Class 2 sites whilst the head was free to move, resulted in step-like addition to the initial, elementary gaze change of further eye–head movements, quite normal in appearance, for as long as stimulation was maintained, or until the head reached the limit of movement allowed by the head-holder. If the head was fixed and stimulation prolonged then, rather than the addition of saccades to produce a staircase as in class 1, the eye movement amplitude was increased by the addition of a slow drift phase. This is shown in Fig. 4*A*, while Fig. 4*B* contrasts this slow extension of the eye movement when the head was fixed, to the nystagmoid movement when the head was free to move and each saccade was followed by a compensatory movement in response to the head movement.

When the head was free the whole gaze change appeared completely normal and co-ordinated. The counter-rotation of the eyes in response to each evoked head movement returned them towards the central resting position thus allowing subsequent saccades which would otherwise have been impossible because of the limited ocular motility (Fig. 4*B*). The resulting series of saccades were regularly spaced at intervals of 150–180 msec and took the form of an initial, large saccade followed by several much smaller ones (Fig. 4*B*). In Fig. 5 the effectiveness of a head movement

electrically evoked from a typical class 2 site in returning the eyes to the central position is examined. In the examples illustrated in Fig. 5*A* the mean end position of the saccadic part of the movements was 22 deg from the centre of the orbit (range ± 4·5 deg) but the subsequent compensatory movements brought the eye back to 13 deg left of centre (range ± 7 deg). The head-holder exerted little restraining influence on head movements carried out within its range; movements obtained with the animal entirely free of the superstructure (Fig. 5*B*) overlap with those obtained before (*A*) and after (*C*) in the holder.

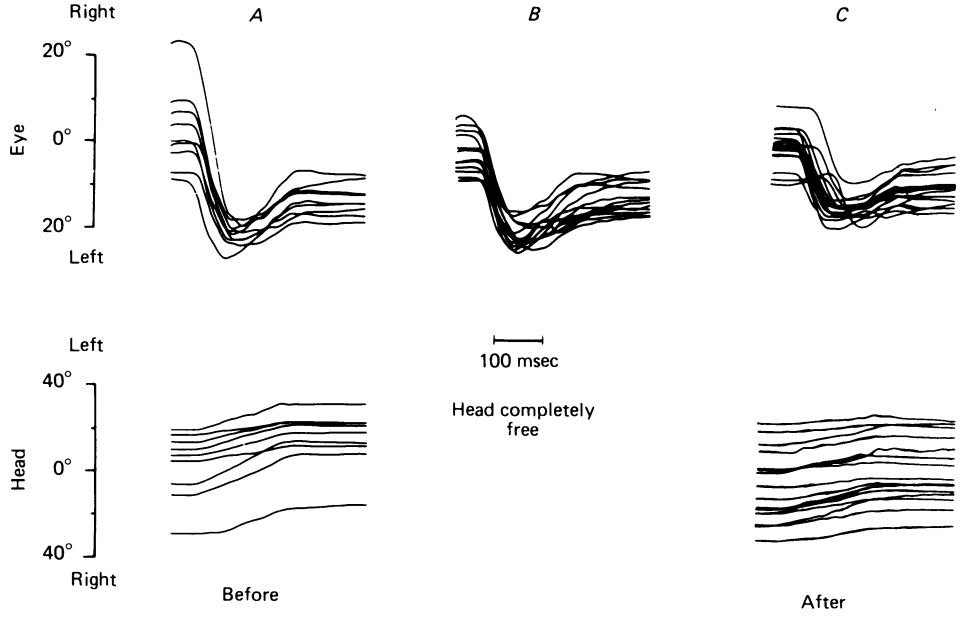

Fig. 5. In order to reveal possible restrictions imposed by the head holder on an evoked head movement, horizontal eye movements were recorded while a class 2 site was stimulated with the head completely free of the holder (*B*). Comparison with the records obtained in response to stimulation of the same site while the animal was free to move its head in the holder before (*A*) and after (*C*) shows no difference in the amplitude of the slow compensatory phase after each saccade, which is caused by the head movement. Therefore the head-holder seems to impose little or no restriction on the speed and size of head movements. In all cases the head movement is smaller than the eye movement and the eye is thus not returned completely to its starting position in the orbit. The head movement traces have been inverted with respect to the eye, as shown in the calibration scales on the left.

Failure to observe 'goal-directed' eye movements

Straschill & Reiger (1973) and Crommelinck *et al.* (1977) have reported that electrical stimulation of the cat's superior colliculus can produce eye movements that take the eye to a fixed position in the orbit whatever its initial starting position. Such eye movements have been called 'goal-directed'. Stein *et al.* (1976) suggest the following criteria for describing 'goal-directed' eye movements: (i) prolonged stimulation results in a movement that goes to a fixed point in space, the 'goal', independent of the starting point of the eye, and stays there; (ii) repeated stimulation when the eye is at the goal results in no movement, and (iii) if the eye is initially

directed further contralateral in space than the 'goal', ipsiversive movements should be seen.

