CONVERGENCE OF SLEEP-WAKEFULNESS SUBSYSTEMS ONTO SINGLE NEURONS IN THE REGION OF CAT'S SOLITARY TRACT NUCLEUS

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INTRODUCTION

It has been claimed that the region of the solitary tract nucleus (NTS) in the medulla oblongata may be capable of triggering slow wave sleep (SS). Activation of the baroreceptive afferents (2, 18, 28), electrical stimulation of the NTS region at low frequency (21), and perfusion of the NTS with serotonin (17), are able to induce behavioral sleep or EEG synchronization. It has been suggested that activation of the bulbar inhibitory system leads to deactivation of the midbrain reticular formation (MFR) (1, 4). Many bulbar reticular neurons readily respond with excitation or inhibition to electrical stimulation of the MFR (22, 23, 30, 31). There is electrophysiological evidence for the existence of reciprocal connections between the MRF and the NTS (5).

There are anatomical observations that caudal portion of the NTS directly projects to the spinal cord, the cerebellum and various forebrain structures, including the hypothalamus (8, 29, 36). Histochemical investigations have revealed that the NTS region is intimately linked with the monoaminergic system (3, 7, 9). These morphological findings indicate that the neurons in the NTS region occupy a strategically important position to exert influence over wide-spread areas in the CNS.

The above-described, different lines of evidence point to the importance of the bulbar structures, including the NTS, in the genera-

tion of SS. It may follow that the neurons in this area which have greater discharge rate during SS than during wekefulness (W) will have something to do with SS machanism. However, it is hard to conceive a CNS neuron, particularly inter- and reticular neuron, which is devoted to a single function alone. In fact, pontomedullary reticular neurons which showed altered firing rate in association with the shift of the level of consciousness, showed also a change in firing rate synchronously with the occurrence of various motor phenomena, such as postural adjustments during W and rapid eye movements (RMEs) during paradoxical sleep (PS) (35, 37). Therefore, it will be important to specify the characteristics of individual neurons in terms of the nature of the converging inputs. In this context, in the present experiment, neurons in the NTS region were examined for their spontaneous discharge rate during sleep and waking, and also for the change which may occur: *i*) during motor activity in W, *ii*) at the transitional phase from SS to PS, *iii*) during REM burst in PS, *iv*) following electrical stimulation of the MRF. In other words, this is an attempt to describe the modes of convergence onto single neurons of various subsystems which come into play at appropriate moments to participate in the elaboration of different phases of sleep and wakefulness.

A part of this study has already been published elsewhere (11).

Methods

Experiments were carried out on 11 adult cats weighing 2.8-3.8 kg. Under pentobarbital anesthesia (40 mg/kg, *i. p.*), electrodes for monitoring the EEG, ocular movements, and nuchal muscle tone were implanted chronically. They were connected to a 9-pin socket on the skull. A bipolar electrode made of stainless steel wire of 0.1 mm diameter and with a tip separation of 1.0 mm was implanted stereotaxically to stimulate the MRF (A 3.0, R 3.5 V —0.5). Occipital trepanation was performed to permit the unitary recording from the NTS region at the co-ordinates of P 13-15, LR 1.5-3.0. A metal cylinder to mount the micromanipurator was fixed over the trepanned skull with dental acrylic. After the animal recovered from surgical wound, it was trained to sleep in a cage with a painless head-restrainer.

Units were picked up with glass-coated tungsten microelectrodes described by Merrill and Ainsworth (24). Glasscoated Elgiloy wires and glass micropipettes filled with 0.9% NaCl solution were also employed. The impedance of these electrodes was between 2 and 5 MΩ when measured at 1 KHz. Rectangular pulses of 0.1 msec duration were delivered every 2.5 sec to the MRF. The stimulation intensity was set at about 60% of the threshold of any visible motor response of facial musculature. Injection needles were inserted into the extremities to record the electrocardiogram on the polygraph. The respiratory cycles were also recorded with a thermistor placed in front of the nostril. After the experiment, the

animal was deeply anesthetized and anodal current of 10 μA was given for 90 sec to mark the stimulated and recorded sites. The brain was fixed with 10% formalin and serial sections of 20 μm thick were stained by Klüver-Barrera method. Special attention was paid to the histological identification of the recording sites. The shrinkage of the brain tissue caused by the fixation procedures was measured on the basis of the distance between the two reference points which had been marked stereotaxically. The positions of the tip of recording electrodes were estimated by correcting the measures on the microstep-driver with the above value.

