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Activity in monkey substantia nigra neurons related to a simple learned movement

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Summary. Single cell activity was recorded in the pars compacta (SNc) and pars reticulata (SNr) of the substantia nigra (SN) in 4 unanesthetized *Macaca fascicularis* to determine the motor role of the nucleus. Animals were trained to perform a simple task that involved moving a lever by elbow flexion-extensions, in the horizontal plane using the hand contralateral to the recording site. Two monkeys learnt to execute the task on both sides. Electromyograms (EMG) of limb muscles were recorded simultaneously with SN neurons. Discharge rate modulation related to specific movement phases was present in 35% of the neurons. A significant positive correlation of the discharge rate with movement velocity and amplitude was found in SNc and SNr neurons. Some SNr cells discharged in anticipation of the EMG, suggesting a participation of the nucleus in the preparation of movement. The activity of SNr neurons was also related to movement of the left and right upper limb. In conclusion, the SN seems to play an important role in the control of specific motor mechanisms, probably modulating movement velocity, amplitude and direction, with little participation of somatosensory feedback. The involvement of the SNr in the coordination of bilateral arm activity is discussed.

Key words: Substantia nigra – Motor behavior – Extracellular activity – Movement-related cells – Awake monkey

Introduction

The substantia nigra (SN) is included within the basal ganglia and has been associated with dysfunctions such as Parkinson's disease. The role of the SN is mostly related to the nigrostriatal dopaminergic degeneration leading to alterations in movements. Of the three main symptoms of Parkinsons's disease: hypokinesia, tremor and rigidity, the former seems to be the most closely related to nigral destruction (Bernheimer et al. 1973) as confirmed by results obtained in primates with SN lesions producing hypokinesia (Schultz et al. 1989; Viallet et al. 1981). Moreover, bradykinesia and akinesia are induced by lesions of the SN pars compacta (SNc) in humans via intravenous administration of 1-methyl-4-phenyl-1,2,3,6 tetrahydropyridine (MPTP), a drug that selectively destroys SNc cells (Langston 1983). Therefore, the nigrostriatal dopaminergic pathway is the most serious candidate in the generation of those disorders, although controversy still exists. For instance, the motor role played by the SNc is not clear enough. It was reported that a small population of SNc cells show a moderate increase in activity during walking (Steinfels et al. 1983) and circling (Diana et al. 1989) while other results showed no relation to phasic movements (Trulson et al. 1981; Trulson 1985). In primates, Schultz et al. (1983) demonstrated that SNc cells modulate their impulse rate in relation to large reaching movements, and showed an impairment in the initiation and execution of movements after the nigrostriatal dopamine pathway was lesioned (Schultz et al. 1989). A point of disagreement results from the observations of DeLong et al. (1983) since SNc neurons were found unrelated to a task where the animals performed controlled forelimb flexion and extensions to varying targets and to passive manipulations. On the other hand, non-dopaminergic cells of the substantia nigra pars reticulata (SNr) represent one of the main output stations for striatal function, and thus a route whereby the basal ganglia may control motor and sensory-motor mechanisms (Cools et al. 1984; Hikosaka and Wurtz 1983; Marsden 1980 and 1982). But reports on this matter are neither extensive nor conclusive although lesions with kainic acid (Di Chiara et al. 1977) indicated that the striatonigral pathway modulates nigral influences on postural movements.

The aim of this work was to gain insight into some of these questions, namely the activity of SNc and SNr neurons in relation to a simple learned motor task. The analysis of the relationships between cell discharge rate

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and different movement variables, using statistical techniques, allowed us to conclude that both subregions play a role in the control of movement. Preliminary results were published in an abstract form (Magariños-Ascone, et al. 1986), and as part of a doctoral thesis (Magariños-Ascone 1989).

Material and methods

Motor task training and surgery

Four monkeys *(Macaca fascicularis)* weighing 3–4 kg sat on a monkey chair with two levers, one on each side. Two animals were trained to move the right lever with the right arm to receive a liquid reward, and the other two learned to move the two levers with the right or left hand, one at a time. Animals had no visual cues and could not see the lever while moving it. The task required the monkeys to move a lever back and forth (in a horizontal plane) between two mechanical stops separated by 20 to 100 mm. Movements consisted of elbow extensions and flexions that pushed and pulled the lever, respectively (here called push-pull). A potentiometer fed by a 1.5 V battery provided a voltage signal proportional to lever position (Fig. 4B), and two microswitches interrupted another voltage signal indicating the rear and forward level stops (not shown). Deflections of the lever record upwards or downwards mean push or pull movements, respectively, in all Figs. A set of DEC logic K-modules was used to control the task.

After training, animals were operated under sodium pentobarbital and a cylinder was cemented over the left hemisphere according to stereotaxic coordinates (Shantha et al. 1968) centered on A 7.5 and L 5. The dura within the cylinder was removed and the cortex was covered with a layer of sylgard (Dow Chem.). A system to immobilize the animals' head was used during recording (see Magariños-Ascone et al. 1988).

