

Tonic activity during visuo-oculomotor behavior in the monkey superior colliculus

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Abstract

The purpose of this study was to examine whether the superior colliculus is involved in intermediary cognitive processes such as memory, movement preparation, and peripheral attention. To answer this question, we recorded single cell activities in the superior colliculus of monkeys trained to perform a series of visuo-oculomotor tasks: delayed saccade task (SACD), saccade task with overlap target (SACO), and attention task (ATT). We recorded 141 neurons showing tonic activities related to the tasks. Depending on the predominance of the activities among the three tasks, we classified the tonic neurons into four types: (1) visuomotor (greater activity in SACO), (2) mnemonic motor (SACD dominant), (3) attention (ATT), and (4) nonspecific. Among 108 neurons recorded in the intermediate layer, 13 were of a visuomotor type, 15 were of a mnemonic motor type, and 13 were of an attention type. The other 67 neurons were of a non-specific type. Of the 33 neurons in the superficial layer, many neurons were of the non-specific type. These results suggested that the tonic activities in the superior colliculus are related to memory of the target location, preparation of saccades and peripheral attention.

Keywords: Superior colliculus; Eye movement; Attention; Memory; Macaque

1. Introduction

The superior colliculus is unique in its dual role in sensory and motor functions. Most of neurons in the superior colliculus show phasic responses that are either sensory (visual) or motor (saccadic) (Goldberg and Wurtz, 1972; Wurtz and Goldberg, 1972a; Mays and Sparks, 1980). It is thus thought that the superior colliculus plays a key role in sensory-motor conversion, as seen in orienting response (Schneider, 1969; Ingle,

1973). However, motor action is not always an immediate consequence of sensory inputs; it can be selected, remembered, and prepared (Andersen et al., 1987; Goldman-Rakic, 1987; Hikosaka et al., 1989c; Goldberg and Bruce, 1990). The objective of the present research was to examine whether the superior colliculus is involved in such intermediary cognitive processes.

For this purpose, we trained the monkeys to perform the following visuo-oculomotor tasks and recorded single cell activities in the superior colliculus while the monkey was performing the tasks. In a delayed saccade task (SACD), the monkey was required to make a saccade to a remembered position of a peripheral target light which had been cued a few seconds before (Hikosaka and Wurtz, 1983a; Matsumura et al., 1992). In a saccade task with overlap target (SACO), a peripheral target light remained on, and the monkey was required to make a saccade to the visible target a few seconds later (Hikosaka and Wurtz, 1983a; Hikosaka et

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al., 1989a). In an attention task (ATT), the monkey was required, while keeping his gaze on the central fixation point, to respond to the dimming of a peripheral target light by releasing a lever (Wurtz and Mohler, 1976a; Robinson et al., 1978). If a neuron in the superior colliculus is related to the above three cognitive processes, it should respond tonically during the delay period in the three tasks (Hikosaka and Wurtz, 1983a; Hikosaka et al., 1989a; Petersen et al., 1985).

We found that neurons in the superior colliculus responded tonically during the delay period of the three tasks (SACD, SACO, and ATT). Nearly half of the neurons in the intermediate layers were significantly more active in one of the three tasks compared with others. These findings suggest that the intermediate layer, rather than the superficial layer, of the superior colliculus may be more differentially related to the preparation of saccade, peripheral attention and memory. Some of these findings have been reported previously (Kojima and Hikosaka, 1991).

2. Methods

2.1. Experimental animals

We studied single-cell activities in the superior colliculus of three Japanese monkeys, *Macaca fuscata* (body weight 6.5, 6.5 and 8.0 kg). The monkeys were kept in separate primate cages (1 m × 1 m × 1 m) in an air-conditioned room. At each experimental session, they were brought to the experiment room. The monkeys were given restricted fluid before recording or training. Their health conditions, such as body weight and appetite, were checked daily. Supplementary water and food were provided daily.

2.2. Surgical procedures

Monkeys were anesthetized with pentobarbital sodium (initially 15 mg/kg and supplemented with 5 mg/kg/h) while the following surgical procedures were performed with aseptic techniques in an operation room. About twenty acrylic screws were implanted on the skull. These screws were fixed with acrylic resin and acted as anchors for a derlin head holder which was used to restrain the head during the experiment. A derlin chamber for microelectrode recording was also fixed to the skull with acrylic resin. The chamber was tilted back 45° from vertical in the midsagittal plane so that the electrode tracks passed through the superior colliculus approximately perpendicular to its rostral-caudal orientation.

Eye positions were monitored by the scleral search coil technique (Robinson, 1963). Search coil of teflon-coated stainless-steel wire was implanted monocularly

under the conjunctiva using a method by Matsumura et al. (1992). The animals received an antibiotic (sodium ampicillin 25 mg/kg intramuscularly each day) after the operation.

