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# Role of the cat substantia nigra pars reticulata in eye and head movements I. Neural activity

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**Summary.** 1. Single unit activity was recorded in the Substantia Nigra pars reticulata (SNpr) of cats trained to orient their gaze toward visual and/or auditory targets. 2. Cells in the SNpr have a steady high rate of spontaneous activity ranging from 35 to 120 spikes per second. The neurons respond to sensory stimuli or in relation to saccadic eye movements with a decrease or a cut-off of the spontaneous discharge. 3. Among 109 cells recorded in the SNPR 60 were responsive to visual stimuli (mean latency = 118 ms). Most of the receptive fields which were plotted were large encompassing part of the ipsilateral field. 4. Thirty nine (39) cells were responsive to auditory stimuli (mean latency = 81 ms). A majority of these cells showed a better response for stimuli located in the contralateral hemifield. 5. In a few cells, the sensory responses were modulated by the subsequent orienting behavior of the animals. 6. Thirty one (31) cells showed a response in relation to saccades. These units typically stopped discharging between 50 and 300 ms prior to the onset of the saccade. 39% of these units also responded in relation to spontaneous saccades in the dark. 61% of the saccadic cells also responded to sensory stimuli in the absence of saccades. Six (6) cells were found to respond to active head movements. 7. These results are discussed in the framework of the role that the basal ganglia might have in the selection of the sensory stimuli that trigger orienting behaviors.

**Key words:** Substantia nigra pars reticulata – Single units – Eye and head movements – Selective neglect

## Introduction

For a long time, information regarding the role of basal ganglia in eye and head movements derived mostly from clinical material showing that in parkinsonism and in Huntington's chorea voluntary saccades are impaired (Starr 1967; Dejong and Melvill Jones 1971; Teravainen and Calne 1980). These observations showed that the basal ganglia played a part in oculomotor coordination but no precise information was available regarding the organization of their output to oculomotor structures. This situation has now changed since it has been demonstrated anatomically that the basal complex has, beside the globus pallidus, another major output station: the pars reticulata of the Substantia Nigra (SNpr). This structure projects heavily on the intermediate layers of the Superior Colliculus (Graybiel 1978) where neurons display visuomotor properties and on the most medial part of the VA–VL–VM complex that in turn projects to the neck and the face area of the motor cortex. These projections suggest that the SNpr might be the structure channeling visuomotor information coming from the striatum onto oculomotor and cephalomotor centers. This hypothesis has been recently confirmed in monkeys (Hikosaka and Wurtz 1983, I).

The present experiments were aimed at understanding the role of the SNpr in oculomotor functions and orienting behavior in cats. They will be reported in two parts. In this first paper we will concentrate on the information processed by SNpr cells during eye and head movements towards visual and auditory targets. A brief account of parts of this work has already been published (Joseph and Boussaoud 1982). In a second paper (Boussaoud and Joseph 1985) we will study oculomotor deficits following pharmacological injections in the SNpr.

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## Methods

Under alfatesine anaesthesia, 10 cats were implanted with 4 electro-oculographic electrodes. A dental cement pedestal was built on the skull to fixate the head to a stereotaxic frame. The skull was opened and two oblique recording cylinders were cemented to the bone with their centers in frontal planes A4 or A5.

Two or three days after surgery, the cats were placed in a hammock in a sound-attenuated, light-proof room, facing a tangent screen located 130 cm in front of them. The screen could be used to present discrete auditory and visual stimuli by means of 195 loud-speakers and 195 red light emitting diodes (LED). Each diode is located in front of a loud-speaker with respect to the cat's gaze. The set "Loud-speaker + LED" is referred to in the text as "the target". These targets are 5° apart from each other with respect to the center of the cat's head. The whole set of targets sustends a 70° angle of vision horizontally and 60° vertically. On a typical trial, a target is turned on for 1.5 s. During this period the LED is ON and the loud-speaker delivers clicks (20 pulses per second).

The horizontal and vertical derivations of the electro-oculogramm (EOG) and of the target are displayed on the same 608 Monitor Tektronix and on a paper chart (10 cm/s).

The experimental paradigm used for training the cat is basically the one used by Schlag and Schlag-Rey (1977) for the study of the Internal Medullary Lamina in cats. Its main characteristic is that there is no attempt to immobilize the gaze by a behavioral procedure before presenting the targets, and that the animals are free to orient their gaze or not at their own initiative. During a 2–3 weeks period, cats are trained to make orienting saccades alternately towards one of four fixed targets, 20° right, left, above and under the center of the screen. This makes it possible to adjust the gain of the horizontal and vertical EOG by comparing the amplitudes of the recorded saccades between these four known positions to their actual distance on the screen of the monitor and to eliminate the cross-talk. Cats were rewarded with water or milk. This behavioral procedure succeeded in inducing the cats to perform orienting saccades towards any target on the screen. Later on, as soon as the cats had reached a stable level of training, parameters of stimulation could be varied, regarding either temporal relationships of the visual and auditory stimuli or the use of "visual only" or "auditory only" targets. It was noticed that orienting responses of the eyes towards purely auditory targets were less frequent.

The activity of single cells was recorded by using movable glasscovered tungsten microelectrodes plated with black-platinum (Merryl and Ainsworth 1972) and driven by a Trent Wells motorized microdrive through a guide tube. For the plotting of the visual receptive field of a cell, repetitive stimulation of a particular region of the retina, irrespective of the cat's gaze position, was performed by electronically adding the retinal coordinates of that particular region to the actual coordinates of the gaze. The target closest to these coordinates was turned on, but because targets positions were discrete, precision under 5° was not available. The same set-up made it possible to stimulate the cat with two visual targets symmetrically located with respect to the position of the gaze. At any time during the study of a cell, the animal's head could be made free to move in the horizontal plane by releasing the stereotaxic frame attached to the skull. The center of rotation above the neck was in a position that gave the cats a minimum of discomfort during the movement. Intertrial interval was random, between 3 and 6 s on the average.