Crommelinck *et al.* (1977) have reported that electrical stimulation of the caudal half of the cat's superior colliculus can produce goal-directed eye movements that satisfy all of the criteria of Stein *et al.* The results described here are rather different. The pattern of eye movement evoked by brief stimulation from class 2 sites with the head fixed, when plotted in spatial co-ordinates (Fig. 6*A*), never appeared to be 'goal directed'. That is they did not terminate at a point precisely fixed with respect to the head and not the retina. None of the criteria of Stein *et al.* (1976) for a goal-directed movement was satisfied. However, brief stimulation of class 2 sites produces quite large eye movements and there is a slight tendency for the end points of the family of movements evoked from one site to converge towards a particular position in the orbit (Fig. 6*A*). This is most likely due to constraints on the direction and size of eye movement imposed by the limited range of ocular motility.

For class 2 sites that produced a somewhat converging array of saccades, like that shown in Fig. 6*A*, stimulation produced a very similar pattern of saccades if the head was free to move (Fig. 6*B*), before the compensatory movement induced by the accompanying head movement. If these saccades are replotted in terms of gaze changes in visual space, taking into account the varied starting positions of the head (Fig. 6*C*), it is quite clear that there can be no question of a goal in space.

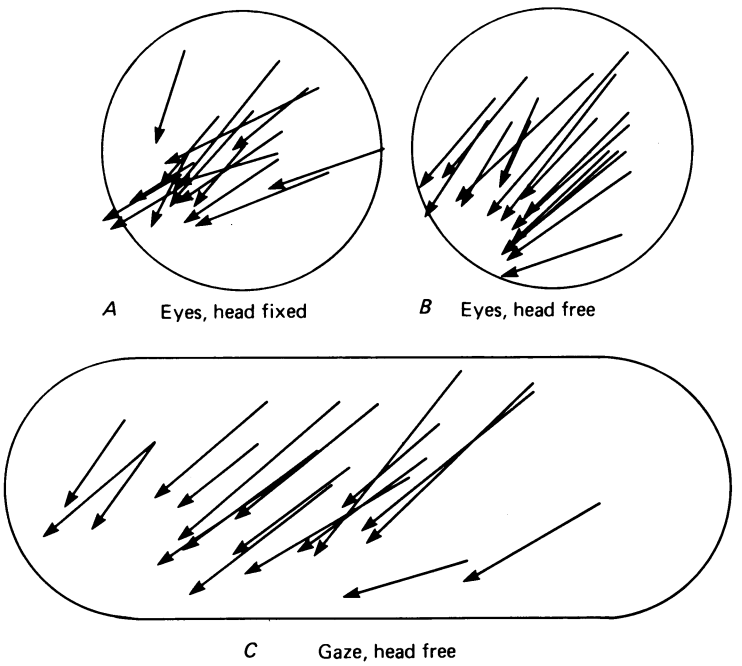

Fig. 6. The eye movements evoked by brief stimulation pulse trains from a class 2 site are plotted with respect to the orbit, as in Fig. 1*A* and *B*, with the head fixed (*A*) and free (*B*). The circles have a radius of 20 deg. *C*, the same movements plotted in *B* are replotted as gaze changes in space, taking account of the different starting positions of the head. The surrounding line represents the approximate range of gaze movement possible with the head free in the head holder, the length of the oval being 100 deg of visual field.

The possibility of the eye adopting a very loose goal in the orbit is, however, harder to dismiss. Although none of the criteria of Stein *et al.* (1976) was fully satisfied, it was true that prolonged stimulation at class 2 sites with the head fixed produced a single, large, saccadic eye movement followed by a very slow drift in the same direction, but without further saccades. However, the end points of the first saccades were always quite close to the edge of the normal range of movement so that a further large eye movement was impossible. Ipsiversive eye movements towards a supposed orbital goal *never* occurred contingent on electrical stimulation of class 2 sites, even when the starting position of the eye was near the contralateral edge of its range of motility.

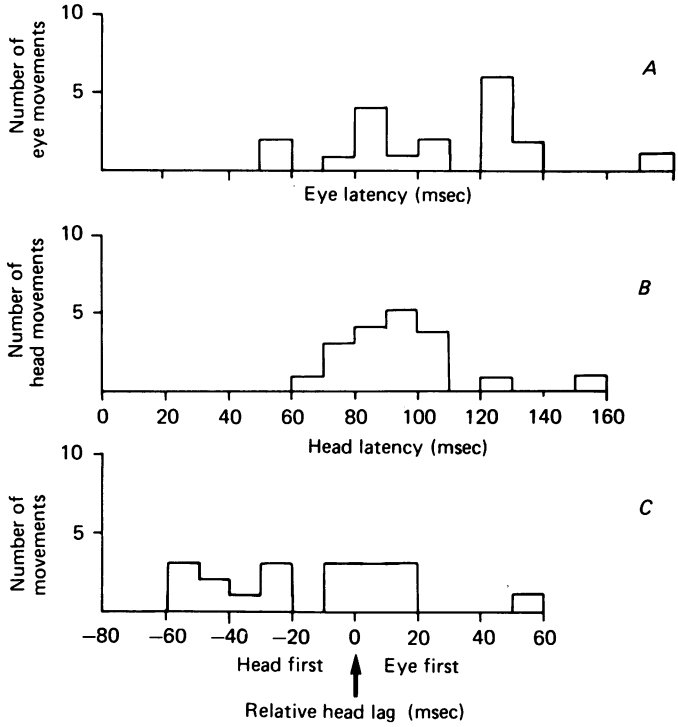

Fig. 7. The latency of eye and head movements evoked from a class 3 site, with the same format as Fig. 3.