2.3. Behavioral paradigms

Before unit recordings, the monkeys were trained to perform five visuo-oculomotor tasks (Fig. 1, Matsumura et al., 1992). The monkey sat on a primate chair with his head fixed in a dimly lit and sound attenuated room. When the monkey pressed a lever on the chair, the center fixation point came on in front of the tangent screen (57 cm from his face). In the eye movement tasks, he had to make a saccade to the target spot after the center fixation point off. In the no-eye

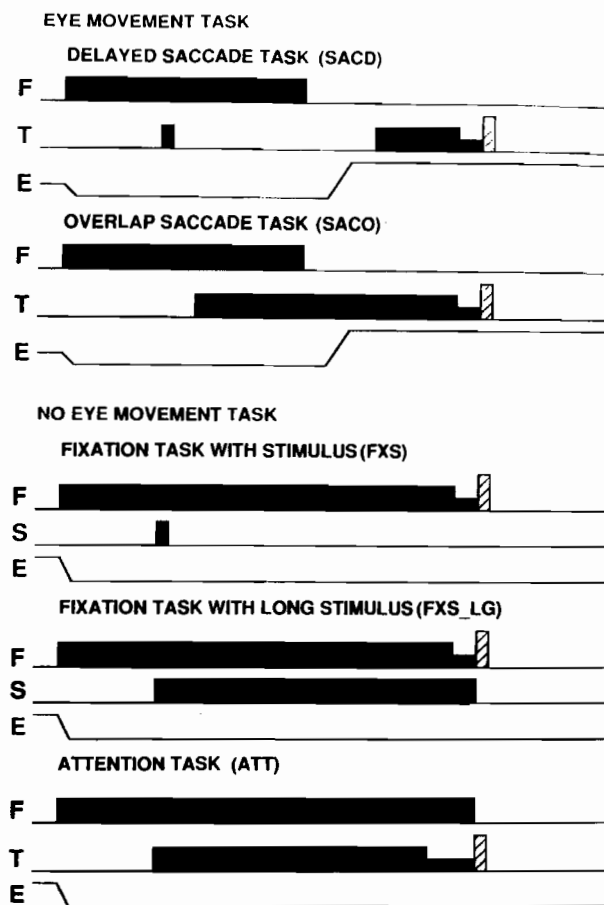


Fig. 1. Behavioral paradigms. F, fixation point: a central spot of light that the monkey must fixate to start a trial. S, stimulation point: a spot of light that was used as a stimulus to study visual responses. T, target point: a similar spot of light that appeared as a final target on the screen. Filled area: time during which the spot of light was on. Depression at the end of filled area indicates dimming of the spot, which was followed by delivery of a reward (hatched area) if the monkey released the lever within a limited time (600–1000 ms). E, schematic eye position.

movement tasks, he had to keep fixating the central fixation point. After a random period of time (1.5–2.5 s) the light spot (target or fixation point) dimmed. If the monkey released the lever within a short period of dimming time (0.5–1.0 s), he was rewarded with a drop of water. The center fixation point and the target point were backprojected spots of light by projectors that use light-emitting diode (LED). The spots had a diameter of 3 mm. The locations of the fixation and target points were controlled by an X–Y galvanometer mirror system under the control of a microcomputer.

We used two types of eye movement tasks: (1) the delayed saccade task (SACD); (2) the saccade task with overlap target (SACO), and three types of no-eye movement tasks: (3) the attention task (ATT); (4) the fixation task with stimulus (FXS); and (5) the fixation task with long stimulus (FXS_LG).

2.3.1. Delayed saccade task (SACD)

This task was designed to elicit a memory guided saccade. When the monkey was fixating on the center fixation point in front of the tangent screen (57 cm from his face), another spot (target cue) came on briefly (50 ms), indicating the location of a future target point. The monkey was not allowed to look to the cue stimulus and was required to keep fixating for 2–3 s until the fixation point went off. When the center fixation point went off, the monkey was allowed to make a saccade to the remembered location of the cue stimulus. The target came on 600 ms later, and the monkey was required, to obtain reward, to release the lever immediately after the target dimmed (Hikosaka and Wurtz, 1983a; Hikosaka et al., 1989a; Matsumura et al., 1992).

2.3.2. Saccade task with overlap target (SACO)

While the monkey was fixating the central fixation point, a target spot appeared, but unlike in SACD, it stayed on. The monkey had to keep fixating while the fixation point was present. Only after the fixation point went off, was he allowed to make a saccade to the visible target point. The rest was the same as SACD (Hikosaka and Wurtz, 1983a; Hikosaka et al., 1989a).

2.3.3. Attention task (ATT)

The initial stimulus condition was the same as in SACO. The fixation point, however, remained on until the end of the trial, and thus the monkey was not allowed to make a saccade to the target. The monkey's task was to detect the dimming of the peripheral target spot, not the fixation point, by releasing the lever (Wurtz and Mohler, 1976a; Robinson et al., 1978).

We used two additional tasks for control.

2.3.4. Fixation task with stimulus (FXS)

The initial stimulus condition was the same as the SACD. But the fixation point remained on until it

became dim, to which the monkey had to respond. The monkey was thus encouraged neither to remember the target position (unlike in SACD) nor to pay attention to the target (unlike in ATT).

2.3.5. Fixation task with long stimulus (FXS_LG)

The initial stimulus condition was the same as SACO and ATT. The fixation point remained on (unlike in SACO) and became dim (unlike in ATT). The monkey was thus encouraged not to pay attention to the target (unlike in ATT) and was not required to prepare for a saccade (unlike in SACO).

