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Role of the cat substantia nigra pars reticulata in eye and head movements II. Effects of local pharmacological injections

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Summary. 1. Guided and reflex eye movements were studied in cats trained to make orienting saccades toward visual and auditory targets. Injections of a GABA-agonist (Muscimol) or GABA-antagonists (Bicuculline and Picrotoxin) were made in the Substantia Nigra pars reticulata (SNpr). 2. Bicuculline and Picrotoxin, whether unilaterally or bilaterally injected had no effect on the posture nor the oculomotor performance of the animals. Neck muscle activity remained symmetrical. 3. Unilateral injections of Muscimol produced oro-facial akinesia, reduction of the number of eye movements, contralateral head turning, visual neglect mostly (but not only) for ipsilateral visual space. Balance between the gains of the vestibulo-ocular reflex (VOR) in the two directions of movement was changed. Gain was decreased for the ipsilateral rotation. The optokinetic nystagmus (OKN) was not affected. Contralateral neck muscles were hypertonic. 4. After bilateral injections of Muscimol, the cats did not orient. The VOR was normal when the injections induced no postural asymmetry. Hypertony was bilateral. 5. Implications of these results for the role of the basal ganglia in motor control are discussed. We suggest that in Parkinson's disease the fixed inhibitory drive of the SNpr on the tectum and on the thalamus is disrupted.

Key words: Substantia nigra pars reticulata – Eye movements – GABA-agonists – GABA-antagonists

Introduction

In the first part of this study (Joseph and Boussaoud 1985) we showed that activity of cells in the Substantia Nigra pars reticulata (SNpr) is related to orientation of the eyes and the head toward visual and auditory targets. These results suggest that lesions of this structure would lead to dysfunction of the oculomotor system and orienting behavior.

We have also shown that the modulation of discharge in SNpr cells related to visuo-motor activity was characterized mostly by an inhibition of the firing rate. Although neurotransmitters in the SNpr are numerous this inhibition might set into play the GABA-ergic striato-nigral pathway. Moreover, it has been shown (Arnt et al. 1979; Scheel-Krüger et al. 1977, 1981) that local injection of GABA agonists in the SNpr leads to behavioral effects very similar to those produced by Kainic acid lesions (Di Chiara et al. 1979; Olianas et al. 1978). Thus it would appear that this GABA-ergic transmission at the level of the SNpr may play the most important role in channeling striatal information to structures subserving oculomotor and postural mechanisms.

In order to delineate more clearly the role of GABA-ergic transmission in orienting behavior, we have studied the effects of local injections of various GABA-agonists and -antagonists on guided and reflex eye movements.

Material and methods

Five animals were used in this experiment. They were fitted with DC electrodes that made it possible to record eye position in the orbit. The electromyographic activity of the right and left biceps, triceps and splenius was also recorded in one cat.

Three cats had been used in the previous experiment (Joseph and Boussaoud 1985) and had already been trained to produce guided eye movements. To avoid disturbing particularly fruitful recording sites, drug injections were made on one side only so that histological reconstruction of microelectrode recording sites on the other side would remain possible. These three cats were tested with guided and reflex eye movements.

Two additional cats could not be fully trained and were only tested with reflex eye movements and were injected both unilater-

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ally and bilaterally. For these two cats, the SNpr was localized with microelectrode recordings by using the different electro-physiological features of SNpr cells (steady rate of discharge ranging from 50 to 100 spikes/s, cells driven by visual, auditory, somesthetic stimuli) and by its borderline with the Peduncle.

All drugs used – Bicucullin and Picrotoxin (SIGMA) which are GABA-antagonists and Muscimol (SIGMA) which is a strong GABA-agonist – were dissolved in 0.9% NaCl and titrated to pH 7 if needed (except for Bicucullin which was titrated to pH 3.5). Concentration of Muscimol, Picrotoxin and Bicucullin were respectively 100, 200 and 300 ng per µl. Drugs were injected by means of a Hamilton microsyringe in a volume of 1 to 2 µl over one minute, after which the needle was kept in position for one more mn. Recording sessions started as soon as head turning was observed, i.e. most of the time immediately after the injection. Drug effects were compared to effects of saline injections performed in the same conditions. Animals were recorded every day. SNpr in each side was injected with each of the drugs and with saline at least three times.