Unit discharges were recorded with an 8-channel FM tape recorder at frequency response of 2.5 or 5.0 KHz. They were fed to a pulse-counting tachograph to display sequentially on the polygraph the number of spikes for 1 sec. The postimulus time histogram (PSTH) was made for the response to electrical stimulation of the MRF. Excitatory and inhibitory responses were calculated by the following equation:

$$\text{magnitude} = \frac{|\,R - BG\,|}{T}$$

where T is the number of the accumulated responses, R is the number of the spikes during evoked response in a given phase, and BG is the number of the spikes assumed to be spontaneously occurring during the response period, which was calculated from the mean background discharge rate.

It is also possible to calculate the response magnitude in other ways; for example, the intensity of the response relative to the background discharge rate and the change in the duration of the response (11, 33) may be taken into account. However, the results calculated with these parameters included, were not significantly different from those with the above-described, simpler equation.

Results

A total of 72 units was recorded from the NTS region. About 60% of these units were found to be located in the NTS or in the reticular formation ventral to it (Fig. 1). The holding time of the units ranged from 3 to 32 min. Forty neurons could be held for at least one complete sleep-wakefulness cycle.

Sixty-seven neurons could be studied during both W and SS. The mean discharge rate in W was 12.9 imp./sec (0.89-56.38) and that in SS was also 12.9 imp./sec (1.20-51.66). The ratio of the mean discharge rate in SS to that in W ranged from 0.27-3.33. Since variation in spontaneous discharge rate in the same two phases occurring at different time was usually less than 30% in the reticular neurons of the lower brain stem (31), the difference greater than 30% was regarded as significant. On this basis, the neurons were classified into three groups: group I, $SS/W > 1.3$; group II, $SS/W < 0.7$; group III, $1.3 \geqq SS/W \geqq 0.7$. About one third of the neurons (22 out of 67) belonged to group I (Fig. 2*a*), and a half of this group

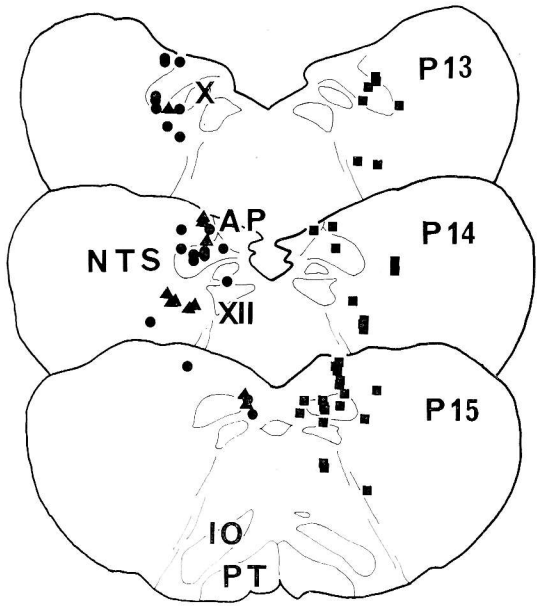

Fig. 1. – *Localization, at the co-ordinates of P 13-15, of the neurons classified into three groups according to the ratio of their mean discharge rate in SS to that in W.*

At the left, group I (●) and group II (▲). Group III (■) at the right. AP: area postrema; IO; inferior olive; NTS: solitary tract nucleus; PT: pyramidal tract; X: dorsal motor nucleus of vagus; XII: motor nucleus of XII nerve.

was within the NTS (Table I). The mean SS/W ratio was 1.8 (1.33-3.33). The increase in discharge rate during SS became obvious neither prior to the appearence of slow waves in the EEG nor only

TABLE I. – *Number of neurons in three groups, recorded from the NTS and the surrounding region (non-NTS).*

Group	NTS	non-NTS	Total
I	10	12	22
II	2	9	11
III	8	26	34
Total	20	47	67

at the initial part of this stage. The increase usually proceeded in good parallelism with the development of EEG slow waves. Group II neurons (Fig. 2*b*) were 11 in number and their mean SS/W ratio in discharge rate was 0.47 (0.22-0.67). Remaining 34 units fell in group III, and 6 of them showed a discharge related to either the cardiac rhythm (n = 5) (Fig. 3) or respiratory cycle (n = 1). These 6 neurons and additional 10 short-lived neurons of similar properties were all encountered at the area close to, but out of the NTS.