Neuronal activity recording

Stainless steel microelectrodes of 180 μm diameter, electrolytically etched, and insulated with epoxy resin except at the tip, were used. A hydraulic micromanipulator fixed to the cylinder and handled from outside a sound-proof room, lowered the electrode to the SN. Extracellular action potentials records (+ up) were only accepted if they fulfilled criteria designed to reject fibers, artifacts, or confusion with the background noise.

Experimental steps

Initially, the animal sat quietly in the chair, a situation named resting, and was unable to grasp the levers because there were compartments preventing the monkey from reaching them. Neurons were first recorded for 1–3 min in that condition. Then, the right (i.e., contralateral) lever compartment was opened from outside the experimental room (by a simple silent, manual device) and the monkey was free to move the lever. The two animals which moved the two levers, were allowed first to move the contralateral, while the ipsilateral one was covered, and then the ipsilateral lever while the contralateral lever was covered. The electromyographic (EMG) activity of biceps and triceps muscles of the right or left arm were studied. Motor action potentials were recorded with two 60 μm diameter factory insulated nichrome wires inserted into the muscles through thin hypodermic needles which were then withdrawn. When the activity of a cell was related to movements of the lower limb or the tail, the EMG of the appropriate muscle was recorded.

Eye movements were recorded in the first animal by placing bitemporal electrodes. Silver-silver chloride electrodes were used and voltage deflections calibrated.

Data logging and processing

Data from the SN microelectrode and EMG electrodes were amplified, bandpass filtered (0.1–10 kHz) and tape-recorded together with signals from the lever position and microswitch stops. Subsequently, the tapes were played-back, action potentials transformed into brief electrical pulses by a "Schmitt-trigger" circuit, and stored, usually with a 10 ms accuracy (occasionally 5 ms), using a PDP 11/50 digital computer. The lever position signals were sampled at 100 Hz and stored in the computer. Whenever the movement reached the lever stops a program generated timing signals (i.e. "point processes" of time) which retrospectively served as zero reference to calculate averages or perievent histograms (PEH). When the movement did not reach the stops another program generated point processes at the onset of the pull and push from the lever position signal. The following functions were calculated with previously stored data: (*a*) averages between point process, either of lever displacement push or pull, and the lever displacements to determine the corresponding average movement trajectories; (*b*) PEHs between the same point processes as in *a* and the cell discharge or the motor action potentials to determine the discharge rate modulation in relation to the movement trajectories (e.g., Fig. 5); (*c*) autocorrelation histograms (ACH) to characterize the temporal occurrence of the impulses (e.g., Fig. 11); (*d*) average movement trajectories (*a*) and averages of eye position, calculated by taking either lever pushes or zero crossings of eye movements to the right as timing signals (i.e., point processes; e.g., Fig. 3).

A cell was considered as movement-related when the peak-to-peak PEH amplitudes were significantly different from peaks of a histogram calculated with the same data but after shuffling at random the relative position of the first-order inter-discharge intervals (Moore et al. 1966; Perkel et al. 1967). The shuffled histogram shows no correlation and tends to be flat. Siegel and Tukey's modification of Wilcoxon's test was used to compare both histograms (Langley 1971).

Velocity-amplitude study. Although the task was performed rhythmically, lever movements were not always exerted at the same pace (e.g., Fig. 4B). To identify cells related to movement velocity and amplitude, lever displacements were separated into fast-slow and large-small groups by a computer program. The program measured peak-to-peak amplitude and duration for all individual movements and separated them into amplitude quartiles and velocity (i.e., amplitude:duration) quartiles. It then calculated movement averages and PEHs for the higher and lower quartiles separately, and together for the two intermediate amplitude and velocity quartiles. Therefore, a total of 6 averages were obtained, 3 for amplitude and 3 for velocity quartiles. Movement variable-discharge rate relationships were also calculated for individual movements. The impulse rate was measured between the lower and upper movement turning points and the velocity (i.e., amplitude:time) was estimated for movements of similar amplitudes (inset, Fig. 8). Rate was plotted as a function of velocity and evaluated with a linear regression analysis. The same analysis was performed with movement amplitude for movements of similar velocity and discharge rate was plotted as a function of amplitude.

X-ray and histological controls

On the initial experimental day lateral and transverse radiographs were taken with a microelectrode positioned in the SN to gross check its localization. On the final day electrolytic lesions (50 μA, 20 s) were made through the microelectrode at selected recording sites with the animal anesthetized with sodium pentobarbital. Finally, animals were perfused intracardially with physiological saline,