Class 3

For six collicular sites, representing 12% of the total, short latency head movements were also evoked but an unusual pattern of eye–head co-ordination was produced. The head often moved before the eyes and the pattern of additions to the evoked movement caused by prolonged electrical stimulation was markedly different from that for class 2 sites. Fig. 7*B* is a histogram of the latencies of the head movements elicited from a typical class 3 site. The mean latency of the head was similar to that of class 2 sites (95 msec, S.D. ± 10 msec in the example shown). A histogram of the relative lag of the head is shown in Fig. 7*C*. The head often began to move before the eyes (mean head lag −14 msec, S.E. ± 7 msec in this example). This was only rarely seen in a class 2 response and is also uncommon in natural eye–head gaze changes.

Increasing the stimulation duration produced a smooth continuation of the evoked head movement. This contrasts with the addition of distinct eye–head movements seen as a result of prolonged electrical stimulation of class 2 sites. Superimposing traces of head movements obtained with stimulation pulse trains of varying durations (Fig. 8*C*) shows that, within limits, the peak velocity of the evoked head movement was constant, at approximately 100 deg/sec, and independent of the amplitude which was determined almost exclusively by the duration of the stimulation pulse train (or the limits of permitted movement). For class 3 sites, all the saccadic eye movements of a sequence accompanying a head movement were of similar amplitude. Regular, step changes of gaze were thus produced by prolonged stimulation of this class of site (Fig. 8*A*). These sites therefore differed from class 2 sites, in which a large initial saccade accompanied by a head movement was followed by a sequence of smaller saccades.

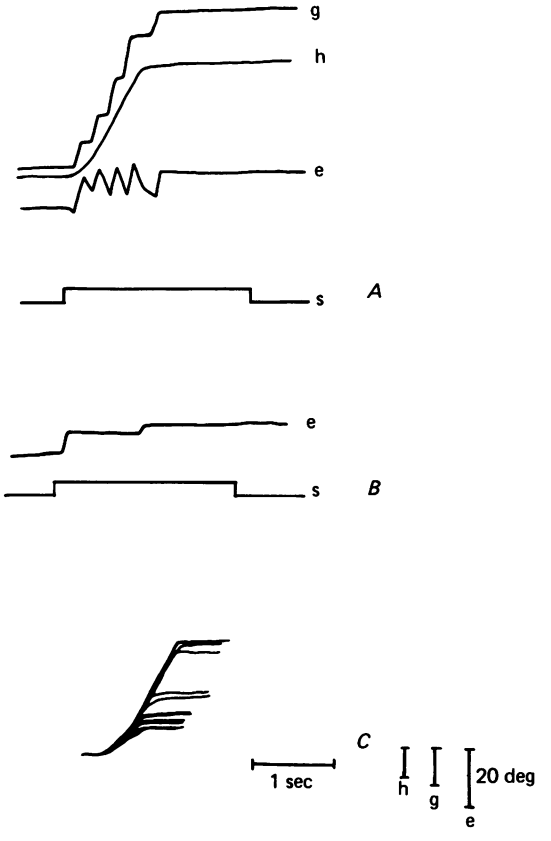

Fig. 8. *A*, a gaze change (g) involving horizontal movements of the eye (e) and head (h) evoked from a class 3 site. Note the initial small compensatory movement (downwards deflexion) of the eye. The head movement is prematurely terminated by the mechanical limit of the head holder. Up represents movements to the left. s = stimulation duration. *B*, eye movements evoked from the same class 3 site while the head was fixed. *C*, head movements evoked from a class 3 site with varying stimulation durations are smooth with approximately constant velocity. The movements whose starting points are superimposed here were carefully selected to exclude those limited by the head holder's range. Amplitude calibrations for head (h), gaze (g) and eye (e) are shown below.

If the head was fixed in the holder a staircase of small saccadic eye movements (< 10 deg), separated by long intervals (> 80 msec), was found to be evoked by prolonged stimulation of a class 3 site (Fig. 8*B*). These saccades did not approach foveation since class 3 sites lay in the caudal part of the colliculus and were thus associated with cells with visual receptive fields of eccentricities greater than 25 deg. They were not 'goal-directed'.