At the end of the experiments, lesions were made by passing a current (20 μA for 60 s) through the microelectrode, in different tracks surrounding the fruitful tracks and at two different levels in depth, aiming at the dorsal and ventral borderline of the SNpr. Then, cats were given an overdose of barbiturate, perfused with saline and 10% formaldehyde. Frozen sections 80 μm thick were made in the frontal plane and stained with cresyl violet. Penetrations were reconstructed with respect to the marking lesions and cells were placed in the SNpr by comparison with the atlases of the cat's brain of Jasper and Marsan (1960), Berman and Jones (1968). For 2 cats, the localization of the cells was based on the cells discharge characteristics and localization of the ends of the guide tube only.

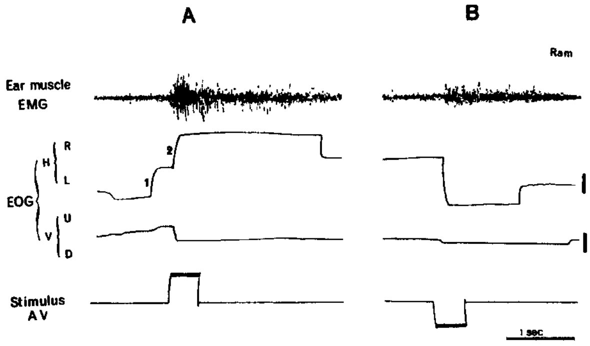

**Fig. 1A and B.** Synergy of eye and ear movements made toward an "auditory and visual" target. **A** and **B** are the records of two successive orientations. From top to bottom: Electromyogram of ear muscles (bipolar recording of right and left Elevator Auris Longus). – Horizontal (H) and Vertical (V) electrooculograms. 1. Spontaneous saccade, 2. Guided saccade. – Time of onset of the AV (Auditory and Visual) stimuli 20° to the right (A) and to the left (B) of the center of the screen

## Results

### *Orienting behavior towards auditory and visual targets*

Orienting saccades towards the targets were performed by the animals mostly towards the visual stimulus. Auditory signals often triggered only saccades towards the center of the screen that were then followed by an orienting saccade when the light came on. Nevertheless, such a strategy was not stable. It may change for day to day and often it was possible to record saccades towards purely auditory targets (see below). The responses were also different depending on the side: a cat might orient preferentially to the left to the visual stimulus and to the right to the auditory stimulus. Orienting saccades toward visual targets were more precise in term of distance of the final position of the gaze with respect to the position of the stimulus than saccades towards purely "auditory" or mixed "visual and auditory" targets, even if both stimuli were delivered at the same time. In the latter case, the cat apparently needed no fine adjustment of its gaze.

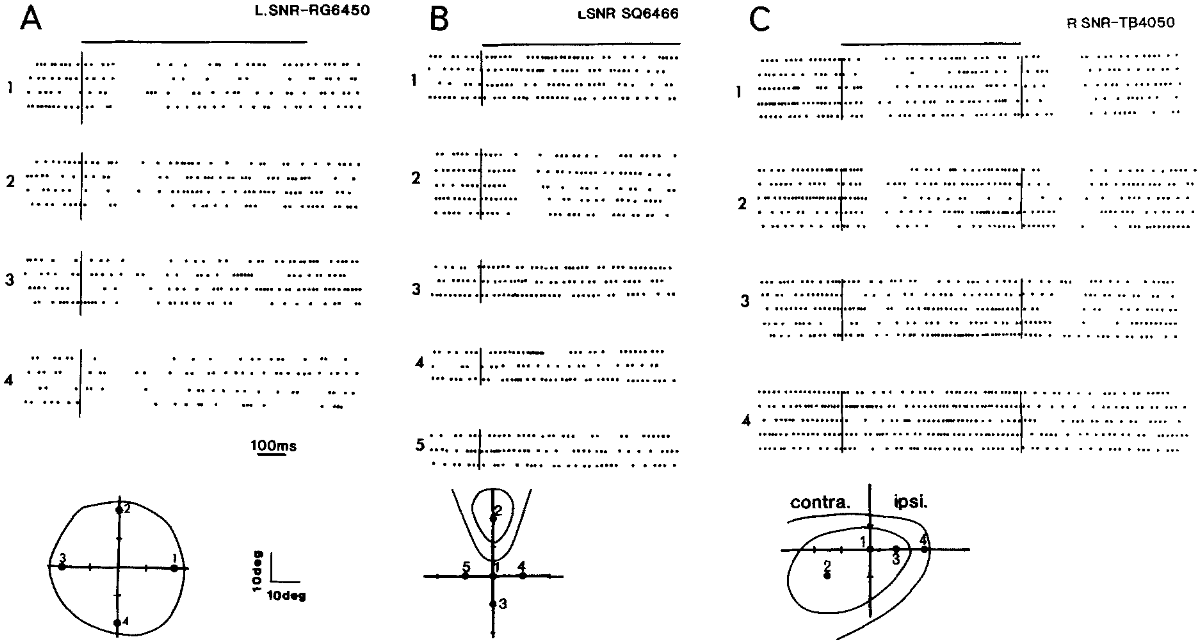

**Fig. 2A–C.** Visual response of three SNpr cells (A–C)) with receptive fields of different size to the onset and offset of a visual stimulus. Duration of the stimulus is indicated by the horizontal line at the top of the rasters. Single dots indicate single action potential. Successive horizontal lines, aligned with the onset and offset of the stimulus indicate consecutive trials. Rasters 1, 2, 3, 4 and 5 show the response of the cells to visual stimuli located respectively at points 1, 2, 3, 4 and 5 of the visual field which is represented below in a schematic way. Contour lines on the visual field demarcate areas where decrease of discharge rate was approximately the same. Time scale is indicated in the lower right corner. Reference of the cells (recorded side, cat, track number and height given by the microdrive) are indicated above the rasters. All subsequent figures use the same conventions

Observation of the animals shows that orienting saccades were accompanied by ear movements. We studied this phenomenon quantitatively in one cat by implanting electrodes in the pinnae muscles and by recording EMG along with saccades. Results showed that in 90% of cases (396 times out of 450), eye movements towards mixed "auditory and visual" or even pure "visual" targets were accompanied by EMG volleys. These volleys may be interpreted as caused by orientation of the pinnae. There is no evidence of a shorter reaction time of either eye or ear movements depending on whether the stimulus was auditory or visual. Thus, during guided orientation, both receptors, eye and ear, seem to move in synergy. In contrast, during spontaneous orientation, either receptor moves in an independant way (Fig. 1).