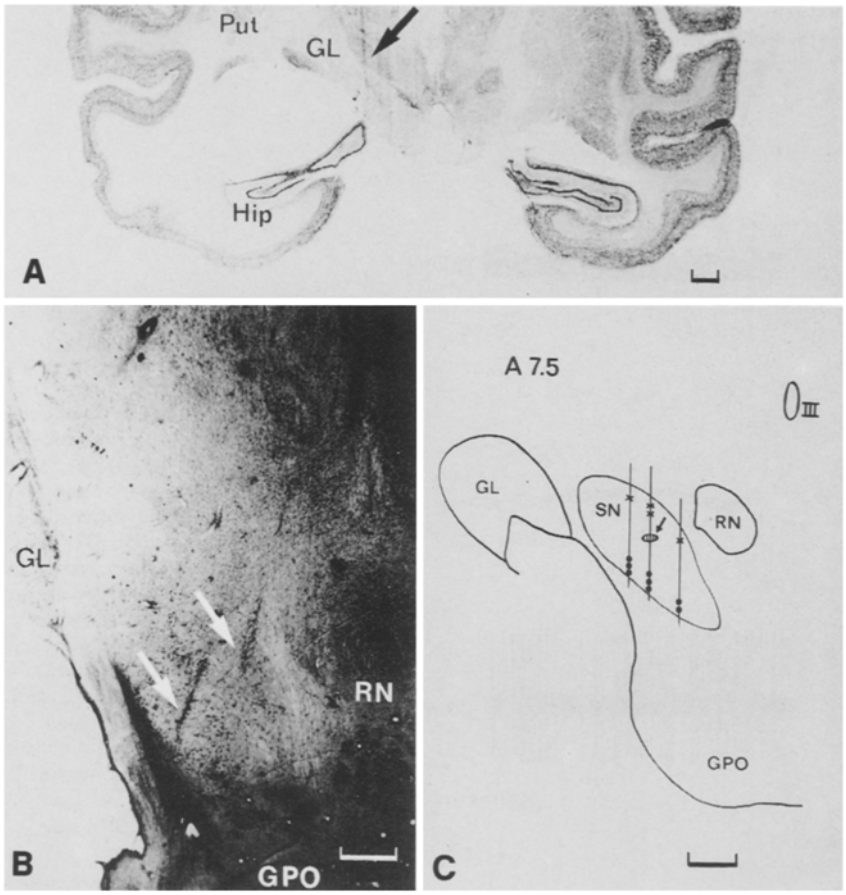

Fig. 1A–C. Coronal sections (**A, B**) through the SN and electrode penetration reconstruction (**C**). **A, B** Photomicrographs of cresyl-violet stained sections of the brains of two monkeys showing SN electrode tracks and electrolytic lesions (arrows). **C** Reconstruction showing some recorded neuron sites in the SNc (crosses) and SNr (circles) calculated from a marking lesion (arrow) in another animal. Abbreviations: GL, lateral geniculate; GPO, griseum pontis; Hip, hippocampus; Put, putamen; RN, red nucleus; SN, substantia nigra. Calibration bars 1 mm

followed by 10% formalin and the brains sectioned at 50 μm and stained with cresyl-violet. Penetration tracks and recording sites were reconstructed with the atlas of Shantha et al. (1968). All cells included in this report were confined to the SN and were separated as belonging to SNc or SNr. Figure 1 displays histological sections with tracks and marking lesions of two monkeys and the reconstruction of some recording sites in another animal.

Results

Cell identification

SNc cells discharged single action potentials at low rates (0.5/s to 9/s; mean = 3.7/s) (see Table 1 and Fig. 2B1). Action potentials were of long duration (> 2 ms) with a marked inflexion on one of the branches or close to the peak (Grace and Bunney 1983; Guyenet and Aghajanian 1978; Schultz 1983), and amplitude variations (Grace and Bunney 1983). SNc cells also discharged in doublets or bursts at low rate (2–8/s; Fig. 11A1; Grace and Bunney, 1983). On the other hand, SNr neurons discharged at higher rates (15–120/s; mean = 31/s) with brief (about 1 ms) and stable action potentials (see Table 1 and Fig. 2B2; Schultz 1986). Figure 2 displays some of the electrophysiological features described (B) and histograms showing discharge rates (A) for SNc and SNr cells. Cells responding to somatosensory stimulation were only found in the SNr and cells activated by visual stimulation were seen in both SNc and SNr; they are not included here (Magariños-Ascone et al. in preparation).

Eye movements were uncorrelated with limb displacements as illustrated in Fig. 3. They were not phase-locked in this experimental paradigm as also reported elsewhere (Magariños-Ascone et al. 1981 and 1988), suggesting that our sample probably did not contain cells related to both movements. A one-way window allowed the confirmation of this observation in all animals. The head was immobilized, and sitting diminishes the activity of postural muscles in a push-pull movement (G. Stelmach et al. 1990). Moreover, there are some data suggesting that anticipatory postural adjustments and focal muscles (arm muscle activation) involve separate motor commands (Brown and Frank 1987). Thus, under these conditions, co-contractions involving neck muscles should not contribute. However, neck EMG was not recorded and a direct demonstration is lacking.

Discharge rate changes related to movements

One hundred and twenty-two neurons were recorded during the performance of the motor task. Forty-three of them (35%) modulated the discharge during lever movements; 14 SNc and 29 SNr cells. Table 1 shows the distribution within the SN. The animals typically displaced the lever rhythmically at 2–4 Hz (Magariños-