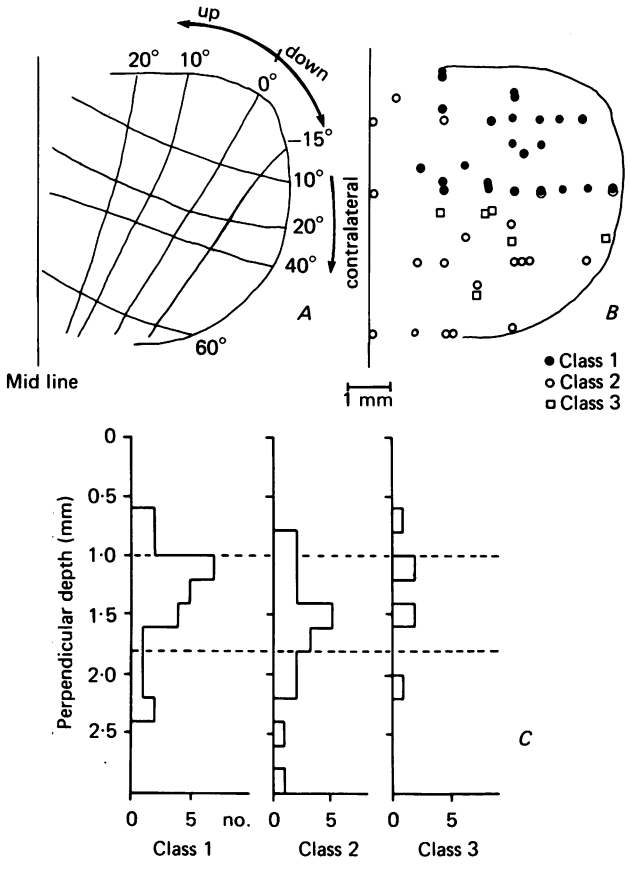

Fig. 9. The distribution of stimulation sites from which responses of class 1, 2 or 3 were evoked are shown in *B* projected onto a surface view of the right colliculus. This distribution may be compared to the retinotopic map of visual receptive field positions shown in *A*. *C*, distribution in depth of minimal threshold points for each class of site measured perpendicular to the collicular surface. The dashed lines represent the approximate depths of the upper and lower borders of the stratum griseum intermediale.

Distribution of classes of stimulation sites

The distribution of evoked responses showed a clear division between anterior (class 1) and posterior (classes 2 and 3) parts of the colliculus (Fig. 9), closely following the contour of retinotopic eccentricity corresponding to the limit that the cat can reach with a single gaze change (about 20–25 deg). The retinotopic map in Fig. 9*A* was derived from the plots of visual receptive fields of single units and was superimposed on the outline of the colliculus with reference to lesions made during acute

recording sessions as described in the methods section. The stimulation sites have been represented on a dorsal view of the colliculus in Fig. 9*B* with compensation for the angle of entry. Fig. 9*C* shows the depths within the colliculus of all sites that elicited responses with threshold currents of less than 20 μA. Threshold current was defined as that current that produced responses on 70% of trials of 200 msec pulse train duration. The depth was measured perpendicular to the collicular surface, taking into account the angle of entry and the surface curvature. The dotted lines correspond to the approximate perpendicular depths of the boundaries of the intermediate layer.

These data suggest that the cat's superior colliculus may be divided into an anterior portion concerned with movements of the eyes and a more posterior area concerned also with movements of the head. This division is further supported by observations of single unit activity.

PART II

Single unit recording from the superior colliculus of the alert cat during head and eye movements

Ninety-nine cells were recorded from the right superior colliculi of three cats whilst they made spontaneous and visually-elicited eye and head movements. The cells were classified into four types based on their responses, or lack of responses, during or preceding gaze changes. The properties of these categories are summarized in Table 1.

Type 1. Cells with no change in activity preceding gaze changes

The superficial layers of the superior colliculus contained almost exclusively visual cells whose activity did not change before movements of the eyes ($n = 55$). Thirty-nine of these cells responded to movements of patterns through their receptive fields irrespective of whether the retinal image motion was created by stimulus movement within the external world or by movements of the eyes which produced a shift of the external world across the retina (type 1*A*).

Sixteen cells responded only to external movement and remained entirely unaffected by retinal shift due to active movements of the eye as the animal looked around the illuminated laboratory (type 1*B*). This observation is in agreement with other reports of the activity of cells of the cat's colliculus (Straschill & Hoffmann, 1970; Straschill & Schick, 1977). Histograms were accumulated using a computer synchronized to eye movements (see Methods) to be sure that there were no responses to image shift due to eye movement. Cells were described as unaffected by such retinal shift if no effect was revealed after twenty eye movements had been averaged. It appears unlikely that the difference could be due solely to these latter cells having very specific velocity or direction selectivity of such a type that spontaneous eye movements were unlikely to generate adequate retinal stimulation. Although these features were not measured quantitatively, simple qualitative examination suggested that the stimulus requirements of such neurones were not any more specific than those of cells that were excited by retinal movement caused by eye movement. Direction selective cells were certainly found in both classes.

In the deeper layers of the colliculus 'bimodal' cells were found with both auditory

and visual receptive fields (type 1*C*; $n = 27$). The effects of changes in eye and head position on the visual and auditory properties of such neurones will be discussed in a separate paper.

TABLE 1. A summary of the response characteristics and frequency of cells isolated in the cat's superior colliculus

Type	Number	Sensory responses	Response during gaze changes
1*a*	39	Vis	Respond to retinal shift caused by eye movements in the light
b	16	Vis	No change in activity associated with gaze changes
c	27	Vis/Aud	No change in activity associated with gaze changes
2	4	Vis	Inhibited before and during all saccadic eye movements
3	9	Vis	Discharge precedes saccadic eye movements in the light
4	4	Vis	Discharge precedes head movements in the light or dark
Total	99		