### *Overall features of SNpr cells*

All cells reported in this paper were recorded between frontal planes 4.0 and 7.0 in the pars reticulata of the substantia nigra. These cells were first identified by their high rate of discharge (Hikosaka and Wurtz 1981). Subsequent analysis showed that the rate of discharge is steady and ranges from 35 to 120 spikes per second. There was no correlation between the rate of discharge of a cell and its response – or lack of response – to a particular event.

Decrease of discharge rate in relation to visual stimuli or saccades were further used for locating the SNpr (Hikosaka and Wurtz 1981). Indeed almost all cells of the SNpr responding to visual or auditory stimuli or to saccades did so by a decrease or a cut-off of their discharge and only a few cells by an increase of their firing rate. Histological reconstructions showed that all cells were located in the middle part of the SNpr and corresponded well to the area labelled by HRP injections in the superior colliculus (Beckstead et al. 1981).

Not all cells of the SNpr were modulated by the occurrence of a stimulus or a saccade. In the best cases, 4 to 6 cells were recorded in one single track, out of which one at most was driven. In ten cats, out of more than 500 cells recorded from the SNpr, 109 showed a response. We will now describe the features of the visual, auditory, saccadic, and cephalic responses separately.

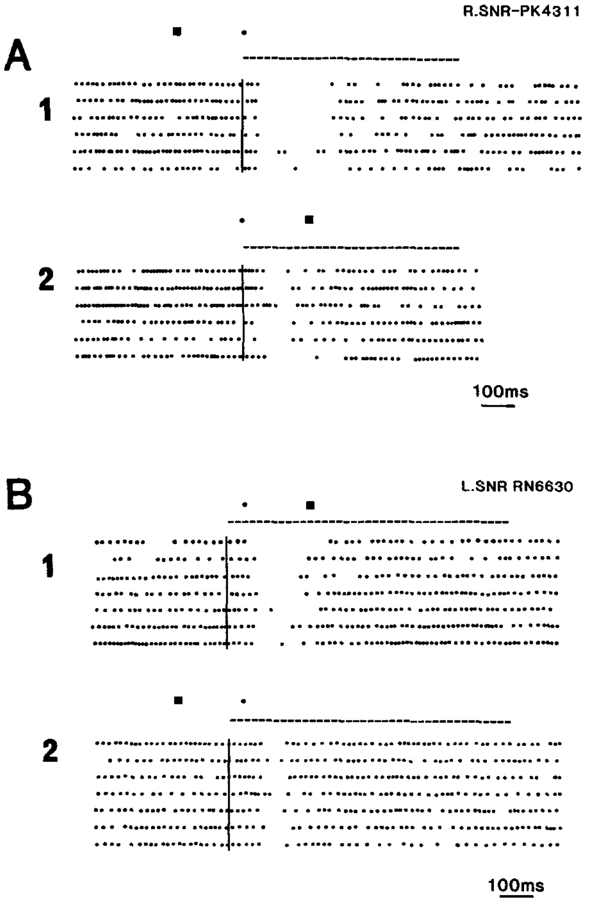

**Fig. 3A and B.** Auditory response of two SNpr cells. **A** and **B** are two cells located respectively in the right and left SNpr. Duration of the stimulus (f = 20 pulses per second) is indicated by the dashed line on the top of the rasters. The dot and the square represent the positions of the gaze and of the loud-speaker respectively. The stimulus was presented on the contralateral (A1 and B1) and on the ipsilateral (A2 and B2) side at 30° of eccentricity with respect to the center of the screen

### *Responses to visual stimuli*

Sixty cells were responsive to visual stimuli. Latencies ranged from 50 to 250 ms (mean latency – 118ms) and duration from 100 to 1400ms depending on the cell considered. In all cases except one, the response was a decrease of the firing rate. Fifty one cells responded to the onset of the stimulus. Nine cells responded both to the onset and offset of the stimulus. For these cells, latencies and duration of the response were the same for both stimulations.

The visual receptive field was systematically explored for 25 cells (Fig. 2). Usually receptive fields were large: 15 cells showed a receptive field extending on both visual hemifields. For 4 cells, the responses were the same whether the stimulus was located 20° on the right, on the left, above or below the fixation point, but for the majority there was a clear directional response. Responses were more vigorous for stimuli located in the contralateral visual field. Six cells showed a more restricted visual field located either around the fovea, either in the upper-field (20° above the gaze position) or in the contralateral visual field only.

### *Responses to auditory stimuli*

Thirty nine cells showed an auditory response. Latencies ranged between 50 and 100 ms (mean latency = 81 ms) and durations between 50 and 400 ms. All cells responded to the onset of the stimulus, only one also showed an off-response. For most cells, the response was a decrease of the firing rate but 3 cells showed an increase of their discharge rate in response to the stimulus. The dependence of these responses upon the frequency of the stimulus was not studied.

Among the 20 auditory cells with no visual response, 15 showed a better response to stimuli located on the contralateral side (Fig. 3). Only one showed a better response to stimuli located in the ipsilateral field. For the 19 bimodal cells, the lateralization of the response was less clear-cut: 6 cells only had a preference for contralateral stimuli.

### *Modulation of responses to visual and auditory stimuli*

In the group of 19 bimodal cells responding to visual and auditory stimuli, interaction between sensory stimuli was often encountered. In particular, the response to a first stimulus, let it be visual or auditory, sometimes overshadowed the response to the delayed occurrence of the second one (Fig. 4). This was seen in 4 cells.