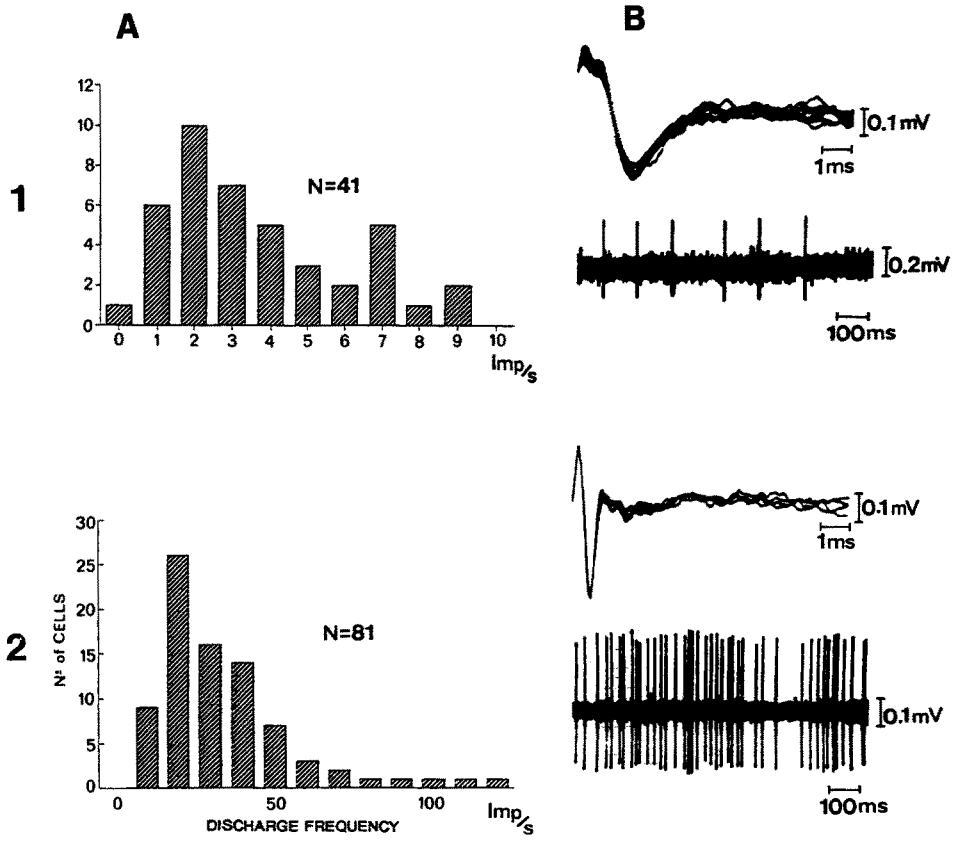

Fig. 2A, B. Histograms of discharge rate (**A**) and main electrophysiological features of SN cells (**B**). **A1, A2** Distribution of SNc ($n=41$) and SNr ($n=81$) cells, respectively, according to their discharge rate. **B1, B2** Main features of SNc and SNr neurons, respectively. Superimposed sweeps in the upper trace of B1 and B2 show action potential waveform characteristics. A notch close to the peak, a long duration and low discharge rate distinguishes the SNc cell. A stable, brief waveform, and higher impulse rate individualizes the SNr neuron

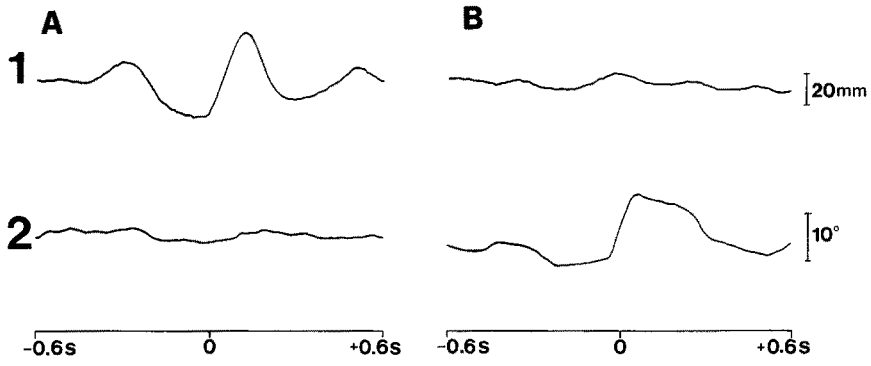

Fig. 3A, B. Eye and lever movement relationships. **A1, B1** Lever movement averages. **A2, B2** Eye movement averages. The lever push displacement was taken as reference for lever (**A1**) and eye movements (**A2**). Saccadic eye movements towards the right were taken as reference for lever (**B1**) and eye movements (**B2**). Note absence of phase-locked peaks indicating no correlation between lever (**A2**) and eye (**B1**) movements. Forty trajectories were processed in **A** and **B**

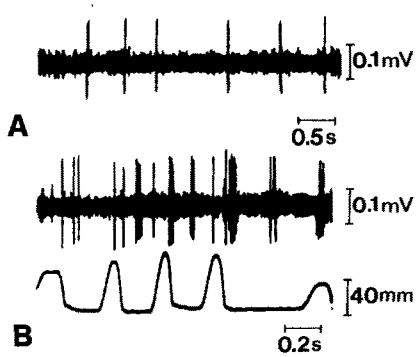

Fig. 4A, B. Raw electrical recordings of movement related SNc cell. **A** Low discharge rate at resting. **B** Discharge modulation (upper) related to movement (lower)

Table 1. Distribution of movement-related cells within the SN

	SNc	SNr	SN
Neurons tested	41	81	122
Movement-related	14 (34%)	29 (36%)	43 (35%)
Unrelated	27	52	79