2.4. Experimental procedures

First, we used the FXS task to determine the visual receptive field of recorded neurons. The best position to the visual stimulus was determined by the activity of phasic visual on-responses by using a sound monitor of unitary spike discharges on the FXS task. After the determination of the visual receptive field, the target was fixed to its center. Second, we used the SACO task to search for tonic activity that would appear after the presentation of the target. Once a tonic neuron was isolated, the five visuo-oculomotor tasks were applied, each as a block of 20 trials.

2.5. Recording procedures

We used glass-coated Elgiloy (RMO, USA) electrode for single unit recordings (Suzuki and Azuma, 1976; 8–12 M Ω measured at 10 Hz, exposed tips 15–20 μ m). The electrodes were driven by a hydraulic micro-manipulator (Narishige, MO-95, Japan) with an X–Y coordinate which was attached to the chamber. We used the magnetic search-coil technique for eye movement recording (Enzanshi-Kogyo, MEL2U, Japan). The eye positions were measured and digitized at 500 Hz, and stored during the whole block of trials. The neural spike events were collected with a resolution of 1 ms. The unit activities were led through the window discriminator and digitized. The behavioral tasks, storage of data and display of data were controlled by a 32 bit computer (PC 9801 RA, NEC, Japan).

At the time of the experiment, the layer of each tonic neuron was determined tentatively depending on the presence or absence of saccade-locked activity: (1) superficial layer if saccadic activity was absent; and (2) intermediate layer if saccadic activity was present. This classification was based on many previous studies and now seems unanimously accepted (Goldberg and Wurtz, 1972; Wurtz and Goldberg, 1972b; Mays and Sparks, 1980). Our determination was later confirmed by histological examination of the marking sites of tonic neurons.

2.6. Histology

In 14 different penetrations we made marking lesions where typical tonic cells were recorded. These lesions were placed by passing positive current (5 μ A, 200 s) through the recording electrode. At the end of the experiments, the monkey was perfused transcardially with saline followed by 4% paraform aldehyde under deep anesthesia (sodium pentobarbital, I.V.). The cut plain of the mid-brain area was tilted back by 45° from vertical, parallel to the electrode penetrations. The brain was postfixed for two weeks. Serial sections (thickness, 50 μ m), parallel to the electrode penetrations, were cut on a cryotome and stained with cresyl violet. Each marking lesion was identified based on the stereotaxic X–Y coordinate system and on the distance from the surface of the superior colliculus.

2.7. Data analysis

Tonic neurons were so defined as having activity of a long duration (> 400 ms) in either of the three main tasks (SACD, SACO, and ATT) after the cue stimulus or target presentation. This criterion was thought to be reasonable, because the duration of phasic response, whether visual or saccadic, were usually less than 200 ms. Most of the tonic neurons in fact responded tonically until the onset of saccade in the eye movement tasks or the offset of the target in the no eye movement tasks.

Tonic activities observed in different tasks may represent different characteristics of saccade. It may indicate the memory of the target location in SACD task, the preparation of a saccade in SACO, or the peripheral attention in ATT. To classify the tonic activity of each neuron, we compared the numbers of spikes that occurred in the three tasks. We set two windows on the raster displays (600 ms in duration), one for the control period (background activity) and the other for the test period (tonic activity), and counted the number of spikes that occurred within each window for each task trial. The control period was set just before the onset of the fixation point. For the two eye movement tasks (SACD and SACO), the test window was set so that its end was 200 ms before the saccade onset; this was to avoid possible inclusion of presaccadic activity. For the attention task (ATT) the test window started 200 ms after the target onset so as not to include a phasic visual response.

'Response magnitude' was defined for each task trial by subtracting the number of spikes within the control period from the number of spikes within the test period.

$$\text{Response magnitude} = N(\text{test}) - N(\text{control})$$

(Here N indicates the number of spikes for each trial.)

Table 1
Classification of tonic neurons

Types of neurons	Superficial layer	Intermediate layer
Visuomotor	4	13
Visual attention	3	13
Mnemonic motor	0	15
Nonspecific	26	67
Total	33	108

We then compared the response magnitude between all possible pairs of tasks (SACD, SACO, ATT and, if necessary, FXS_LG) by using Mann-Whitney's U -test (unpaired comparison). The number of success trials for each task (SACD, SACO, ATT and FXS_LG) was always set to 20. If the response magnitude was significantly stronger in one task than in other tasks, the neuron was classified into one of the three specific types (see Table 1). Otherwise, the neuron was classified into a nonspecific type.

3. Results

In the present study, we concentrated on the tonic neurons in the superior colliculus. Although many neurons showing only phasic responses were encountered along electrode penetration, we did not attempt to isolate their activity for further analysis. Neurons were determined to be tonic in nature if its activity was sustained for more than 400 msec in either one of the main tasks (SACO, SACD, and ATT). A total of 141 tonic neurons were recorded from the superior colliculus in three monkeys. We found tonic neurons in both the superficial ($n = 33$) and intermediate layers ($n = 108$).

3.1. Classification of the tonic neurons in the superior colliculus

Table 1 summarizes the types of tonic neurons. We used the SACD, SACO, ATT (and FXS_LG, if necessary) tasks to classify the tonic neurons. They were classified into four types: (1) visuomotor type, if tonic activity in the SACO task was significantly stronger than those in the other tasks; (2) fixation type, if tonic activity in the ATT task was significantly stronger than those in the other tasks; (3) mnemonic motor type, if tonic activity in the SACD task was significantly stronger than those in the other tasks; (4) non-specific type, if the neuron could not be classified into either of the above three types. Neurons of the non-specific type could be classified into several sub-types; some neurons showed significantly enhanced activity in two or three of the four tasks; some neurons showed no significant difference among the four tasks.