Modulation in the intensity of sensory responses during repeated stimulations was found to occur in accordance with the orienting behavior of the cat. Visual cells sometimes displayed responses that might disappear after two or three stimulations if the cat did not orient to the stimulus (Fig. 5B). We do not know however, in the absence of monitoring of lid closure, if the visual responses disappeared in relation to habituation or because the cats, dozing off and keeping their eyes half-open, did not see the stimulus. However, this phenomenon was also observed with auditory responses where such lid closures did not matter. This is best seen in Fig. 5A where the auditory response of a cell completely disappears after 8 contralateral stimulations distributed over a 60-s period and intermixed with the same

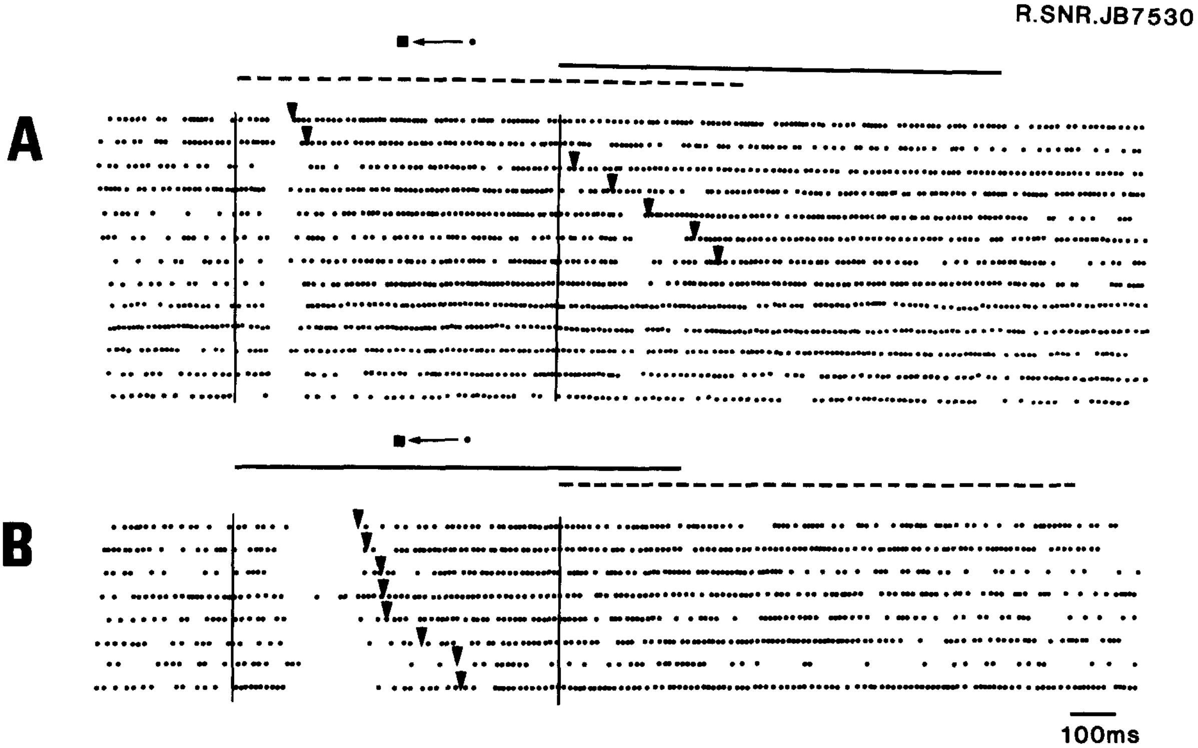

**Fig. 4A and B.** Modulation of the auditory response by a visual stimulus and of the visual response by an auditory stimulus in a SNpr cell. Both stimuli were located at 20° eccentricity to the contralateral visual field. In **A** the auditory stimulus comes on first, followed by the visual stimulus. In **B** the visual stimulus comes on first, followed by the auditory stimulus. Arrows on particular trials indicate the onset of orienting saccades. All subsequent figures use the same symbols to indicate the beginning of saccades

number of ipsilateral stimulations. Orienting saccades in Fig. 5A, represented by triangles, are directed toward the target (first orientation) then towards the center of the screen (next 4 orientations) and finally, away from the present target, toward the expected location of the next target (last 3 orientations). In this case, if the cat was alert but neglected part of the sensory field, sensory responses to stimuli located in this field might completely disappear.

Modulation of the discharge rate in relation to saccades was studied also in order to see whether a phenomenon described in the monkey as the "enhancement effect" might be recorded in cats when the animals used the stimulus for an orienting movement. The term "enhancement" is used in all cases when the magnitude of a sensory response is increased by a subsequent motor event but not when a better sensory response may be interpreted as an overlap or a summation of a sensory and a saccade related response. Both responses often could be separated in our experiments because the animals frequently delayed the orienting saccade with respect to the onset of the stimulus. Enhancement could be reliably studied in 55 cells. There were 10 visual and 3 auditory cells whose responses were enhanced with saccades toward the stimulus (Fig. 6). This enhancement was either a prolongation of the response or a better cut-off of the firing. In four cells, sensory responses only or mostly appeared if there was an orienting saccade toward the stimuli (Fig. 6B and C). Due to the insufficient cooperation of the animals, and the small numbers of cells displaying the enhancement effect, the spatial selectivity of this phenomenon could not be reliably studied. However, in case of a stimulation with two stimuli located symmetrically with respect to the cat's gaze center, if the response was not altered when the saccade was directed toward the stimulus located in the receptive field of the cell, it was not altered either if the saccade was directed toward the second stimulus located outside the receptive field.