For the three animals tested with guided eye movements, the methods of training and data analysis have been fully described in the companion paper. In this experiment, however, a simplified version of the paradigm was used: the animals were required to direct their gaze to 4 targets only, located respectively 20° right, left, above and under the center of gaze. These 4 targets consisted of 1 second visual signal, superimposed on an auditory signal (clicks at 20 Hz). Targets were presented every 30 s in a random sequence. On the average, each target was presented 8 times during a recording session and 25 times over the successive sessions.

Reflex eye movements were studied by placing the animals in a hammock with their head secured at the center of rotation of a servo-controlled turntable. The horizontal Vestibulo-Ocular Reflex (VOR) was tested in the dark, by using sinusoidal oscillations at different frequencies (0.03, 0.04, 0.05, 0.06, 0.12, 0.24 Hz) with a peak velocity of 10° per second. Visual suppression of VOR was tested by attaching a visual stimulus (randomly distributed spots of light) to the turntable in front of the animal. Sinusoidal oscillations similar to the above were applied to the turntable. Opto-Kinetic Nystagmus (OKN) was tested in the horizontal plane by rotating at uniform speed, spots of light randomly distributed on a hemispheric screen surrounding the cat's head. Rotations were performed in each direction (clockwise and counterclockwise) at constant velocities ranging from 5 to 140° per second.

Horizontal eye position recordings were displayed on a paper chart. The Slow Cumulative Eye Position (SCEP) was reconstructed manually. The gain of the VOR was defined as the ratio of the average peak-to-peak values of SCEP during clockwise and counterclockwise rotation over several cycles and the corresponding table displacement. The shifts between the reversal of eye position and the corresponding reversal of head position during responses to sinusoidal oscillations were also measured and analyzed. OKN was characterized by its gain defined as the ratio of the slope of the SCEP and of the velocity of the corresponding stimulation, by the frequency of the nystagmic beats and by the duration of the optokinetic after nystagmus (OKAN I).

At the end of the experiments, all animals were anaesthetized and perfused intracardially with 10% formalin. Serial sections were stained with cresyl violet and used to reconstruct the injection sites.

Results

All injections were centered in the SNpr.

1. Behavioral changes following injections of GABA-agonists and -antagonists

In control experiments performed on 3 cats, the injection of saline, Muscimol, Bicuculline and Picrotoxine 3 mm above the selected area of SNpr did not produce any detectable behavioral effects.

Unilateral or bilateral injections of 1 to 2 µl of saline in the SNpr induced no characteristic effects. Locomotion and standing posture were normal. In one cat only, a slight contraversive head turning and circling was observed after the first unilateral injection. Bicuculline and Picrotoxin unilaterally or bilaterally injected induced no rotation nor behavioral stimulation. In one cat only, one unilateral injection of Picrotoxin induced a slight ipsiversive head turning and circling. EMG activity of biceps, triceps and splenius was normal.

In contrast to these two drugs Muscimol unilaterally injected consistently induced changes in the standing posture and locomotor behavior of the animals when the dose injected was larger than 0.5 µl. Contraversive head turning and sometimes forced circling toward the contralateral side were observed. These effects started shortly after the injection, reached their maximum after about 1 h and lasted 2–3 h. Except for circling, locomotion was normal. The animals sometimes appeared to be restless.

After the injection, the animals remained obviously hungry and thirsty but they were unable to eat. This impairement was not due to the circling which sometimes kept them from getting the food with the mouth but seemingly, to an oro-facial akinesia.

With bilateral injections of Muscimol, the behavioral picture was different. In one animal, fixed uncontrolled jerky movements of the head toward both sides were observed. The head was vertically raised and slightly turned toward one side. In the other cat, posture ressembled that induced by unilateral injection except that the direction of head turning changed over successive trials. Neither one payed attention to what happened around them. They were akinetic. When they were frightened their motor behavior was one of escape but in fact they only exhibited a circular motion. We did not observe compulsory sniffing or biting.

Unilateral Muscimol injections also induced an hypertonic activity in the contralateral splenius but not in the biceps and triceps (Fig. 1).