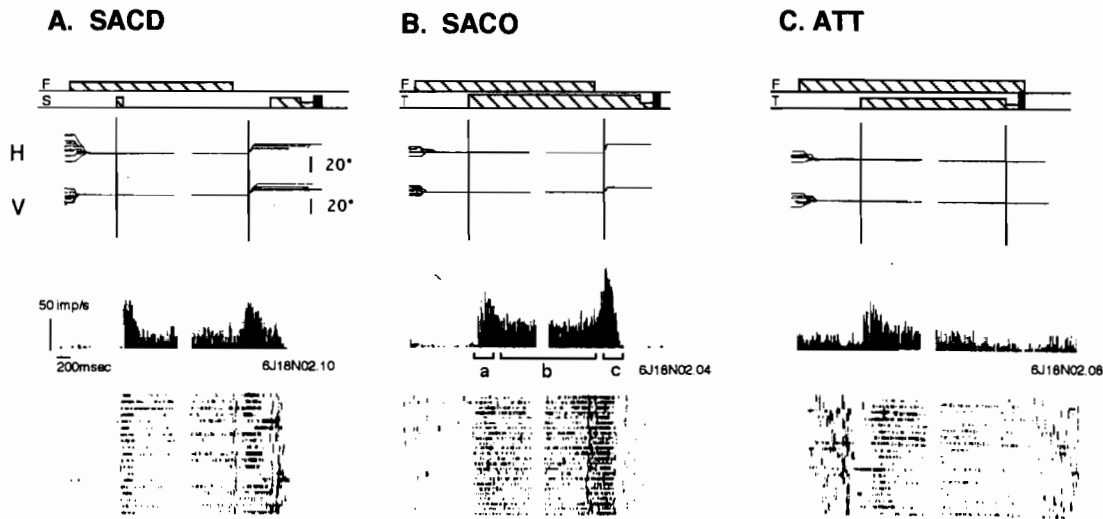


Fig. 2. A neuron of the visuomotor type in the intermediate layer. Its activity is compared between three tasks: SACD (A), SACO (B), and ATT (C). Top: durations of fixation point (F) and target point (T) or visual stimulus point (S). The target presented at 12° to the right and 10° up from the center. Middle: horizontal eye position (H, (up): rightward, (down): leftward), vertical eye position (V, (up): upward, (down): downward). Eye position traces for all trials were superimposed. Bottom: Cell activity is shown as raster display, each dot indicating a single action potential and each line indicating a single trial of task. Averaged activity is shown above the raster display as a spike time histogram. (a), (b), and (c) indicate phasic visual response, tonic activity, and saccadic activity, respectively. The left half of the raster-histogram in (A) is aligned at target cue onset and the right half in (A) at saccade onset. The right halves in (C) are aligned at dim onset, and that in (A) and (B) is aligned at saccade onset. Small vertical ticks on the left side of raster indicate the onset of fixation point. Those on the right side indicate the offset of fixation point and the onset of target point. The spike discharge rate (mean standard error, imp/s) was 20.7 ± 4.0 (A) ($n = 19$), 35.4 ± 3.9 (B) ($n = 24$), and 15.4 ± 3.7 (C) ($n = 20$). All subsequent figures use these conventions unless otherwise stated.

The results can be summarized as follows. First, a majority of tonic neurons were of the non-specific type. Second, the specific types were more common in the intermediate layer, where the three specific types were similarly common. Third, in the superficial layer no cell was classified to be of a mnemonic motor type. In fact, among the superficial layer neurons, none showed significant activity in the SACD task, whereas most tonic neurons in the intermediate layer showed some tonic activity in this task. In the following, we describe the representative tonic activities recorded in neurons in the intermediate layer.

3.1.1. Visuomotor type

Fig. 2 shows an example of an intermediate layer neuron that was classified as a visuomotor type. In the SACO task (Fig. 2) this neuron showed: (a) a visual on-response; (b) tonic activity during visual stimulation; and (c) the presaccadic response. It was thus suggested that the tonic activity was related to preparation of a future saccade. In the SACD task (Fig. 2A) a similar saccade was prepared, but now to a remembered position; yet the tonic activity was significantly weaker. The relation to attention was also excluded by the experiment using the ATT task (Fig. 2C). Statistical comparison confirmed the difference:

the tonic activity was strongest in the SACO task among the three tasks (Mann-Whitney's U -test, $P < 0.05$).

3.1.2. Attention type

Fig. 3 shows an example of an intermediate layer neuron that was classified as a visual attention type. The activity started with a visual response, and lasted until a targeting saccade in the SACO task (Fig. 3B). The tonic discharge in the SACD task was smaller than that in the SACO task (Fig. 3A). However, the tonic activity was further enhanced in the ATT task compared with the SACO task (Fig. 3C). On the other hand, the tonic activity in the FXS_LG did not continue until the dimming of the fixation point (Fig. 3D). The enhancement in the ATT task was confirmed statistically (Mann-Whitney's U -test, $P < 0.05$). This neuron was judged to be related to peripheral attention rather than eye movement.