Ascone et al. 1988) and the neuron's discharge rate modulation involved rhythmic accelerations and decelerations (increases of up to 3-fold above controls) at specified phases of the movement cycle (e.g., Figs. 4 and 5). Figure 4 shows a brief segment of the spontaneous discharge (A) and of the movement related activity (B). This

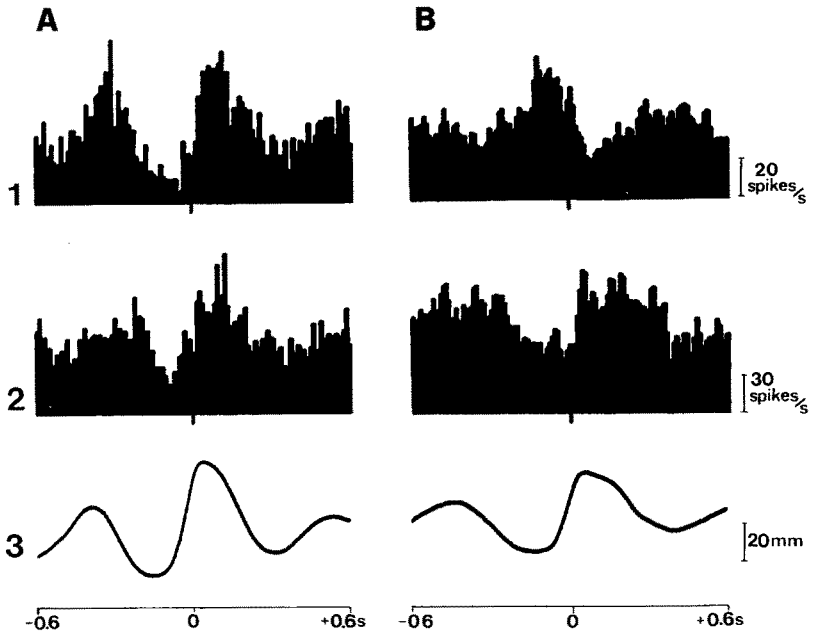

Fig. 5A, B. Discharge rate modulation of SNr cells with movements. **A1** and **B1** Perievent histograms (PEH) of neural discharges. **A2** and **B2** PEHs of the EMG triceps brachii. **A3, B3** Averages of the lever displacement (zero reference push). Peak rates are in phase with push (**A**) and pull (**B**). Sixty lever trajectories were processed in each case

SNc cell increased its discharge rate in relation to pulling movements.

The encoding of movement direction (i.e., pull or push) is illustrated in Fig. 5A and B. Twenty-five cells were related to extension (8 SNc and 17 SNr neurons) and 18 to flexion movements (6 SNc and 12 SNr cells). The lever displacement averages (record 3) show successive pull-push sequences of similar amplitude, indicating stable rhythmic movement cycles. The PEHs of two neurons (record 1) illustrate the rhythmic rate modulation in relation to movement trajectories. The rate modulation depth of both cells (1) closely followed the waveform of the lever displacement averages (3), but neuron peak discharge accelerations were in opposite phase (pull A1; push B1) with respect to the EMGs. Triceps EMG activity (record 2) incremented with arm extension during push.

Velocity and amplitude neurons

Figure 6 shows an example of an SNc velocity-dependent cell. Movement averages and PEHs for the higher (A) and lower (B) velocity quartiles are illustrated. Although velocity was clearly different in A and B, it should be noted that mean peak-to-peak amplitude was also larger in A, for it was impossible to distinguish both movement variables completely (see below). Figure 7 illustrates an SNr neuron related to movement amplitude. Panels A, B and C, show averages and PEHs for the larger, two intermediate, and smaller amplitude quartiles, respectively.

As there was a high correlation between both variables (i.e., amplitude, velocity) all neurons showing a relationship with those movement variables were studied for each individual movement (see Methods). The analysis shown in Fig. 8, revealed that discharge rate was well described by a positive linear function of movement

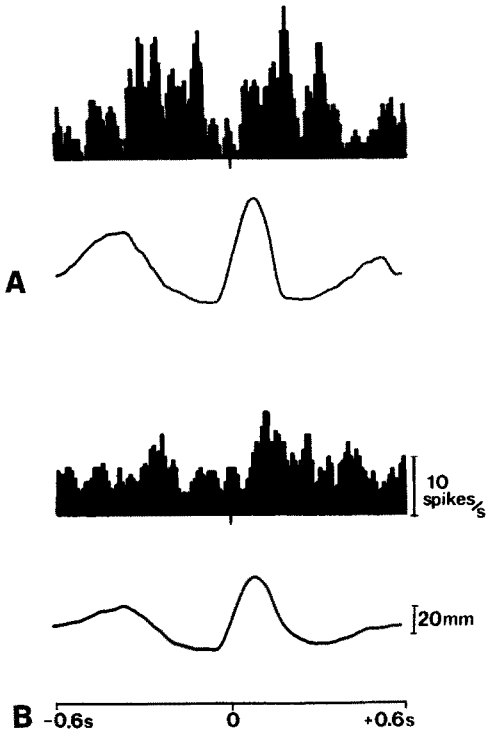

Fig. 6A, B. Discharge modulation of SNc neuron with rapid (**A**) and slow (**B**) movements. PEH (upper) and lever displacement averages (lower); 25 movements were averaged. The cell shows a vigorous movement-related acceleration, larger for rapid movements (**A**)

velocity. Ten SNr and 4 SNc neurons out of the 43 movement-related cells (32%) demonstrated a velocity-dependent discharge rate relationship. All the velocity-related neurons that increased the rate showed the same type of functional relationship ($p < 0.01$, range of correlation coefficient $r = 0.68$–0.90 for $n = 12$, and $p < 0.05$, $r = 0.75$ and 0.87 for $n = 2$). The discharge rate was a