### *Saccadic responses*

Thirty one cells showed a response in relation to saccades. Responses were a decrease of the firing rate, ranging from 300 to 50 ms before the saccade for 28 cells (Fig. 7A), or just at the onset of the saccade for 3 cells. The decrease might last up to one

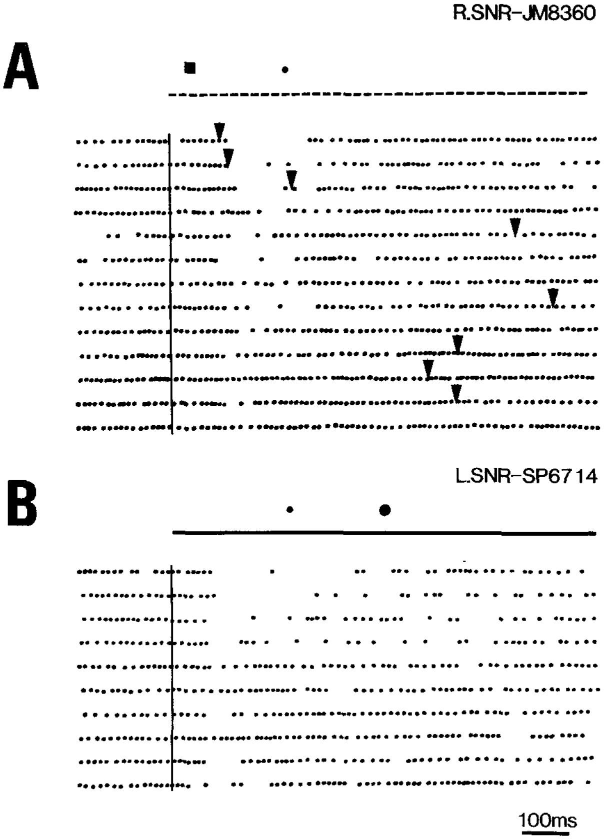

**Fig. 5A and B.** Habituation of the auditory **A** and the visual **B** response of two SNpr cells. In **A** the auditory stimuli, located at 20° eccentricity horizontally to contralateral side with respect to the center of the screen, come on approximately every 8 seconds. The first saccade only is directed toward the target. In **B**, the visual stimuli located at 20° eccentricity to contralateral side with respect to the center of gaze come on approximately every 4 s

second after the end of the saccade. Only 3 cells showed an increase of the firing rate.

The majority of the saccade cells (22) only responded to saccades toward a visual stimulus, not to those occurring in the dark. In this group, responses to saccades toward purely auditory targets were sometimes encountered but responses were weaker. We also recorded 9 cells that displayed a slight decrease of discharge rate for spontaneous saccades executed in the dark (Fig. 7C).

Twenty one cells showed a response only when saccades were directed toward one side of the visual space. Four cells were not directional. Regarding relationships between visual receptive field and movement field, we observed that saccadic responses appear mostly for saccades directed toward stimuli located in the receptive field in 16 cells. Two cells showed a response to saccades directed in all directions although they had a limited receptive field (Fig. 7B).

### *Combination of sensory and saccade responses*

Among the 90 sensory cells, bimodality was often encountered: 31% of the visual cells had an auditory response and almost half of the auditory cells had a visual response. 61% of the saccadic cells had a sensory response.

### *Cells associated with head movements*

Head movements were studied in the horizontal plane. The range of possible movement on each side was 90° with respect to body axis. Cells referred to in this section did not show any visual, auditory, vestibular or oculomotor response. Position of the head did not modify their firing rate.

Seventeen cells were influenced by head movements. Responses were in most cases a decrease of the firing rate. Increased firing rate was observed only in two cases. Eleven cells responded to passive head rotations only and 6 to active head movements. Among these 6 cells however, 3 cells showed a stronger response for passive than for active movements (Fig. 8B). The activity of cells responding to active head movements was modulated by orienting movements toward a stimulus as well as by spontaneous movements in the dark. These cells were directional: five cells responded to movements toward the contralateral side and one toward the ipsilateral side. Responses started slightly before the movement for 2 cells (Fig. 8A) and at the onset of movement for 4 cells. Cells active only with passive head movements were also directional. Most responded with passive movements toward the contralateral side.

## Discussion

### *Inhibitory responses of the SNpr cells*

We have shown that activity of SNpr cells is modulated by sensory and oculomotor inputs. These inputs may reach the SNpr by way of the subthalamic nucleus (Hammond et al. 1978), the locus coeruleus (Collindridge et al. 1979), the raphe nuclei (Dray et al. 1976) and the cortex (Goswell and Sedgwick 1973). But the main afference comes from the caudate nucleus. This nucleus receives in turn afferents from all cortical areas but mostly from associative and frontal areas (Webster 1965; Royce 1982) and from the Internal Medullary Lamina of the thalamus. All such afferents to the caudate nucleus