3.1.3. Mnemonic motor type

Fig. 4 shows an example of intermediate layer neuron that was classified as mnemonic motor type. The neuron did not show a strong tonic response in either the SACO (Fig. 4B) or ATT task (Fig. 4C), in which the target was continuously present. It showed the

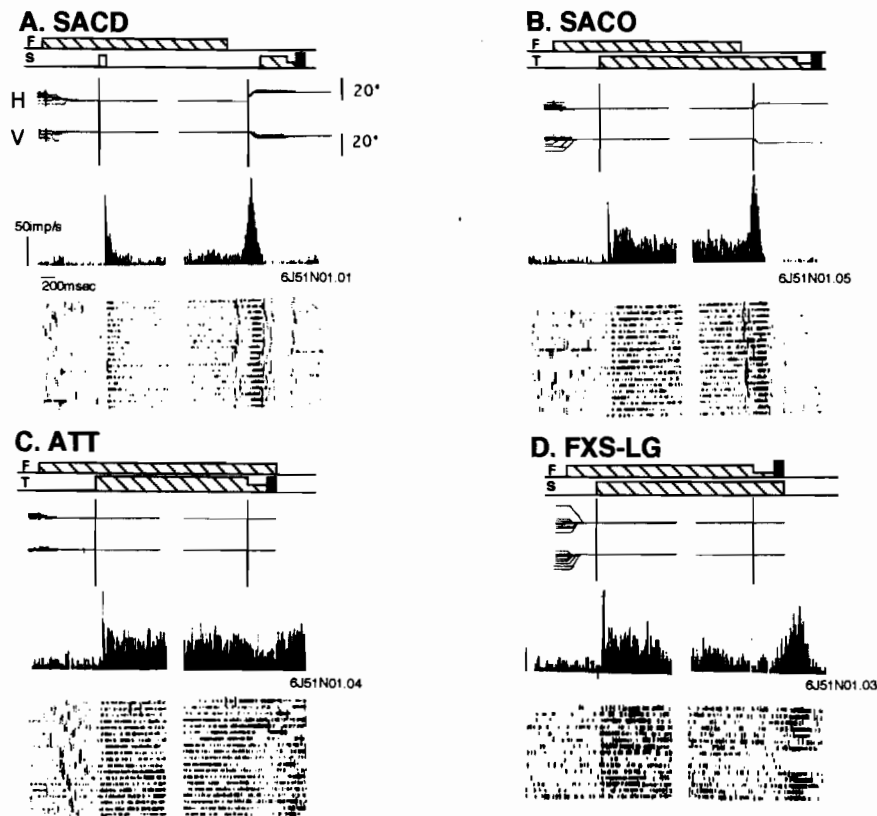


Fig. 3. A neuron of visual attention type in the intermediate layer. The target presented at 10° to the right and 8° down from the center. Arrangements of each raster and histogram are the same as Fig. 4. The spike discharge rate (mean standard error, imp/sec) was 6.1 ± 3.6 (A) ($n = 20$), 30.8 ± 3.1 (B) ($n = 20$), and 38.6 ± 5.1 (C) ($n = 20$).

strongest tonic activity in the SACC task, in which the monkey had to memorize the location of the target (Fig. 4A). This was confirmed statistically (Mann-Whitney's U -test, $P < 0.05$).

3.2. Histological data

To confirm the location of the tonic neurons, we made small marking lesions at some of the recording sites which were identified later by histological examination. Examples are shown in Fig. 5.

All of the histologically identified marks are shown in Fig. 6, as projected onto a representative plane. There was no tendency for differential distribution among different types of tonic neurons.

4. Discussion

We examined the nature of neurons in the monkey superior colliculus that showed tonic activities during different types of visuo-oculomotor tasks. The experiments showed that tonic neurons in the superior col-

liculus were classified into four types: visuomotor; attention; mnemonic motor; and nonspecific types. A majority of neurons in the superficial layer were classified as the nonspecific type, although some were of the visuomotor and attention types. In contrast, nearly half of the neurons in the intermediate layers were classified as specific types, either visuomotor, attention or mnemonic motor type. These findings suggest that the intermediate layer, rather than the superficial layer, of the superior colliculus may be more differentially related to preparation of saccade, peripheral attention and memory. In the following discussion we will concentrate on the tonic neurons in the intermediate layer.

4.1. Comparison with previous reports

Our tonic neurons are similar to quasi-visual cells (Mays and Sparks, 1980), prelude bursters (Glimcher and Sparks, 1992), or build-up cells (Munoz and Wurtz, 1995a,b), all of which were found in the intermediate layers of the monkey superior colliculus.