2. Effects of GABA-agonists and -antagonists on spontaneous and guided eye movements

Spontaneous saccades were studied in animals with their head restrained, placed in a dimly illuminated room and facing a blank tangent screen.

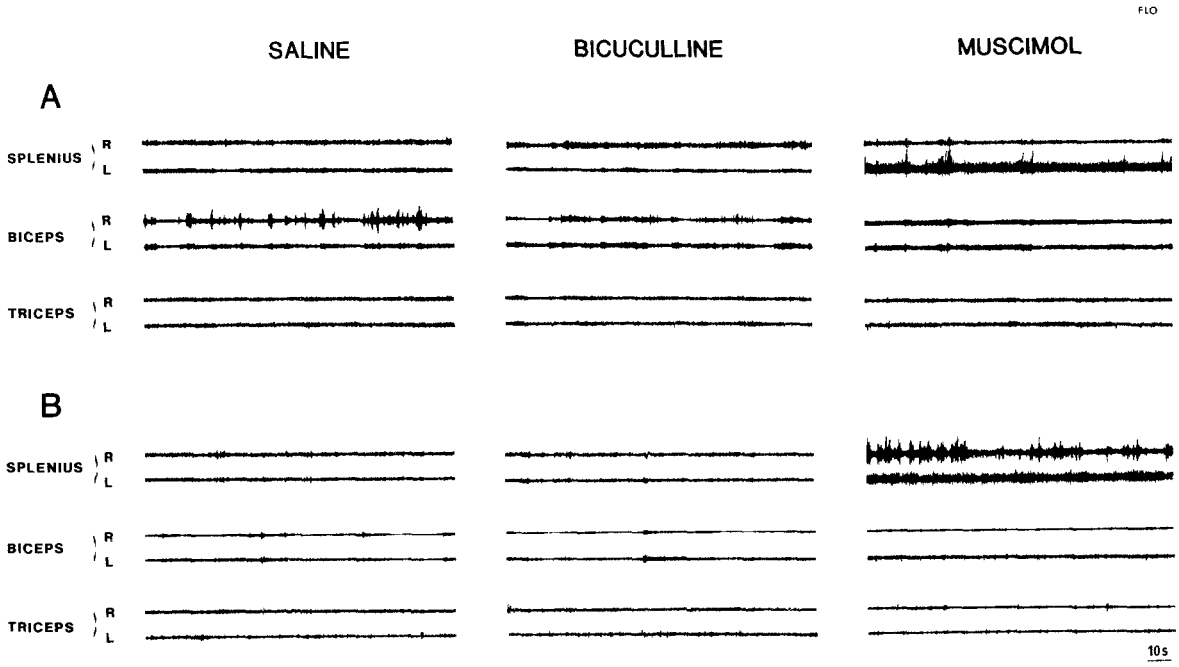

Fig. 1A and B. Comparison of muscular tone after saline (left), Bicuculline (center) and Muscimol (right) injections (2 µl) in the SNpr. Electromyographic recordings of the right and left splenius, biceps and triceps after injection in the right SNpr in **A** and after injection in the right and in the left SNpr in **B**. Time scale is in the lower right corner. During the recording sessions, head was kept straight, in the direction of the body axis

Unilateral injection of Bicuculline or Picrotoxin had no effect on spontaneous saccades. The average number of saccades and their amplitude were normal. There was no systematic deviation of the gaze. In one cat the relation between amplitude and speed of the horizontal component of saccades was studied. This relation was comparable to that obtained in normal animals. Frequency, latencies and precision of orienting saccades toward any one of the four targets were not modified after injections of Bicuculline, Picrotoxin or saline.

In contrast, unilateral injection of Muscimol resulted in a dose dependent decrease of spontaneous eye movements. The gaze was consistently rotated toward the contralateral side. Oculomotor exploration was thus often limited to this part of space. The animals could execute saccades toward the ipsilateral side but fixation could not be maintained (Fig. 2). When tested for guided eye movements, all three animals showed a neglect of the ipsilateral and inferior targets. This neglect was characterized by a reduction of the number of orienting saccades compared to those obtained after saline injection and by a reduction of their precision with regard to the position of the targets (Fig. 3). Undershooting was a common feature but the animals did not try (except one cat in one recording session) to correct their aim by additional saccades