Type 2. Cells with inhibition preceding gaze changes

Four cells were isolated in the colliculus that responded briskly to movement of targets in any direction across their receptive fields but that were inhibited during spontaneous eye movements in any direction, both in the light and dark. Examples of the behaviour of a typical cell of this type are shown in Fig. 10. These cells were always non-selective for the direction of stimulus movement across their visual receptive fields (Fig. 10*A*) and were inhibited during eye movements of all directions both in the light (Fig. 10*B*) and dark (Fig. 10*C*). The inhibition began up to 120 msec before an eye movement (mean 66 msec, S.D. $\pm$ 56 msec in the example illustrated in Fig. 10). It could therefore not be due either to retinal image movement caused by eye movement (in any case it continued in total darkness) or to afferent feed-back from muscle receptors. This inhibition must therefore have originated from an 'efference copy' (von Helmholtz, 1866) or represented an integral stage in the production of eye movements. These neurones may be functionally similar to those type 1 cells that appear to distinguish external from self-induced movement (type 1*B*). Some of the latter cells had very low spontaneous discharge which would render undetectable any possible inhibition associated with eye movements. Cells that were clearly inhibited during eye movements may simply have been neurones in which the balance between excitation set up by the eye movement and a roughly simultaneous suppressive signal was not perfect. Comparison of the extent of inhibition in the light (Fig. 10*B*) and the dark (Fig. 10*C*) shows that the inhibition was more pronounced in the dark, where there was no competing visual activation.

Type 3. Cells which discharged before eye movements

The responses of cells that discharged before eye movements ($n = 9$) were generally weak (less than 10 impulses/sec. movement) and did not correlate well with the occurrence of an eye movement to a particular area of visual space. This is illustrated in Fig. 11 in which the pattern of responses of a typical cell that dis-

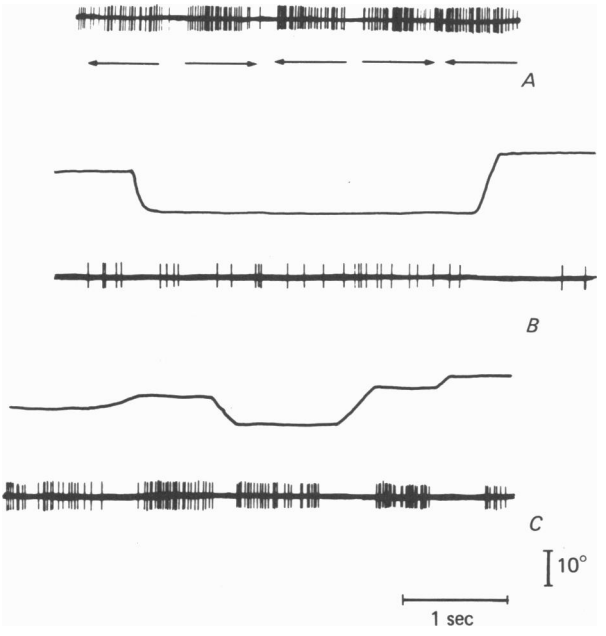

Fig. 10. Oscillograph records of action potentials from a cell whose activity was inhibited during eye movements (type 2). *A*, strong excitatory responses as a small spot of light was moved horizontally back and forth (see arrows below records) across the cell's receptive field while the cat was fixating the centre of the screen. *B* and *C*, inhibition before and during eye movements in the light and dark respectively. The upper trace in each case is horizontal eye position, the calibration for which is indicated below.

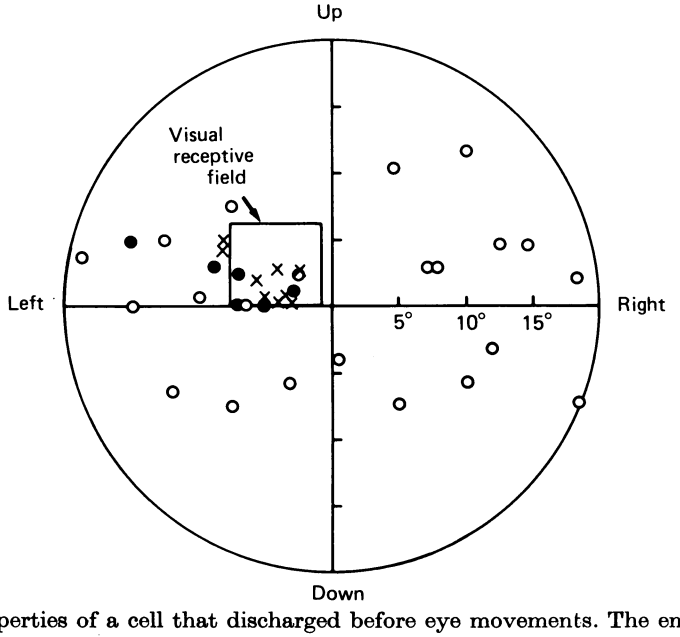

Fig. 11. Properties of a cell that discharged before eye movements. The end point of eye movements observed while such a cell was isolated are plotted with respect to their starting positions which are represented by the centre of the circle. Filled circles are the end points of those eye movements preceded by a discharge of the cell. Open circles represent the end points of eye movements that were not accompanied by a burst in the cell's activity. Also shown are the cell's visual receptive field and the end point of eye movements (×) subsequently evoked from the same site by brief electrical stimulation at 10 μA.

charged before eye movements is represented. In this Figure the end points of eye movements have been plotted with their starting positions superimposed at the centre of the co-ordinate system. The filled circles represent the end points of saccades that were preceded by a discharge from this cell. The end points of several eye movements that were not accompanied by a discharge of the cell are shown as open circles for comparison. Also shown is the visual receptive field of the cell.