Like our tonic neurons, the quasi-visual cells, described by Mays and Sparks (1980), also responded

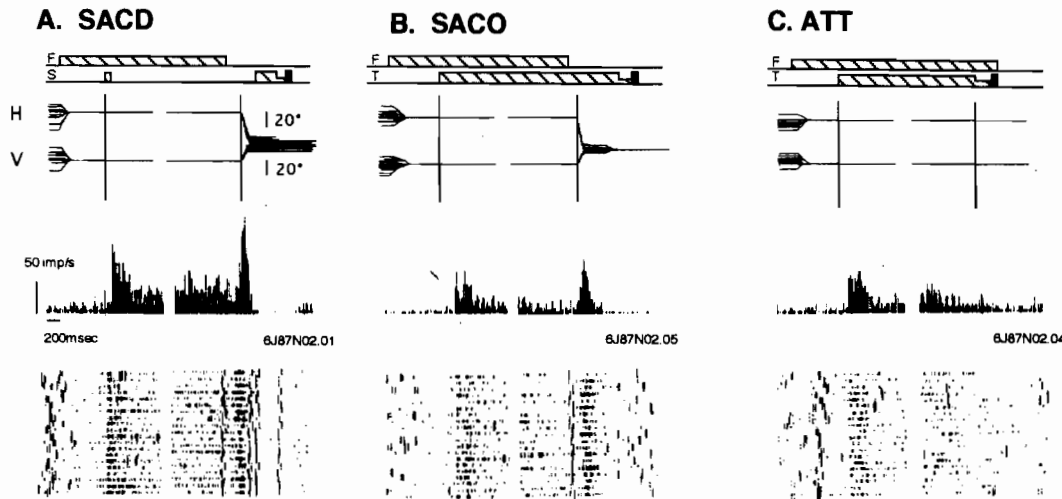


Fig. 4. A neuron of mnemonic motor type in the intermediate layer. The target presented at 36° to the left and 15° up from the center. Arrangements of each raster and histogram are the same as Fig. 3. The spike discharge rate (mean standard error, imp/sec) was 15.5 ± 1.7 (A) ($n = 20$), 4.3 ± 1.9 (B) ($n = 20$), and 7.5 ± 1.3 (C) ($n = 20$).

tonically during the delay period in the double saccade task. The situation at the second saccade in their task was similar to that in our SACD task: the monkey was required to make a saccade to the remembered target. It might be argued that the tonic activities in this study were recorded from the quasi-visual cells. However, the quasi-visual cell did not show a phasic saccadic response. Therefore, we think that tonic neurons in this study are different from the quasi-visual cells.

The prelude bursters (Glimcher and Sparks, 1992), on the other hand, resemble our tonic neurons in that they showed a clear burst with a saccade. They further showed that the prelude bursters encode the vector of an upcoming saccade. Such a saccadic preparatory feature is common to the visuomotor type or the mnemonic motor type which we described in this study. The visual attention type, in contrast, may be different from the prelude bursters.

The build-up cells described by Munoz and Wurtz (1995a) have been characterized in detail. These type of cells showed tonic activity between the signal to make a saccade and its onset, similar to our tonic neurons. Unlike the well-documented burst cells, the build-up cells tended to have open-ended movement fields and their saccadic activity tended to remain after the end of a saccade (partially clipped). Munoz and Wurtz (1995b) further indicated that, the activity of build-up cells, viewed as a population in the superior colliculus, shifted from a caudal zone toward the rostral zone where fixation cells (Munoz and Wurtz, 1993) are located, thereby terminating the saccade.

We did not investigate these properties related to saccadic parameters, and therefore direct comparison is difficult. However, the saccadic activity of our tonic neurons seems to be clipped with the saccade end (see Figs. 2–4), unlike the typical build-up cells. In addition, the estimated locations of the tonic neurons (Fig. 6) are not necessarily at the deeper part of the intermediate layer.

To summarize, although different laboratories have reported new types of superior colliculus neurons that show sustained activity preceding a saccade, they seem to be related to different functions. It will be an important issue to determine whether there are different groups of cells with different functions or they are in fact a single class of cells that have multiple functions.

4.2. Possible sources of the tonic activity

If the tonic activity in the superior colliculus originates in other brain areas, similar tonic activities must be found in these areas. The candidates can be found in the cerebral cortex, basal ganglia, and thalamus. The frontal eye field (Bruce and Goldberg, 1985; Goldberg and Bruce, 1990), supplementary eye field (Schall, 1991), and posterior parietal cortex (Andersen et al., 1987; Barash et al., 1991) are the three major cortical areas. The caudate nucleus (Hikosaka et al., 1989b,c) and substantia nigra pars reticulata (Hikosaka and Wurtz, 1983b) are the two candidate regions in the basal ganglia.

We will discuss the possible origins of each specific type of information on the basis of data currently available.