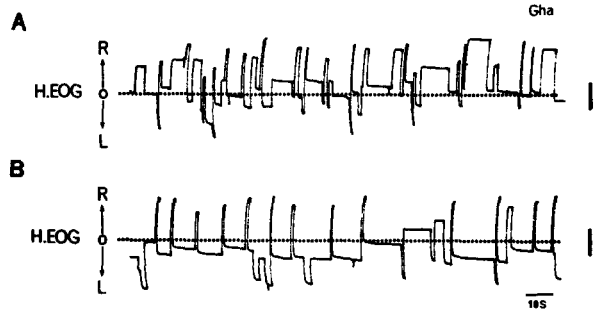

Fig. 2A and B. Effects of an unilateral injection of Muscimol (200 ng) in the SNpr on average gaze position and spontaneous eye movements. Horizontal Electro-oculogram is recorded after saline injection in **A** and after muscimol injection in the right SNpr in **B**. Calibration (20°) is given by the thick vertical bars on the right. R: right side; L: left side; O: center of the screen

that would bring the gaze on the targets. Neglect for contralateral targets was also observed (Fig. 3): After injections of 200 or even 100 ng, cat ERO did not orient toward contralateral targets. In cat GHA, contralateral orienting saccades occurred but were less precise than those recorded in saline conditions. Taken together all saccades corresponding to an orienting movement toward the targets showed increased latencies in Muscimol conditions but there was no statistical difference in latencies between contralateral and ipsilateral saccades (when the latter