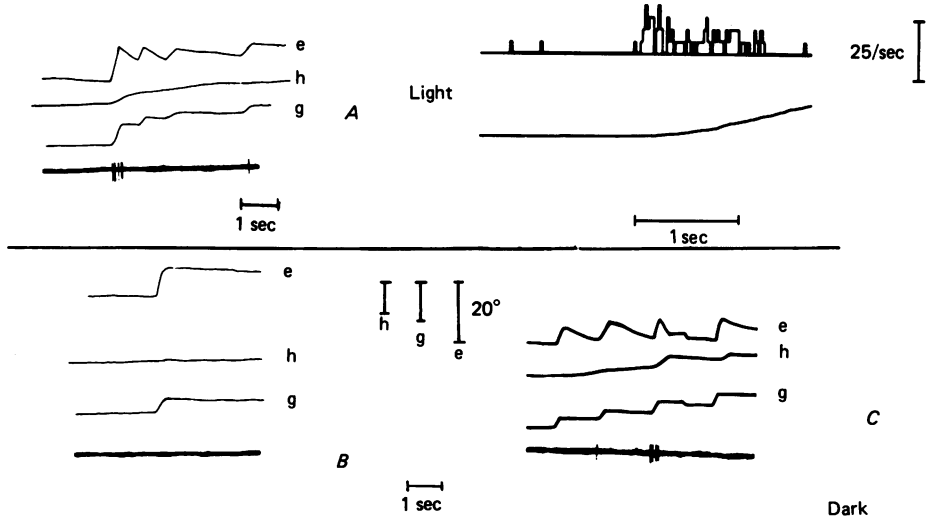

Fig. 12. Properties of a cell that discharge before head movements. *A* shows a sample of record with a burst preceding a head movement (h). Also shown are the associated movements of the eyes (e) and the total gaze change (g). On the right of this record is a histogram of the responses that preceded ten contraversive head movements larger than 5 deg. This was obtained as described in the text. The bin width was 20 msec and there were ten head movements; hence 5 spikes/bin is equivalent to 25 spikes/sec. Below the histogram is the averaged head movement. *B*, a gaze change (g) of approximately equal amplitude to that shown in *A* but that was not accompanied by a head movement (h) although the head was free to move, was not preceded by a discharge from this cell. *C*, oscillograph record showing that a burst of activity is also seen preceding a head movement (h) in complete darkness. Upward deflexion indicates movement to the left in all these records. Amplitude calibrations are next to *B*.

Although generally the amplitude and direction of eye movements accompanied by a discharge of the cell were appropriate for 'foveation' to be achieved, this was not always the case. Only contraversive eye movements were accompanied by a prior discharge but a discharge was occasionally noted preceding an eye movement that took the area centralis to a point well outside that part of visual space previously occupied by the visual receptive field of that cell. Conversely, some eye movements that were appropriate for foveation of the cell's visual receptive field were not preceded by a discharge from this cell. This type of cell had virtually no spontaneous activity and this may be the reason why so few were observed. They discharged prior to saccades around an illuminated environment but did not fire before similar movements in the dark.

Type 4. Cells which discharged before head movements

A few cells were found that began to discharge before movements of the head ($n = 4$). These were all found in the caudal and medial part of the colliculus, within the area in which electrical stimulation evoked normal eye–head gaze changes (class 2 sites: see Fig. 9). Fig. 12*A* shows the pattern of response of a typical cell of this type. On the left of Fig. 12*A* is a record showing a discharge just before a head movement; on the right the response associated with ten consecutive, contraversive head movements larger than 5 deg is shown as a histogram. The histogram was obtained by synchronizing the computer with the head movement signal (see Methods) and an averaged head movement trace obtained from all the head movements used to trigger the computer is shown below the histogram. The onset of the cell's discharge preceded the onset of head movement by up to 160 msec. The response persisted in the dark (Fig. 12*C*) and was not related to changes of gaze as