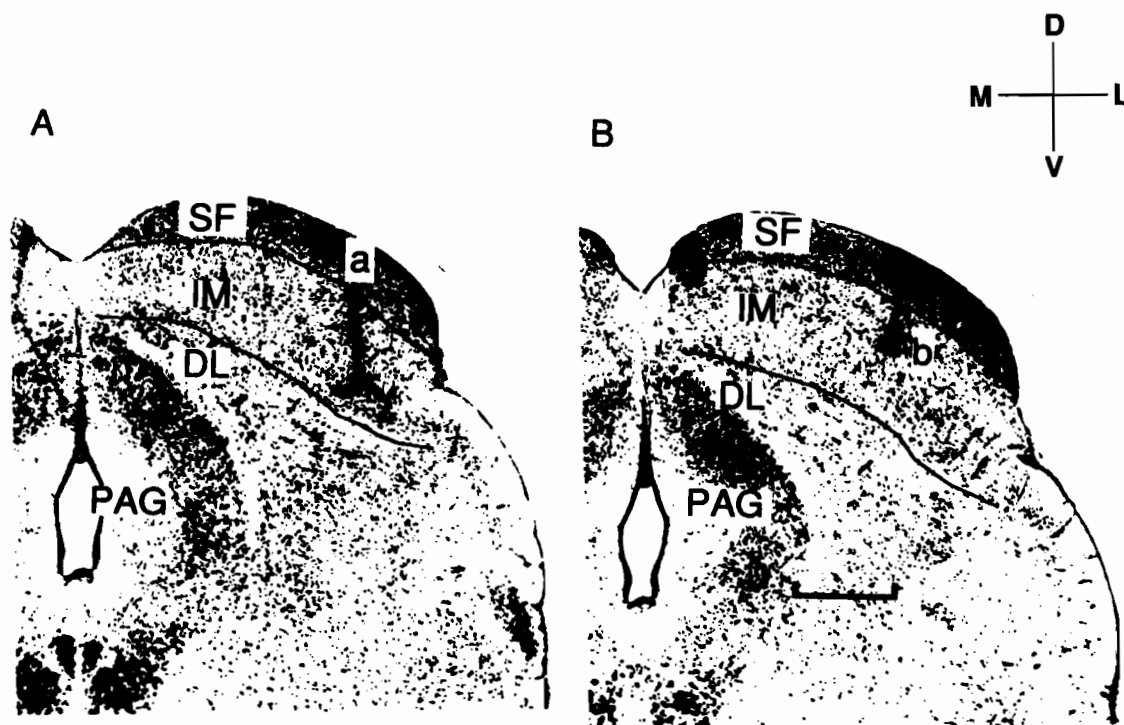


Fig. 5. Photomicrograph of a section, which was tilted back 45° from vertical, showing the superior colliculus. (A), a marking site where a nonspecific type neuron was recorded; (B), a marking site of 3 mm below the site where a visuomotor type neuron was recorded. Abbreviations: SF, the superficial layer; IM, the intermediate layer; DL, the deep layer; PAG, periaqueductal gray matter; D, dorsal; V, ventral; M, medial; L, lateral. Horizontal bar indicates 1 mm.

4.2.1. Mnemonic motor type

The memory-specific nature has been found in the basal ganglia (Hikosaka and Wurtz, 1983a; Hikosaka et al., 1989c) and the prefrontal cortex (Joseph and

Barone, 1987; Goldman-Rakic, 1987; Funahashi et al., 1989).

Some neurons in the caudate nucleus show tonic activity that is specific to memory-guided saccades (Hikosaka and Wurtz, 1983a; Hikosaka et al., 1989c); it was absent before visually guided saccades. The memory-specific role of the basal ganglia was further suggested by the chemical lesion of the caudate nucleus of the monkey (Kori et al., 1995): after injection of MPTP which specifically denervates dopaminergic fibers, the monkey became unable to make memory guided saccades to the side contralateral to the lesion. Similar memory-specific saccadic deficits were observed in human patients of basal ganglia diseases (e.g. Parkinson's and Huntington's disease) (Crawford et al., 1989; Leigh et al., 1983).

The memory-related function of the prefrontal cortex has been widely accepted (Joseph and Barone, 1987; Goldman-Rakic, 1987). This view has further been elaborated by recent studies using saccade tasks similar to ours (Sawaguchi and Goldman-Rakic, 1991; Funahashi et al., 1993). Neural correlates of the memory-specific behavior were found by Funahashi et al. (1989): neurons in the prefrontal cortex show tonic activities in a memory guided saccade task.

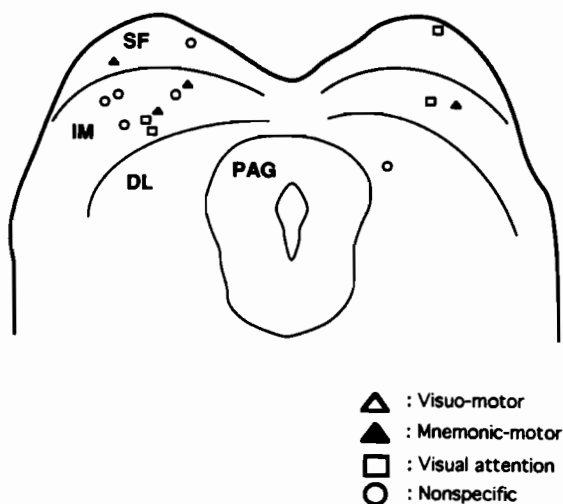


Fig. 6. Marking sites indicating the locations of tonic neurons; visuomotor type (open triangle), mnemonic motor type (filled triangle), visual attention type (filled square), nonspecific type (open circle). Abbreviations: SF, the superficial layer; IM, the intermediate layer; DL, the deep layer; PAG, periaqueductal gray matter.

In sum, it is suggested that neurons of the prefrontal cortex and the caudate nucleus share memory-selective features with the tonic neurons of mnemonic motor type in the superior colliculus. Underlying this correlation may be the strong connection from the prefrontal cortex to the caudate nucleus (Künzle, 1978; Jakobson et al., 1978). Caudate neurons project to the substantia nigra pars reticulata (SNr), which in turn projects to the intermediate layer of the superior colliculus (Jayaraman et al., 1977; Graybiel and Ragsdale, 1979). We would suggest that the information related to short-term memory in the prefrontal cortex is transmitted to the caudate nucleus, and the activity of the mnemonic motor type in the superior colliculus may reflect the activity of the caudate nucleus neurons through the SNr.