Phasic modulation of firing during motor activity in W could be examined in 46 neurons (EMG in Table II). Fourteen neurons

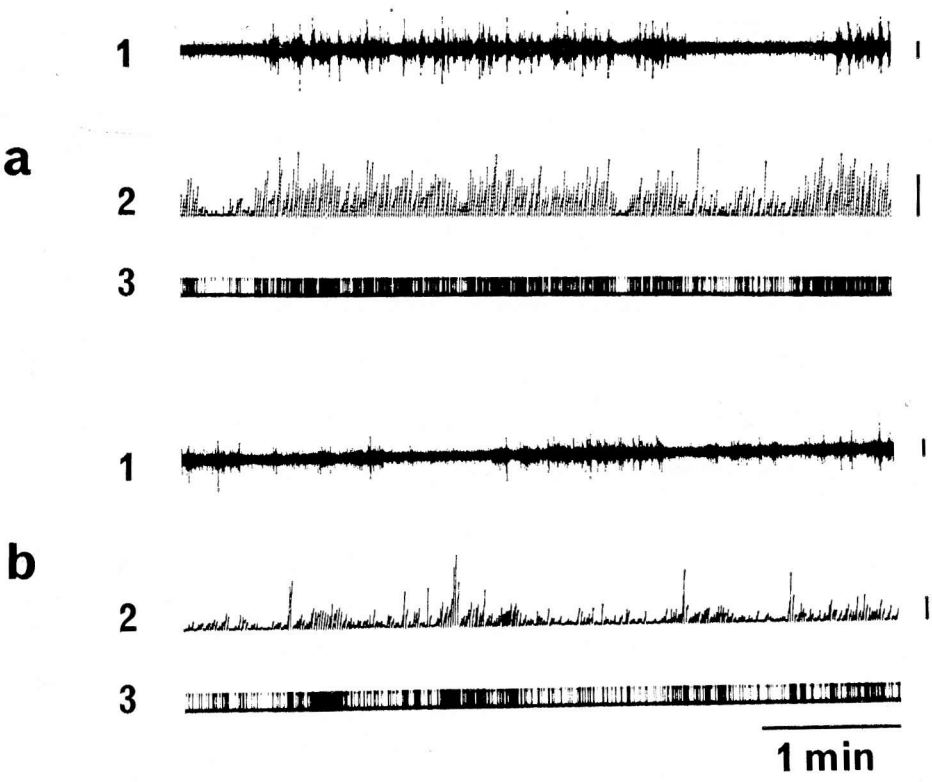

Fig. 2. – *Sequential distribution of unit discharge during SS and W of group I (a) and group II (b) neurons.*

1: EEG; 2: tachogram of the number of spikes for 1 sec; 3: pulse output from a window discriminator. Calibrations: 200 μV (1) and 10 spikes/sec (2). During the development of EEG slow waves, the discharge rate of group 1 neuron increases, whereas that of group II decreases.