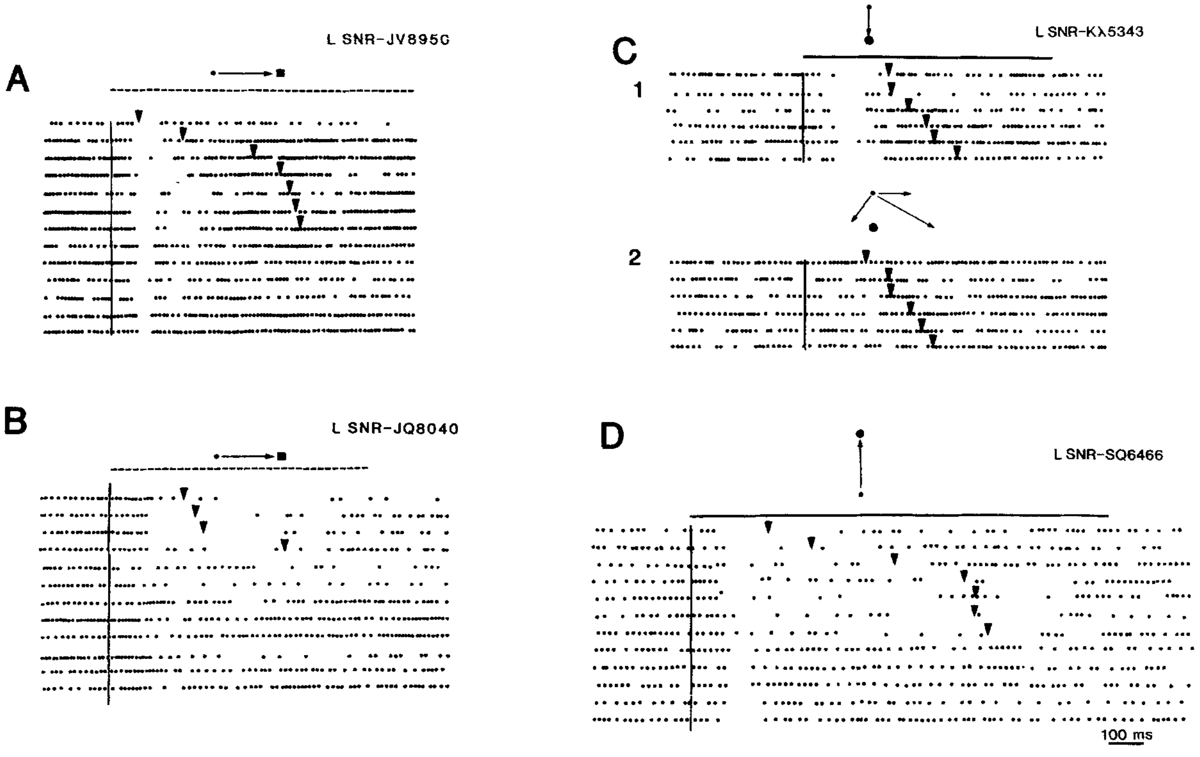

**Fig. 6A–D.** Enhancement of auditory (**A and B**) and visual (**C and D**) responses when the stimulus is a target for a saccade. All trials are ranked according to increased reaction time. In **A** and **B** the click stimulus is presented 20° contralateral to the cat's initial gaze position. In **A**, the auditory response is prolonged when there is an orientation. In **B**, the auditory response is vigorous only if there is an orientation toward the stimulus. Trials in this raster are consecutive. In **C** the spot of light is presented 10° below the cat's initial gaze position. In ($C_1$) the animal saccades toward the stimulus. In ($C_2$) the animal saccades but not toward the stimulus. In **D** the spot of light is presented 20° above the cat's initial gaze position where the cell has its receptive field. The visual response is prolonged when there is an orienting saccade

may indirectly provide the SNpr with sensory information and oculomotor inputs.

We have shown also that SNpr cells have a relatively steady high rate of discharge (35–120 spikes per second) and that their response to sensory signals and to the occurrence of a saccade is a decrease of firing. This decrease might be mediated by inhibition via the striato-nigral pathway. It was indeed shown that stimulation of the caudate nucleus mostly elicits inhibition of SNpr neurons (Yoshida and Precht 1971; Frigyesi and Szabo 1975; Deniau et al. 1976). This inhibition is mediated by the γ-aminobutyric acid (GABA) (Feltz 1971; Streit et al. 1979). The SNpr projects in turn to the thalamus, to the mesencephalic reticular formation and to the intermediate layers of the superior colliculus. All these projections are also reportedly inhibitory (Deniau et al. 1978; Chevalier et al. 1980). This inhibition is also mediated by GABA (Vincent et al. 1978; Di Chiara et al. 1979).

In conclusion, if we make the assumption that the caudato-nigro-tectal GABA-ergic pathway is the main pathway mediating sensory and oculomotor inputs of striatal origin toward the oculomotor centers, we may hypothesize that steady inhibition of tectal neurons and release or modulation of this inhibition in relation to sensory and oculomotor events is the basic mechanism by which basal ganglia participate in saccadic eye movements. In order to understand the proper role of these ganglia, it is nevertheless necessary to go further into the details of the cells' responses.

## *Uni- and multimodality of sensory cells*

One of the most striking results of this experiment is the relative abundance of sensory responses found in a structure that was thought to be mostly motor. This feature is encountered also in monkeys (Hikosaka and Wurtz 1983, I). The characteristics of the visual and auditory responses, i.e. the type of response (mostly inhibitory), latencies, and lateralization also seem to be similar in both animals. There are differences, however, that are important with regards to the role that the SNpr might have in guided