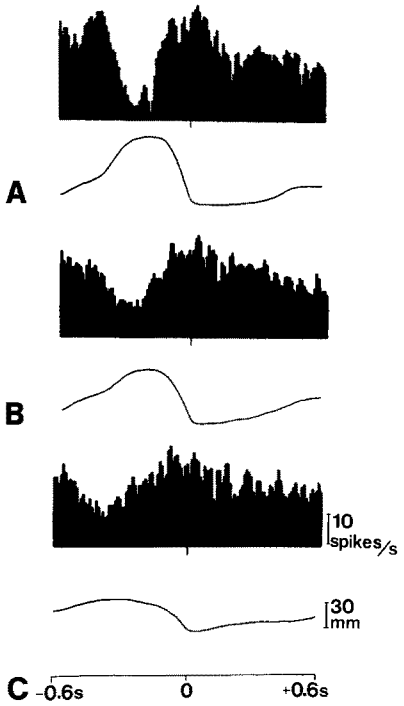

Fig. 7A–C. SNr neuron related to movement amplitude. **A–C** Large intermediate and small amplitude quartiles, respectively. PEHs (upper) and lever displacement averages (lower). The cell accelerates during the pull and more so with larger movements. Twenty-five lever displacements were processed in **A** and **C**, and 50 in **B**

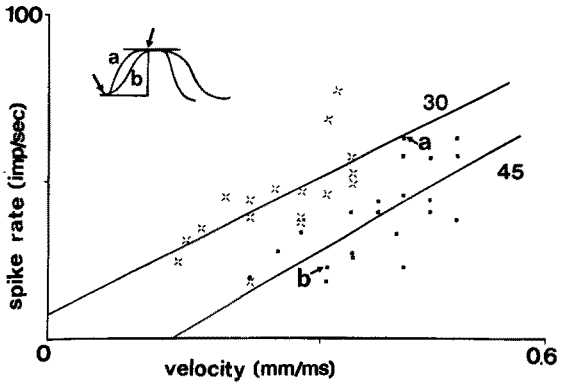

Fig. 8. Plot of SNr cell impulse rate versus movement velocity. The inset illustrates two lever displacement traces having the same amplitude (45 mm) and either a high (*a*) or low (*b*) velocity. The corresponding mean discharge rates measured over each corresponding movement are shown in a and b in the plot. Arrows in the inset indicate the minimum and maximum turning point of the lever record. The discharge rate is a linear function of velocity for amplitude movements of 30 and 45 mm (indicated by the respective numbers). Seventeen and 21 trials were sampled (crosses and squares, respectively)

linear function of the movement amplitude in two SNc and 8 SNr cells ($p<0.01$, range of correlation coefficient $r=0.68$–0.84 for $n=6$, and $p<0.05$, range of $r=0.58$–0.91 for $n=4$). Half of the cells increased their discharge rate with movement amplitude and the rest decreased it.

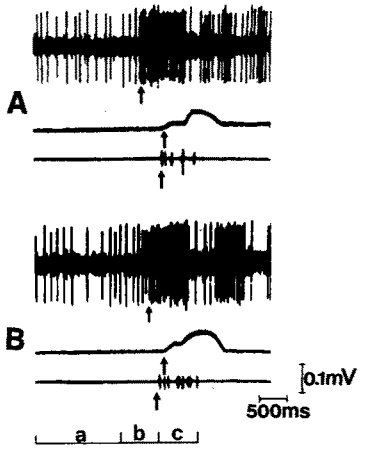

Fig. 9A, B. Movement-related SNr cell showing discharge rate increments before EMG activity. Upper, middle and lower traces, cell activity, lever displacement and biceps EMG, respectively. Arrows indicate the onset for the discharge acceleration, the lever movement and EMG, respectively. The trial was separated into a non-movement (*a*), and a pre-movement (*b*) and movement (*c*) epochs

Increased discharge rate of SNr cells preceding EMG activity

Four SNr cells incremented their discharge rate up to 80 ms before the onset of the biceps EMG activity (Fig. 9). This rate increase was clearly observed only when the animals moved the lever performing a single, isolated, push-pull (which also involved a discontinuity in the lever excursion). The trial was separated into a non-movement epoch (a), a pre-movement (b) and a movement (c) epochs. The mean discharge rate was estimated for the epochs in which this movement was classified. Twelve similar movements were considered for this cell giving as a result a mean discharge rate of 15.2/s (s.d. 5.19) for the non-movement epoch (a), 22.5/s (s.d. 5.7) for the pre-movement time (b), and 31.6/s (s.d. 6.6) for the duration of the movement (c).