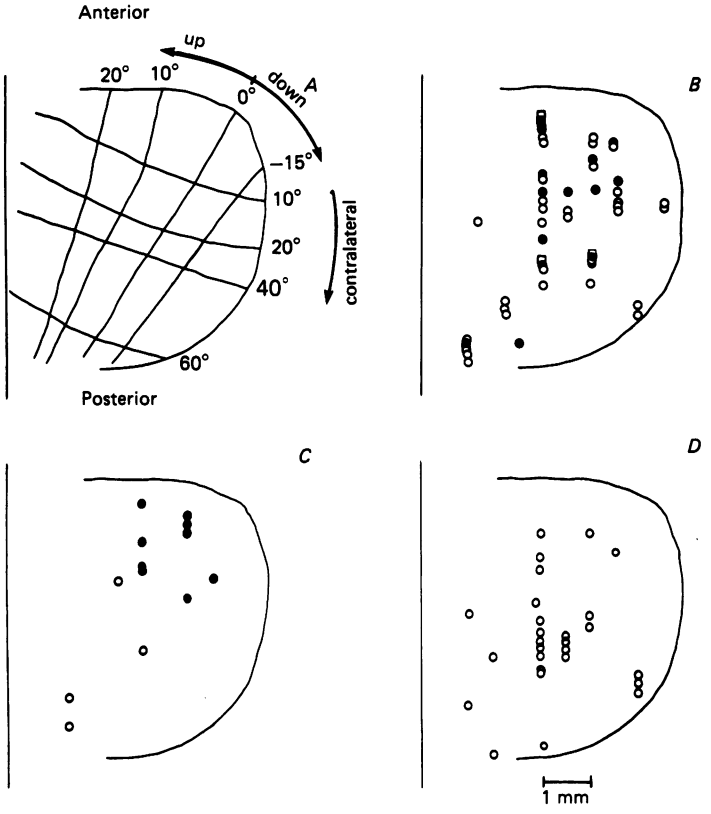

Fig. 13. The distribution of cells characterized in this study are shown projected onto surface views of the right colliculus. *A*, the retinotopic map over the collicular surface as in Fig. 9*A*. *B*, type 1 cells that distinguished between self-induced and external movement (filled circles: see text) and those that did not (open circles) are found scattered over the colliculus. Also shown are type 2 cells that were inhibited before eye movements (open squares). *C*, the distribution of cells that discharged before eye movement (filled circles: type 3) or head movement (open circles: type 4) appear segregated in their distribution. *D*, the distribution of cells with both auditory and visual receptive fields (bimodal cells).

such since an eye movement alone, that produced approximately the same gaze change, was not accompanied by a discharge (Fig. 12*B*). The response only accompanied contraversive movements of the head and was only associated with head movements of velocity greater than 15–20 deg/sec and of amplitude over 5–10 deg. However, there did not appear to be an optimum velocity or amplitude of head movement associated with the discharge of any of these cells. The discharges were generally weak (less than 25 spikes/sec) and the cells had very low spontaneous discharge rates (less than 1 spike/sec).

Distribution

The distributions of cell types over the collicular surface are shown in Fig. 13. The angle of entry has been taken into account as in Fig. 9. Cells whose discharge pattern did not change prior to gaze changes (type 1) are found scattered throughout the colliculus. These are shown in Fig. 13*B* (open circles: type 1*A* visual cells that responded to image movement caused by eye movement; filled circles: type 1*B* visual cells that were unresponsive to image movement caused by eye movement) and Fig. 13*D* (open circles: type 1*C* bimodal cells). The few cells that showed inhibition of their spontaneous discharge (type 2) also appear scattered in their distribution (Fig. 13*B*: open squares). Those cells firing before eye movements (Fig. 13*C*: filled circles) and before head movements (Fig. 13*C*: open circles) are, however, clearly segregated with neurones associated with eye movements clumping within the representation of the central part of the visual field.

DISCUSSION

Comparison of the cat and monkey superior colliculus

Cats usually move their heads as part of the normal orienting behaviour. Although the cat's range of ocular movement is more restricted than that of man or monkey (Stryker & Blakemore, 1972; Blakemore & Donaghy, 1980) cat's eye movements are very similar to those of primates in their integration with head movements (Blakemore & Donaghy, 1974, 1980; Donaghy, 1980).

The superior colliculus has long been thought to be involved in the control of orienting movements and it is therefore not surprising that it should be involved in head movement generation in the cat since head movements are so obviously an integral part of the orienting behaviour of this species. This study has demonstrated that apparently normal, co-ordinated movements of the eyes and head are evoked by electrical microstimulation of the posterior part of the cat's superior colliculus (class 2 responses).

Co-ordinated eye–head movements of short latency have not been reported for stimulation of any part of the monkey colliculus. The visual map over the monkey colliculus, as in the cat, certainly also extends further than the oculomotor range. However, since the monkey's oculomotor range is much larger than that of the cat ($\pm$ 45 deg; Fuchs, 1967), there is only a small crescent at the posterior end of the colliculus that represents the more eccentric part of the field (Cynader & Berman, 1972) which cannot be reached by an eye movement alone. Robinson (1972) showed that stimulation of this region of the monkey colliculus produces eye movements

that fall short of the visual receptive fields of neighbouring collicular cells, but he did not study the effect of such stimulation on head position.

The gaze change associated with the eye–head movement produced by brief electrical stimulation of a class 2 site in the posterior part of the cat's colliculus falls far short of the retinal target that would excite visually responsive cells in the same collicular area. The direction of the evoked movement is, however, always appropriate to the position of the visual receptive fields relative to the area centralis. The behaviour of cells that fire selectively before and during a head movement is consistent with the effect of electrical stimulation. These cells fire before eye–head movements in the direction of their visual receptive fields but the initial associated gaze change is usually inadequate in amplitude to foveate the assumed visual target.

It has been suggested by Straschill & Rieger (1973), Roucoux & Crommelinck (1976) and Crommelinck *et al.* (1977) that some parts of the cat's colliculus may differ from the monkey's colliculus in coding eye movements not with respect to the retina but with respect to the head. They report that for some parts of the cat colliculus electrical stimulation produces so-called 'goal-directed' eye movements that take the area centralis to a constant point with respect to the *head*. I have been unable to produce 'goal directed' eye movements from any part of the cat's colliculus. No ipsiversive reversals of direction were found and if stimulation was continued with the head restrained, the eyes did not remain fixed at a 'goal position' but drifted a little further after the saccadic movement, even though they were always near the normal limit of ocular motility.