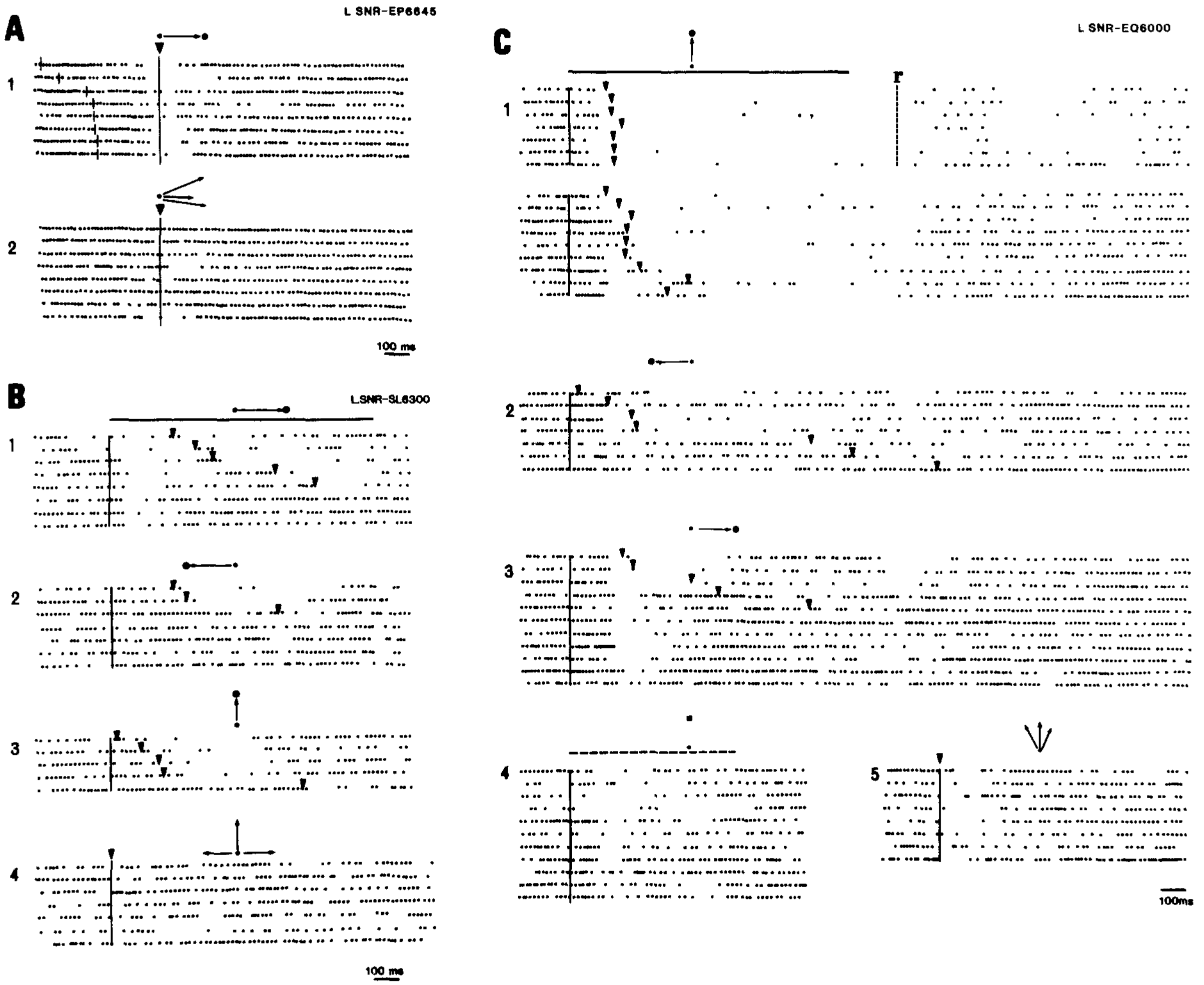

**Fig. 7A–C.** Saccadic and sensory responses of SNpr cells. **A** Saccadic responses of a cell to targets located 20° horizontally with respect to the cat's initial gaze position. Saccades are directed towards the contralateral field. Trials are aligned with the onset of the saccade. In A1 saccades were triggered by a visual stimulus. Stimulus onset is indicated by a small vertical bar. In A2 responses to spontaneous saccades of about the same amplitude and direction as in A1 are illustrated. **B** Visual and saccadic responses of a SNpr cell. In B1, B2, B3 the trials are aligned with respect to stimulus onset. The stimulus was presented 20° contralateral to (B1) 20° ipsilateral to (B2) and 20° above (B3) the cat's initial gaze position. There is a saccadic response in relation to all saccades. There is a visual response only to targets located in the contralateral field (B1). In (B4), the activity of the cell is aligned with respect to the onset of spontaneous saccades in all three directions. **C** Visual, somesthetic, auditory and saccadic response of a SNpr cell. The visual stimulus was presented 20° above the cat's initial gaze position (C1), and 20° ipsilateral (C2) and contralateral (C3). In the first part of (C1), the letter "r" indicates the time of onset of the reinforcement that is followed, 400 ms later, by a somesthetic response. In (C4) the raster illustrates a weak auditory response to the click stimulus presented at 20° of eccentricity upward with respect to the center of the screen. In (C5) the raster shows a decrease of activity in relation to spontaneous saccades directed upwards

behavior. The main difference is that the proportion of bimodal cells seems to be higher in cats than in monkeys. In cats we found many cells with multimodal sensory inputs. We also found a few cells, not fully described here, responding to tactile stimulation of the face or to licking of the spout as well as to visual stimulation. This convergence that is reminiscent of the multimodal sensory inputs to the striatum is not encountered in monkeys where most sensory cells are apparently unimodal. Hikosaka and Wurtz have suggested that unimodality of sensory responses in the SNpr might be one of the physiological bases of the behavioral habituation of the orienting response that is known to be specific to a particular stimulus. This hypothesis is not supported by our data in cats.

### *Involvement of the SNpr in eye and head movement*

In this paper we have described cells whose activities were related to saccades. Most cells showed a

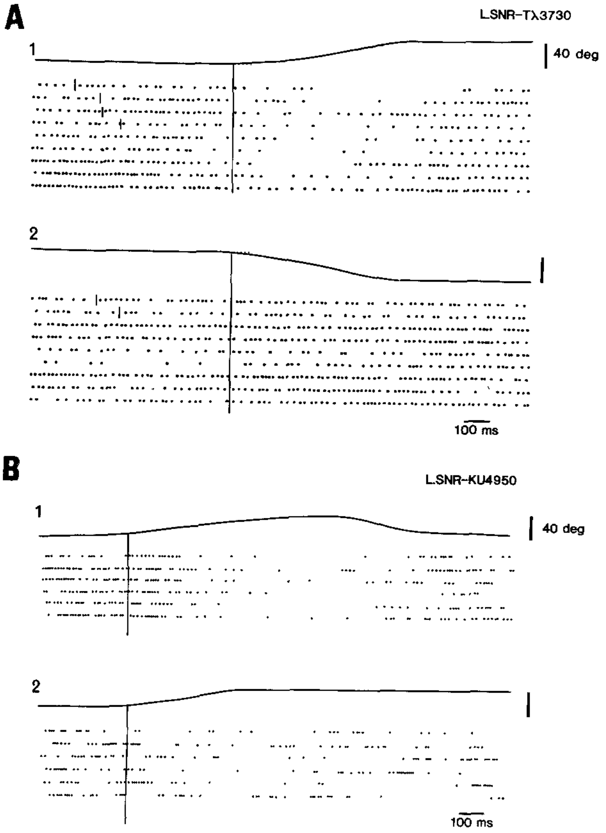

**Fig. 8A and B.** Response of SNpr cells to head movements. Activity of the cells are aligned with respect to the onset of the saccade accompanying the head movement. Calibration of the movement is indicated by the two thick vertical bars on the right of the figure. In **A** response of a cell to the contralateral (A1) and ipsilateral (A2) voluntary head movement. Small vertical bars indicate onset of the visual stimulus triggering the movement. In **B** response of a cell to passive (B1) and voluntary (B2) head movement. Decrease of firing rate is more vigourous for passive than for active movements.

decrease of activity before the onset of the saccades. One feature of these cells in their dependency upon sensory information. This dependency is illustrated by the fact that the movement field and the visual field of a given cell are often the same and that, for the most part, the saccadic response is contingent on visual or auditory stimuli (Fig. 7A and B). For the majority of saccadic cells there is indeed no response if saccades of about the same amplitude and direction occur in darkness.