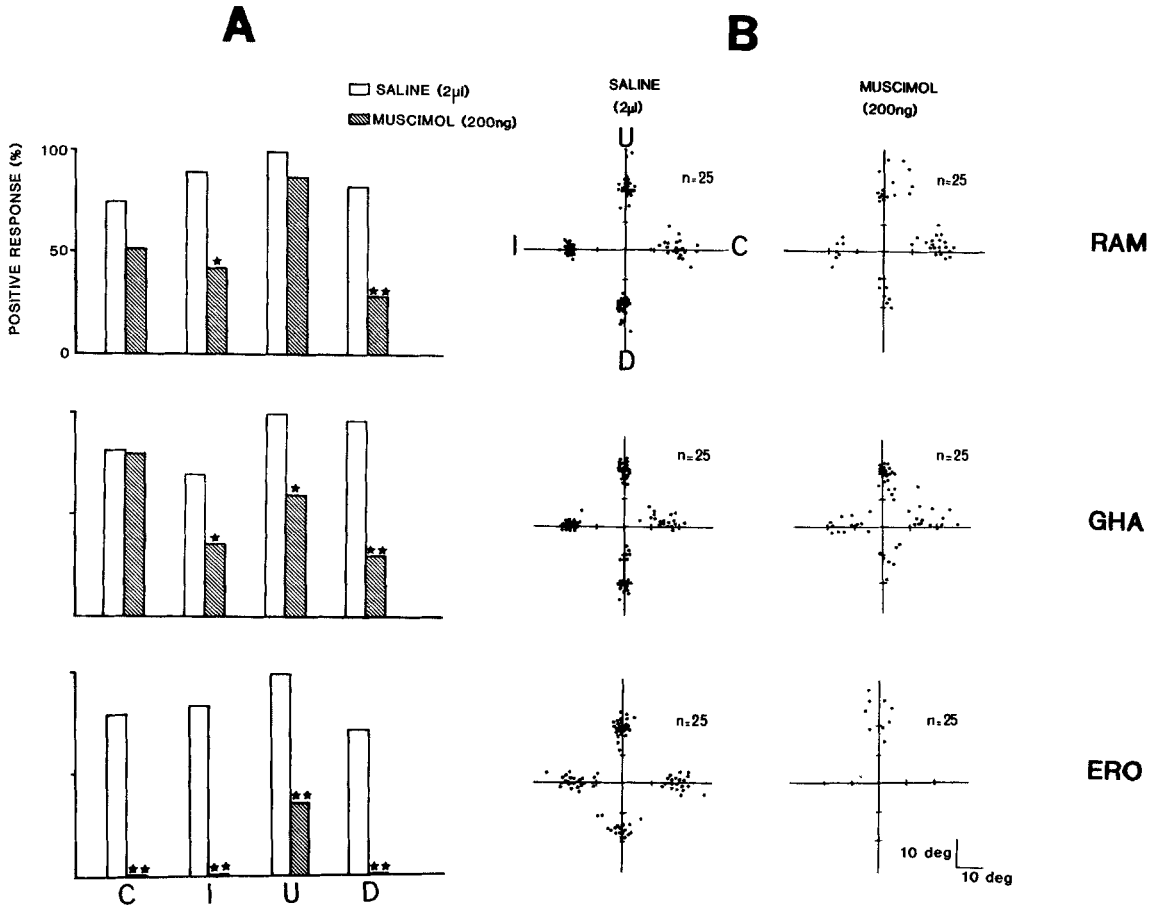

Fig. 3A and B. Effects of an unilateral Muscimol injection (200 ng) in the left SNpr on number and precision of guided saccades in three cats (RAM, GHA, ERO). In **A**: the number (in percentage) of orienting saccades after muscimol injections is compared to the number of orienting saccades after saline injections. Differences are significant at 0.05 (*) or 0.01 (**). At bottom, letters C, I, U, D correspond to saccades contralateral (C) or ipsilateral (I) to the side of injection, upwards (U) and downwards saccades (D). In **B**: the diagrams show the dispersion of the final gaze positions after the orienting saccades. Perpendicular axis represents the two meridiens of the visual field and their intersection the initial gaze position of the cat. Targets are presented at 20° eccentricity. C, I, D, U have the same significance than in **A**. A dot represents the final position of the gaze after a saccade. For each condition (saline or muscimol) and for each direction (C, I, D, U) targets were presented 25 times

occurred). The relation between amplitude and speed of the horizontal component of the saccades was studied in one cat. This relation was similar to that obtained in saline condition.

Bilateral injection of Muscimol resulted in visual neglect for all the surrounding space.

3. Effects of injections of GABA-agonists and -antagonists on vestibulo-ocular reflex and opto-kinetic nystagmus

After unilateral or bilateral injections of saline, Bicuculline or Picrotoxin there was no spontaneous nystagmus in the dark. After unilateral injection of Muscimol, a spontaneous nystagmus appeared in 3 cases out of 7. The slow phase was directed toward the side ipsilateral to the injection. Its speed was low, less than 2° per second.

Vestibulo-ocular responses

Compared to the VOR under saline conditions, the VOR recorded after Picrotoxin or Bicuculline injections was not significantly altered. The gain of the response, the phase relationship between the eyes and the head, the amplitude and the frequency of nystagmus beat were approximately the same.

In contrast, unilateral injection of Muscimol induced a strong VOR imbalance in 6 cases out of 7. VOR gain was larger for rotation toward the contra-