4.2.2. Visuomotor type

In the frontal eye field, visuomovement cells may also respond tonically during the interval between the target onset and the saccade onset (Bruce and Goldberg, 1985). There are some neurons within this group whose tonic activity is stronger before visually guided saccades (SACO) than before memory-guided saccades (SACD) (Goldberg and Bruce, 1990).

The role of the frontal eye field in visually guided initiation of saccade is strongly supported by its massive connection to the superior colliculus, especially to the intermediate layer (Fries, 1984; Huerta et al., 1986; Segraves and Goldberg, 1987; Stanton et al., 1988a). Thus, the visuomotor type neurons in the superior colliculus could reflect the tonic activity in the frontal eye field.

4.2.3. Attention type

Attention is the process by which sensory processing is selectively facilitated. At the neuronal level, attention is revealed by an enhancement of sensory response. This was first described in the superior colliculus by Goldberg and Wurtz (1972).

Subsequent studies showed that a similar saccadic enhancement of visual response is seen in other brain areas: frontal eye field (Wurtz and Mohler, 1976b), posterior parietal cortex (Robinson, 1972; Bushnell et al., 1981; Goldberg and Bushnell, 1981), and caudate nucleus (Hikosaka et al., 1989b). However, only in the posterior parietal cortex were neurons found that showed enhancement when the monkey attended to the target without making an eye movement (Goldberg and Bushnell, 1981). Some of them also responded tonically to the presentation of a visual stimulus (Goldberg and Bushnell, 1981; Andersen et al., 1987). The role of the parietal cortex in attention has also been suggested by lesion studies and clinical observations (Lynch et al., 1977; Lynch and McLaren, 1989; Zihl and Von Cramon, 1979).

These findings suggest that the activity of neurons of the posterior parietal cortex may be the source of the tonic activity of visual attention type in the superior colliculus.

4.3. Possible functions of tonic activities in the superior colliculus

The major output areas of the superior colliculus were classified into the following two areas: the oculomotor areas in the brain stem and the thalamus (Harting, 1977; Harting et al., 1980; Moschovakis et al., 1988; Sparks and Hartwich-Young, 1989).

The superior colliculus is well known to project to the oculomotor areas of the brain stem (Harting, 1977; Moschovakis et al., 1988) which contain burst neurons that drive ocular motoneurons directly to produce a saccade (Hikosaka et al., 1978; Grantyn et al., 1980; Igusa et al., 1980). The tonically active neurons that we recorded might also project to the burst neuron area and influence their membrane potential; this influence may normally be damped by a strong inhibition from omnipause neurons (Keller, 1974; Nakao et al., 1980). According to this scheme the tonic activity in the superior colliculus would change the subthreshold excitability of premotor burst neurons, and the selectivity of the tonic activity is preserved to some extent up to this level.

Another possible projection is to the thalamus, especially their subnuclei such as the ventral anterior (VA), the medial dorsal (MD), the internal medullary lamina nuclei (IML) (Benevento and Fallon, 1975; Harting, 1977). In IML and MD, there are neurons showing visual and saccadic responses (Schlag and Schlag-Rey, 1984). The IML and MD are mutually connected with the frontal eye field and posterior parietal cortex (Pearson et al., 1978; Barbas and Mesulam, 1981; Stanton et al., 1988b). These nuclei also project to the caudate nucleus (Jones and Leavitt, 1974). The VA instead projects to the prefrontal cortex (Jakobson et al., 1978).

These anatomical findings, taken together, suggest that there are loop circuits that are formed by the superior colliculus, thalamus, cerebral cortex, and basal ganglia. These loops might be divided into at least three sectors: (1) thalamus (IML/MD)-frontal eye field-superior colliculus; (2) thalamus (VA)-prefrontal cortex-caudate nucleus-SNr-superior colliculus; and (3) thalamus (IML/MD)-posterior parietal cortex-superior colliculus. Based on the arguments in Section 4.2., we would suggest that these loops may convey different types of signals: preparation of saccade, short-term memory, and visual attention. This may be the reason why there are specific types of neurons in the superior colliculus. Note, however, that a majority

of superior colliculus neurons are non-specific, suggesting that these signals, to a considerable degree, converge onto single neurons in the superior colliculus.

These data suggested that tonic neurons in the intermediate layers act to transform visual inputs to motor outputs. Further, there remains the possibility that the tonic neurons are interneurons (Behan and Appell, 1992). If so, the relatively specific signals observed in the tonic neurons might further be integrated at the next stage, presumably presaccadic burst neurons in the superior colliculus, and then transmitted to saccadic burst neurons in the brain stem.

5. Conclusion

We found that there are a fair number of tonic neurons in the superior colliculus, and some of them are selective for short-term memory, preparation of saccade, and visual attention. Our findings suggest that the superior colliculus is one of the areas where such cognitive signals are translated into oculomotor information. Furthermore, the superior colliculus might participate in the processes in which memory-, preparation-, and attention-related signals are maintained; and this may be accomplished by multiple loop circuits formed with the cerebral cortex, thalamus, and basal ganglia.

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