Bilateral movement-related cells

Neurons related to movements of both limbs were found only in the SNr. Eleven cells out of the 35 studied in two monkeys (31%) were found to be related in this way, as illustrated for a representative cell in Fig. 10. A and B show discharge modulation (record 1) and movements (record 2) of the right (contralateral) and left limb (homolateral), respectively. The peak impulse rate is for contralateral push and ipsilateral pull.

Other movement-related cells

Although many cells in the SNc and SNr were unrelated to the task during its performance, they altered the discharge rate when the monkey made other different movements. These cells (4 SNr and 6 SNc) increased their discharge rate for up to 1 min after the movement. The

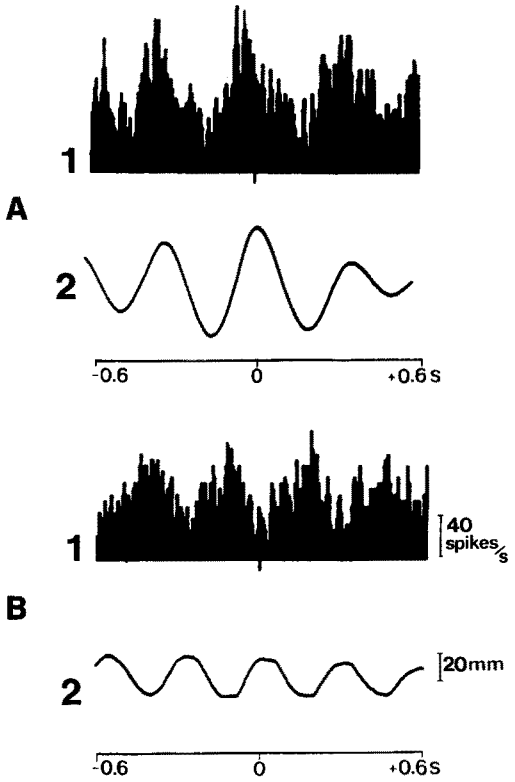

Fig. 10A, B. SNr cell related to right and left limb movements. **A, B** Right and left, respectively. 1, PEHs and 2, lever displacement averages. Peak discharge acceleration was related to push (**A**) and pull (**B**). Fifty lever trajectories were processed

cell shown in Fig. 11 discharged spontaneously with a slight rhythmic tendency as indicated by the two peaks at either side of the zero reference (B1), and became totally rhythmic with a vigorous increase in discharge rate after performing a movement (B2). Cells related to other specific movements were also found in the SN. They were correlated with the EMG of the legs, ears and tail and were not included in Table 1.

Discussion

An important contribution of the SN in movement is deduced from this study regarding the amount of motor-related cells, the encoding of some movement variables, and the motor bilateral activity. No special regional difference was found within the SN except for some SNr cells which showed discharges correlated with movements of both upper limbs.

The movement of the trained limb was uncorrelated with spontaneous eye movements in our experimental paradigm (Fig. 3). Earlier findings indicated that SNr cells decreased their discharge rate in relation to saccade-induced eye movements (Joseph and Boussaoud 1985; Hikosaka and Wurtz 1983). However, most SNr cells reported here enhanced their activity to movements of the limb, suggesting the existence of another SNr population which may be due to the different experimental paradigm, or, as noted by Hikosaka and Wurtz (1983), "one cell may respond in different ways under different experimental conditions".

A considerable percentage of SN cells was related to movements of the upper limb confirming results obtained in the SNc of rats (Diana et al. 1989) and in the SNr of cats (Schwarz et al. 1984) and monkeys (Nishino et al. 1985), but in contrast to other reports (DeLong et al. 1983, Schultz 1983). The differences may be due to the distinct experimental approach followed. In our case the animals executed simple, fast excursions of the arm with no visual cue to indicate a correct target. Furthermore, our results imply that the neurons were related to movements with a duration of about 200 ms which may be considered ballistic and preprogrammed (Desmedt and Godaux 1978). As the peak of the discharge rate increment was not preferentially related to any part of the lever displacement trajectory it was assumed that the stops did not play a significant role as a reference. Therefore, these cells are probably unrelated to somatosensory information provided by the lever stops.