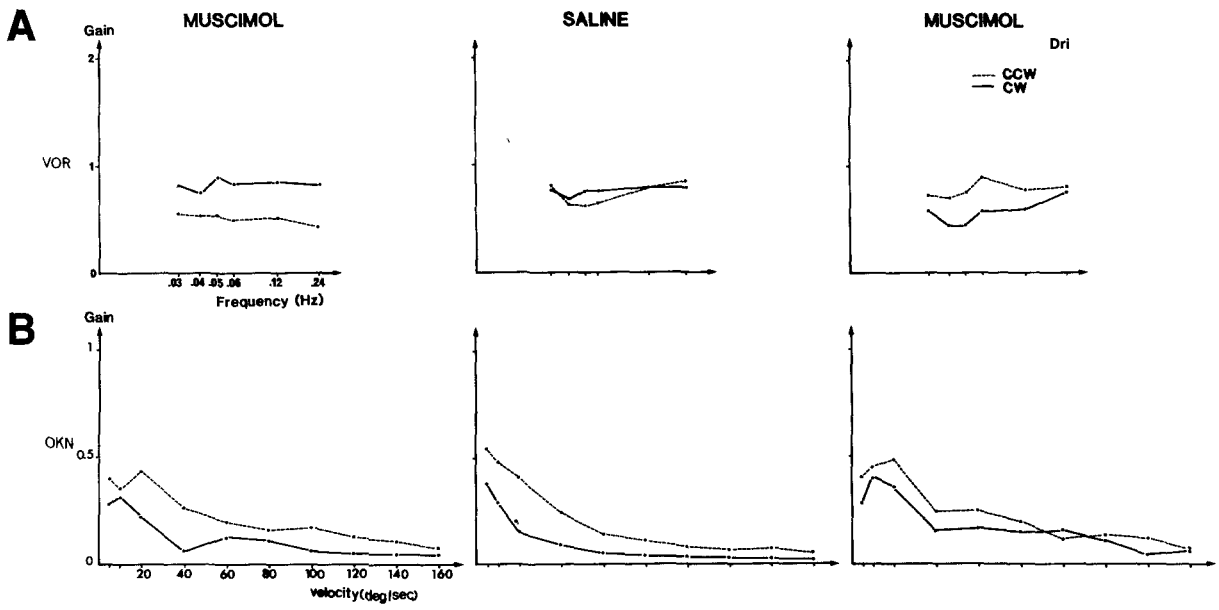

Fig. 4A and B. Effects of an unilateral injection of Muscimol (200 ng) on the vestibulo-ocular reflex (VOR) and on the opto-kinetic nystagmus (OKN). Evolution of VOR gain and of OKN gain as a function of the parameters of the stimulation. – On the right, after injection in the right SNpr; – on the left, after injection in the left SNpr; – in the middle, after bilateral saline injection. Stimulation was clockwise (solide line) or counterclockwise (dashed line)

lateral side. Compared to VOR under saline conditions, this imbalance was mainly due to a decrease of the VOR for the ipsilateral rotation. With contralateral rotation, VOR did not change significantly. The amount of asymmetry was independent of the frequency of the sinusoidal oscillations (Fig. 4). The presence of a spontaneous nystagmus might account for the observed asymmetry. Data were replotted by removing from SCEP the contribution of spontaneous nystagmus, according to the method proposed by Courjon et al. (1977). In Fig. 4 for instance, the gain asymmetry during the two directions of movements is 1.72 and 1.62 at f = 0.05 Hz after Muscimol injection in the left and the right SNpr. After correction these ratios are 1.52 and 1.21. Thus a gain asymmetry is still present. The same observation was made for all the data after correction.

Another effect of Muscimol injection was the change in phase of eye position vs head position. In all cases, the phase-lead of eye movement was reduced for contralateral rotation, compared to values obtained with saline. In 3 cases out of 7, a phase-lag was even observed: the animals inverted their nystagmus after the end of the contralateral rotation (Figs. 5 and 6). Imbalance of the VOR recorded after Muscimol injection also appeared in the pattern of the nystagmic response. During contralateral rotation, frequency of the beat was increased and amplitude was decreased compared to ipsi- and contralateral rotation in saline conditions (Fig. 6). With ipsilateral rotation, frequency of beats decreased slightly.

The visual suppression of the VOR was similar during ipsi- and contralateral rotation. Thus the percentage of asymmetry induced by Muscimol was not reduced by vision. Visual fixation did not change significantly the frequency of the nystagmic beats observed in the dark. However, in all three cases where a phase-lag of the eye movement vs head movement was present, visual fixation restored a normal phase-lead. After bilateral injections, the VOR was normal if there was not strong postural asymmetry. When the latter occurred, the VOR was close to what would have been expected from an unilateral injection inducing the same postural asymmetry.

Optokinetic nystagmus

Changes in VOR resulting from injection of Muscimol were not accompanied by a modification of the OKN reflex (Fig. 4). OKN gain and OKANI duration were not affected. The major difference was the symmetry of OKN which, in the Muscimol condition, consisted of beats of higher frequency and lower amplitude during ipsilateral stimulation. A similar effect on the vestibular nystagmus was obtained with