However, for these cells, it seems that the very presence of the target is not necessary. Our data show indeed that if a saccade is directed toward a target that is already "OFF", there may be also a response. In other terms, as soon as a saccade is aimed at finding a target, there may be a saccade-related response. This may explain the existence of cells displaying a weak response correlated with spontaneous saccades in the dark, if we suppose that part of these spontaneous saccades are aimed at finding a remembered target.

We recorded in the SNpr cells whose activity was modulated by active or passive head movements. Only 3 cells showed a decrease in activity slightly before spontaneous head movements toward the contralateral side and no modulation with passive movements. These cells show that SNpr might be involved in initiation and, certainly, control of cephalic movements. Even if they are not many, the very existence of such cells is not surprising. The SNpr is functionally located between the striatum where Schneider and Lidsky (1980) have found cells whose activity preceeded EMG volleys of the neck muscles accompanying movement of the head, and the superior colliculus where Straschill and Schick (1977) recorded neurons active with spontaneous head movements. However, most cells only responded to passive head movement. This observation shows that proprioceptive signals can reach the SNpr. We noticed that these cells did not respond mostly to a simple stretch of the neck muscles. The response was better if the cat resisted the passive stretch. This feature was seen in another context: we found two cells that neither responded to the passive stretch of the contralateral paw nor to active twitching when the cat pulled it back. But they clearly stopped their firing when the experimenter tried to keep the cat from doing so. In such a case, as in the case of neck muscles, the adequate parameter for driving the cell was not the stretch itself but the stiffness of the muscles due to the animal's effort to counteract the load. Seemingly the context in which the possible role of such cells might be best understood is not the control of head orientation but the control of load compensation and correction of external perturbations occurring during movements and positional tasks.

### *Modulation of sensory responses – enhancement and decrement*

Modulation of sensory responses was studied in relation to the occurrence of saccades. The enhancement of sensory responses observed in visual and auditory cells was very similar to the enhancement effect first described in monkeys in the context of orientation toward visual stimuli (Goldberg and Wurtz 1972). Thus, it seems that our data extend this phenomenon of enhancement both to another sensory modality, audition, and to another animal, the cat. It is true however that this effect can be observed in earlier papers on the cat even though the authors do not comment on these data directly (Schlag and Schlag-Rey 1982). Hikosaka and Wurtz (1983, I) did describe an enhancement of sensory responses in SNpr of monkeys when the visual or auditory stimulus was a target for a saccade. The main difference appears to be that the phenomenon is seen in a greater proportion of cells in monkeys (42% of the visual cells) than in cats (17% of the visual cells). It is not clear however, whether this particular comparison between the two species is meaningful because, in our statistics, we discarded all cells whose sensory and saccade related responses could not be separated and in which an enhancement of the sensory response alone was not clear-cut. Thus, our definition of enhanced cells is apparently more restrictive than the one used by Hikosaka and Wurtz. Comparison is difficult also because of differences in the experimental conditions. In our experiment, there was no opportunity for the cat to prepare systematically for a particular eye movement and the observed changes in the sensory responses can only be explained either by differences in the alertness of the animals or by the selective attention that they spontaneously pay to one part and then another of the visual or auditory space. At the present time, either or both of these explanations are consistent with the data.

In addition to enhancement, decrement of sensory response was also observed in the context of habituation to repeated stimulations and/or in the context of selective neglect. We introduce the term "selective neglect" because decrement of the sensory responses was most often observed in situations in which the oculomotor behavior of the cat suggested "neglect" for one part of space as a consequence of a possible selective attention to another. A good example of decrement of a sensory response in which neglect might have played a role is illustrated in Fig. 5A. It shows that the decrement in the auditory response was related neither to a decline in alertness of the animal which continued to react quickly to stimulus presentation, nor to the brisk saccades made by the animal away from the receptive field, since it also occurred on trials in which no saccades were produced, but was instead related to what seems to be a systematic neglect of the targets presented on one side of space. The behavior of those cells that displayed a sensory response only when the cat oriented toward the stimuli (Fig. 6B and C) may also be interpreted in term of selective attention/neglect. Indeed the sudden reduction in responsivity that was observed as soon as the cat failed to orient toward the target cannot be explained only by a general reduction in alertness, but rather by selective neglect for that part of space where the cell has its receptive field.

In conclusion, it seems that the two related behavioral phenomena – selective attention and neglect – find in the SNpr neural correlates in term of enhancement and decrement of responses in sensory cells. If we consider the great quantity of sensory information continuously and simultaneously impinging on the brain and the single motor act that this stream of information triggers, we may suppose that there must be, at some points, a selection of the sensory information that will be used for the motor act and, correlatively, a neglect for the part of the sensory information that will not be used. Hassler (1978) pointed to the putamen as one of the CNS structures dealing with this selection "The function of the putamen is to focus the attention, the emotional participation and the excitability on one single event by simultaneously suppressing and fading out all other happenings and motivational objects". We do not know whether the responsivity of the SNpr cells is a result of sensory information processing that takes place in the putamen, the caudate nucleus or both, but the modulation of the SNpr cells responses fits well with the hypothesis that selection of that part of sensory information that will trigger a motor act is one of the functions of the basal ganglia.

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