A possible reason for my inability to reproduce the 'goal directed' eye movements of Roucoux & Crommelinck (1976) is the difficulty in getting a cat to maintain a fixation further eccentric than the 'goal', from which position stimulation might produce convincing ipsiversive movements. Such eccentric fixations are only held by a cat for very short periods (typically less than half a second) when the head is restrained and, if the head is free to move, are inevitably accompanied by a head movement that immediately returns the eyes to a more central position in the orbit. Even in the head-fixed condition, therefore, there is a high probability of an ipsiversive movement occurring whenever the eyes are strongly deviated, quite independently of electrical stimulation. Clearly this requires further investigation.

How are natural large gaze changes accomplished by a cat?

Large spontaneous gaze changes are divided into steps. The first is of near maximal amplitude (usually 20–25 deg in the cat), the amplitude being limited by the range of ocular motility and the fact that movements of the head are virtually perfectly subtracted from the eye movement by the vestibulo-ocular reflex (Bartz, 1966; Bizzi, Kalil & Tagliasco, 1971; Dichgans, Bizzi, Morasso & Tagliasco, 1973; Gresty, 1974; Blakemore & Donaghy, 1980).

During the shifting of gaze to a peripheral visual target the following sequence of events occurs. The target excites a certain region of the retina and thus the corresponding region of the retinotopic map in the caudal part of the colliculus. If other factors, for example the appropriate 'readiness to respond', are favourable a co-ordinated eye–head movement occurs producing a deviation of gaze of maximal

amplitude (20–25 deg). Because of the difference on onset times and the fact that the eye moves faster than the head, the eye reaches the initial gaze point long before the head has completed its movement, the eye then counter-rotates and since the vestibulo-ocular reflex has a gain of unity under these conditions (Donaghy, 1980), the visual axis remains fixating the point in space achieved at the end of this initial saccade. The result of this initial eye–head movement is therefore a step change of gaze with the eyes brought back towards the centre of the orbit. This first gaze change cannot achieve foveation of the peripheral target but, if the target is still present, a point further anterior in the colliculus corresponding to the new retinal eccentricity of the target is now excited by it and the process may be repeated until the target is brought within the representation of the central part of the visual field and can be foveated with a single gaze change.

The results of electrical stimulation of the cat's superior colliculus reported in this study suggest the following prediction. It might be expected that a cat would be unable to make the *series* of eye and head movements required to reach a peripheral visual target if the target is extinguished before the completion of the first step of the gaze change. Removing the target at this stage would prevent more anterior collicular sites from being excited following the initial gaze step and thus leave the animal dependent on only the collicular region stimulated initially by the visual target. The results of electrical stimulation suggest that this would be inadequate for foveation of the original site of the target in space to occur. Brief electrical stimulation of sites within the caudal part of the colliculus (class 2: Fig. 9) produces only a *single* eye–head movement and thus a single gaze step, inadequate in amplitude to achieve foveation of the implied peripheral target.

How may the colliculus mediate head movements?

The superior colliculus has appropriate anatomical connections for processing movements not only of the eyes but also of the head. The cervical region of the spinal cord receives an indirect tecto-reticulospinal projection (Anderson, Yashida & Wilson, 1971), a direct tectospinal projection (Altman & Carpenter, 1961; Nyberg-Hansen, 1964) and also projects back to the colliculus with proprioceptive information from the region of the neck (Abrahams & Rose, 1975). The spinotectal pathways terminate in the intermediate layers of the colliculus (Graham, 1977) the cells of which give output to the cervical spinal cord (Abrahams & Rose, 1975). The superior colliculus may thus be involved not only in the initiation of head movements but also in the processing of feedback information required for the rapid and accurate head movements that a cat makes during natural gaze changes.

The results of electrical stimulation suggest that the superior colliculus is involved in the initiation of eye–head gaze changes although both components are almost certainly finally controlled in the reticular formation of the brain stem. The superior colliculus does not project directly to the nuclei of the extraocular muscles (Graham, 1977) but there is a strong projection to the pontine reticular formation (Altman *et al.* 1961; Grantyn, Grantyn & Robiné, 1977). The pontine reticular formation is concerned not only with the eye movement system (see for example Robinson, 1975) but also in the head movement system (Kuypers & Maisky, 1975). The cells of origin of the tectospinal tract are found throughout the colliculus and not only in the

region corresponding to visual receptive fields greater than 25 deg eccentric where class 2 stimulation sites are found (L. R. Harris, in preparation).

Electrical stimulation of some sites in the posterior part of the colliculus produces a head movement that continues smoothly until stimulation ceases and that is co-ordinated with eye movements in an unusual way (class 3). These observations suggest a more involved role for the colliculus in the regulation of head movement. Such evoked head movements may reflect artificial stimulation of a feedback pathway in a servo-regulatory loop, creating a movement to cancel a feed-back 'error'. It could also represent the direct activation of a motor pathway after the site of effect of feed-back information. The results of stimulation at class 3 sites suggest that the superior colliculus may be concerned in feed-back processing of neck muscle proprioceptive information used in the production of accurate head movements.

Taken together these observations from electrical microstimulation and single unit recording in the superior colliculus of alert cats suggest that the colliculus is intimately involved in the production of head and eye movements and their co-ordination. It may also play a regulatory role in their execution.

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