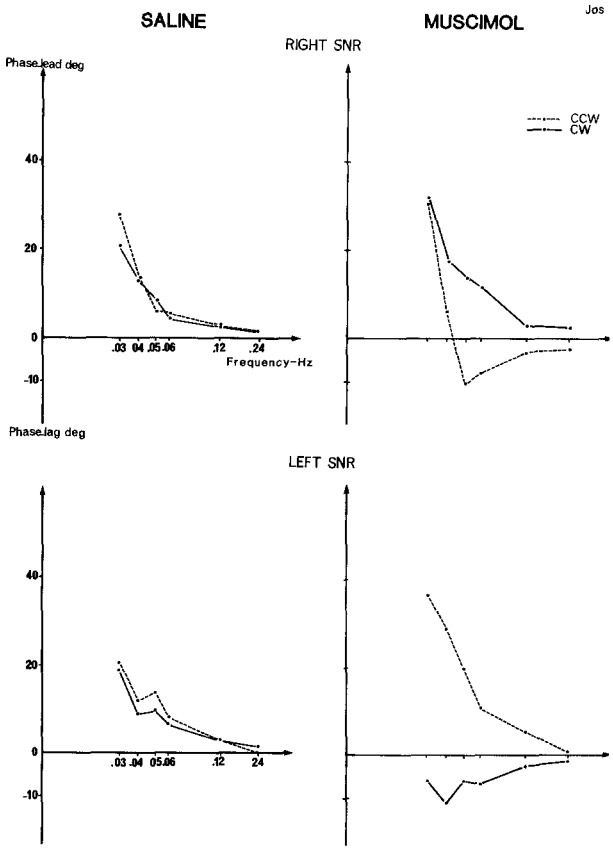

Fig. 5. Effects of a unilateral injection of Muscimol (200 ng) in the SNpr on phase advance of the eyes vs the head position during the vestibulo-ocular reflex. Evolution of phase advance as a function of the frequency of the stimulation, – on the left, after saline injection; on the right, after Muscimol injection; – at top, in the right SNpr; at bottom, in the left SNpr

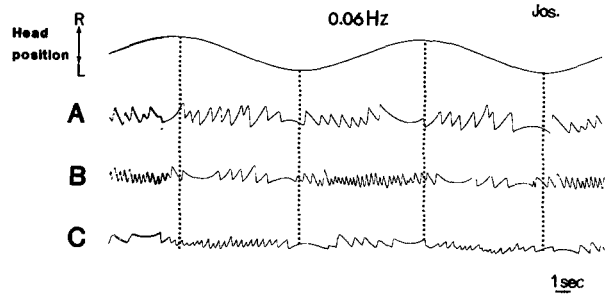

Fig. 6A–C. Effects of a unilateral injection of Muscimol (200 ng) on the phase advance of the eyes vs the head position and on the frequency of the nystagmic beat. From top to bottom: – position of the head; – vestibulo-ocular response after a saline **A** and a muscimol injection in the left **B** or in the right **C** SNpr. In **A** and **C** there was a slow (2°/s) spontaneous nystagmus to the right. In **B**, no spontaneous nystagmus was present

contralateral rotation. The modification of the symmetry was also found in the OKAN responses: Following the OKN with the low beat frequency, the OKAN II was again made up of faster beats of lower amplitude and, conversely, the OKN of higher frequency was followed by a slower nystagmus.

Discussion

The two GABA-antagonists, Picrotoxin and Bicuculline, that were used in these experiments had no effect either on the behavior or oculomotor performances. Although we used different concentrations (up to 800 ng/μl for both drugs) and injected increasing volumes (up to 10 μl), only in one cat did we observe during one recording session a slight overshoot of the orienting saccades toward the ipsilateral side. This result is very different from those in rats reported by Scheel-Krüger et al. (1977). These authors observed head turning and rotational behavior toward the ipsilateral side after injection of either drug. The difference between our results and those of Scheel-Krüger et al. might be due to species differences, although behavioral changes induced in rats are not clear-cut (Tarsi et al. 1975; Scheel-Krüger et al. 1977). In contrast, the results obtained with Muscimol are more in agreement with those obtained by these authors, although the compulsory biting, licking and sniffing observed in rats were absent in our cats.

Although the doses of Muscimol that we injected in the SNpr represented a threshold below which no behavioral effect was observed, it cannot be overlooked that the drug might have diffused into structures surrounding the SNpr and produced the observed deficits. Our control experiments show that injections centered 3 mm above the selected site of the SNpr have no behavioral effects. Similarly, Muscimol injections in the Subthalamic Nucleus – which is located close to the SNpr – does not induce head turning in rats (Scheel-Krüger et al. 1981). Thus, the behavioral changes observed after Muscimol injection can be attributed to an effect on the neurons of the SNpr.