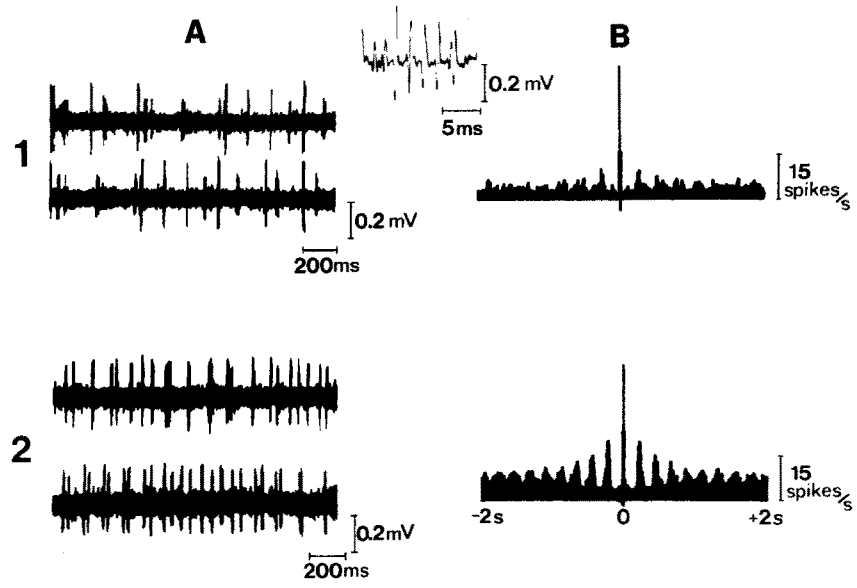

Fig. 11A, B. Post movement rate acceleration in a SNc cell. **A1,** activity in quiet animal; two successive traces (upper and lower as in **A2**). Two cells discharged simultaneously (large and small action potentials). **A2** 10 s after movement; only the large action potential remained. Inset, high velocity sweep showing the decrease in amplitude of the large action potentials along the burst. **B,** ACHs calculated with the large amplitude action potential in quiet (1) and post-movement (2) conditions. The post-movement activity becomes more rhythmic

The fact that the discharge rate peak to pull or push movements depended on the neuron suggests that the cells may preferentially code arm movement direction (see below). Nevertheless, the contribution of some SNc cells to a general motor activation (Schultz 1983) may be found in our group of neurons discharging in an unrelated way to the task although with an increment in discharge rate (e.g. Fig. 11). These cells may be related to a tonic facilitatory action of dopamine (DeLong et al. 1983). Interestingly, other SNc neurons discharged phasically in relation with a specified phase of individual arm movements.

The encoding of limb movement direction by SN cells fits in with similar findings in other structures of the basal ganglia. Thus, cells related to either flexion or extension of the arm were also described in the putamen (Alexander 1987; Crutcher and DeLong 1984) and globus pallidus (Anderson and Horak 1985; Georgopoulus et al. 1983).

The relation of SN cells to movement velocity and amplitude is a novel finding. This means that a group of SNc cells may participate in the control of such mechanisms, and supports the view that the SNr is an important motor output station of the basal ganglia (Cools et al. 1984; Marsden 1980, 1982) capable of influencing other centers (Hikosaka and Wurtz 1983; and see also below). Interestingly, similar neurons were also found in the globus pallidus (Georgopoulus et al. 1983) and in other regions like the pulvinar (Magariños-Ascone et al. 1988) which are also related with the SNr (Motles et al. 1987; Takada et al. 1984).

Some SNr cells discharged in advance of the onset of movement and of EMG activity (see Fig. 9), possibly implying an influence in the preparation of movement. This view is consistent with similar findings obtained in areas anatomically linked to the SN such as the putamen and caudate (Crutcher and DeLong 1984; Hikosaka and Sakamoto 1986), as well as in the pallidum (Anderson and Horak 1985; Georgopoulos et al. 1983; Neafsey et al. 1978).

The cells discharging in relation with bilateral movement offer a new perspective in the consideration of the SN functioning. The peak of discharge of the same SNr cell encoding opposite direction of displacement in both limbs (Fig. 10) provides evidence in favor of a reciprocal bilateral motor coordination. Although a direct anatomical pathway connecting both hemispheric SN regions has not been reported, their close interactivity has been demonstrated on the basis of the effects of drug administration, the spontaneous release of dopamine, and sensory stimuli (Nieoullon et al. 1977, 1978). Furthermore, a reciprocal influence between the SNc and SNr was found by many authors (Grace and Bunney 1980; Hommer and Bunney 1980; Ruffieux and Schultz 1980; Waszczack and Walters 1983, 1986; Magariños-Ascone, Buño and Garcia-Austt in preparation). In addition, bilateral SNr efferent fibers projecting to the superior colliculi (Hopkins and Niesen 1976; Rinvik et al. 1976; Gerfen et al. 1982), the ventromedial thalamic nuclei and the midbrain reticular formation (Beckstead and Frankfurter 1982) have been described. Thus there is a possibility of a SN bilateral motor influence mediated by SNr efferent pathways. On the other hand, it should be noted that the SNr and the internal pallidum output projections make contact in the thalamus with cells channelling the motor circuitry primarily to the supplementary cortical motor area (Schell and Strick 1984), a region having an important role in the bilateral control of movements (Brinkman 1981). Although precise postural adjustments preceding any arm activity may involve co-contraction of neck and other muscles (Bouisset and Zattara 1981), sitting diminishes the need to stabilize the body prior to the execution of push-pull movements (Stelmach et al. 1990) and when stability is high, postural activity is reduced or absent (Cordo and Nashner 1982). Furthermore, it is also claimed that separate motor commands drive postural and arm muscles activation when pulling or pushing a handle (Brown and Frank 1987). Therefore, although we cannot provide further evidence since neck EMG was not recorded it seems reasonable to think that postural adjustments are of little importance in our experimental paradigm.

In conclusion, the movement-related activity of neurons found in this work is a clear indication of the role of the SN in motor mechanisms, in consonance with results on nearby structures and with current models of basal ganglia function (Alexander and Crutcher 1990; DeLong et al. 1990).

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