The two major efferent pathways of the SNpr, the nigrotectal and nigrothalamic pathways, appear to play different roles in the observed behavioral changes. Head turning and circling might be due to imbalance between the two superior colliculi induced by the unilateral injection. It was shown that after the injections of GABA-agonists in the SNpr, the integrity of the superior colliculus was necessary for head-turning to appear (Kilpatrick et al. 1982). The release of inhibition from the SNpr on one side produces a fixed excitatory drive on the contralateral cervical motoneurons through the tectospinal pathways (Anderson et al. 1971; Chevalier et al. 1984). It also

results in the deviation of the gaze toward the contralateral side and a difficulty for the cats to orient toward the ipsilateral side.

Oro-facial akinesia observed after unilateral and bilateral Muscimol injections could be due to a dysfunction of the thalamic targets of the SNpr. The major target is the ventromedial nucleus (VM) of the thalamus (Hendry et al. 1979) which in turn projects to the face area of the motor cortex. Dysfunction of this nucleus might explain the observed difficulty for the cats to open the mouth. Schneider and Lidsky (1981) have described a heavy somatosensory projection of the face and the mouth on the striatum. It is possible that the basal ganglia use this input to modulate facial or mandibular movements.

It seems more difficult to isolate a possible dysfunction of the nigrostriatal dopaminergic pathway. An inhibitory drive of the SNpr on the dopaminergic neurons of the SNpc does not account for head turning observed after unilateral injection. Akinesia observed after bilateral injection may be a side effect of the severe orienting problems encountered by the animals. Moreover, the dysfunction of the nigrostriatal pathway would have probably induced a generalized hypertonic muscular activity, which would not be restricted to the neck and face.

Another consequence of Muscimol injections is an asymmetry of the VOR resulting from a decrease of the gain with the rotation of the head toward the intact side. The possibility of a control of the vestibular functions by the basal ganglia has already been suggested (Potegal 1982). There is anatomical evidence supporting this theory as there are numerous vestibular projections on the striatum, via the cortex and the intralaminar thalamic nuclei (Magnin and Kennedy 1979; Kotchabhakdi et al. 1980). There is however no direct link between the SNpr and the vestibular nuclei. Only an indirect one, involving thalamic or subthalamic targets of SNpr efferents, could be responsible for the modulation of VOR gain by this structure. The superior colliculus might be one such target (Flandrin and Jeannerod 1981). It possibly controls the VOR by a crossed pathway linking its intermediate and deep layers to the nucleus prepositus hypoglossi (Magnin et al. 1983), the latter projecting in turn on the vestibular nuclei (Pompeiano et al. 1978). Nevertheless, our data do not firmly establish the existence of a neuronal loop controlling VOR via the basal ganglia. Although the VOR was recorded with the head restrained in the direction of the body axis, unilateral hypertony of the neck muscles might have induced an imbalance in the vestibular nuclei. Accordingly, the VOR asymmetry might be a consequence of this imbalance of peripheral origin.

In conclusion, there is a striking similarity between the disorders induced in cats by unilateral or bilateral injection of Muscimol – reduction of spontaneous and guided eye movements, oro-facial akinesia and neck-muscle hypertony – and the orienting disorders, the oro-facial dyskinesia and the hypertony observed in patients with Parkinson's disease (Damasio et al. 1979; Villardita et al. 1983). Our hypothesis is that the SNpr in Parkinsonism is functionally identical to that of cats after injection of Muscimol. This hypothesis suggests that some of the neural events associated with Parkinsonism include 1) dysfunction of the dopaminergic pathway linking the Substantia Nigra pars compacta (SNpc) and the striatum, 2) consequent disruption of the fixed tonic activity of the SNpr cells, 3) abolition of the inhibitory effect of these cells on the thalamus and the tectum (Deniau et al. 1978; Chevalier et al. 1980), 4) hyperactivity of target cells in the thalamus and the tectum.

This hypothesis implies that hyperactivity of the neurons of the motor nuclei of the thalamus (VA-VM-VL complex) is the direct source of most of the parkinsonian symptoms. It would account for the fact that electrolytic lesion of these nuclei has long been the only successful treatment of parkinsonian disorders.

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