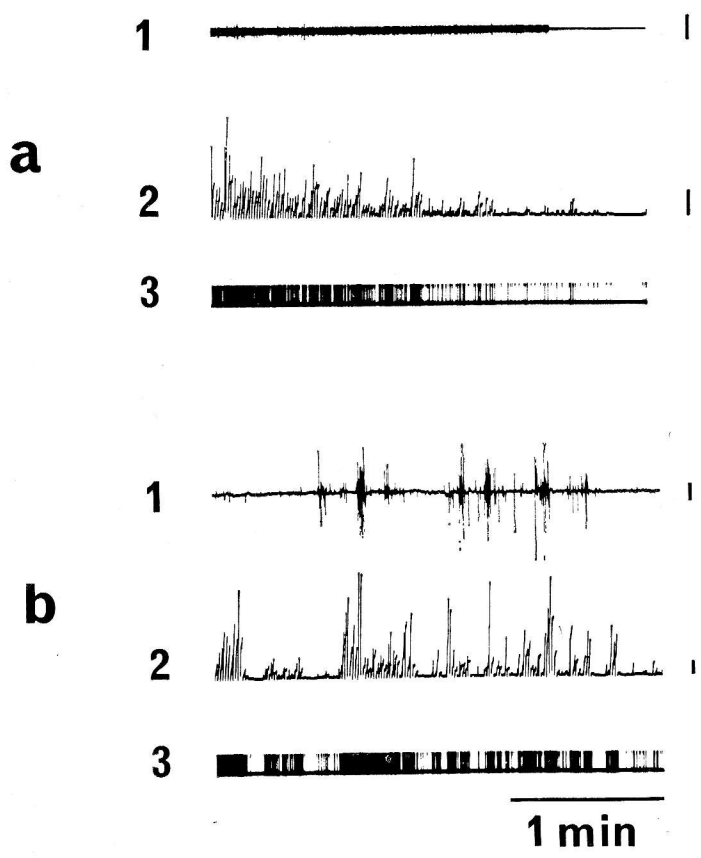

Fig. 5. – *Changes in unit activity during PS.*

a (group II neuron): alteration in firing during transitional phase from SS to PS. 1: neck EMG. Neuronal discharge progressively decreased prior to disappearance of tonic EMG activity. *b* (group II neuron): bursting discharge synchronous with REMs during PS. 1: EOG; 2 and 3: the same as in Fig. 2. Calibrations: 200 μV (1) and 10 spikes/sec (2).

latency of group II neurons was often relatively short (Table III). The duration of inhibition was generally shorter during SS and more so during PS, while that of facilitation was less variable across different phases and neuron groups. During SS, the magnitude of the excitatory responses tended to be slightly greater than that during W (Fig. 6, EXCIT). On the other hand, inhibitory responses had, in a majority of cases, definitely, smaller magnitude during SS as compared with W (Fig. 6, INHIB). During PS, The magnitude of both

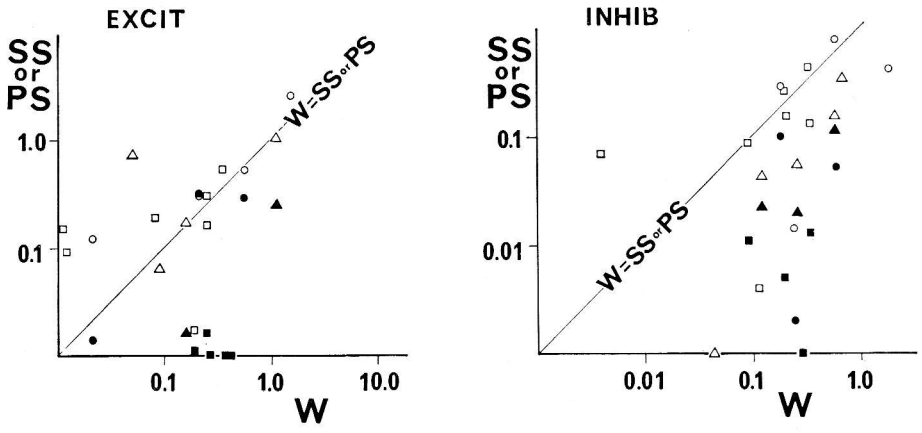

Fig. 6. – *Magnitude of excitatory (EXCIT) and inhibitory (INHIB) responses to electrical stimulation of the MRF.*

Abscissa: magnitude in W, ordinate; magnitude in SS (empty symbols) or in PS (filled symbols). Group I (●), group II (▲), and group III (■) neurons. Most inhibitory responses are below the 45° line, indicating greater magnitude during W.

TABLE III. – *Latency and duration of excitatory and inhibitory responses.*

Group	Latency during W (msec)		Duration relative to W			
	excitatory	inhibitory	excitatory		inhibitory	
			S/W	P/W	S/W	P/W
I	7.3 (2.0-12.0)	21.0 (2.0-50.0)	0.94 (0.83-1.0)	0.72 (0.17-1.0)	0.35 (0.003-0.56)	0.095 (0.05-0.14)
II	4.5 (2.0-12.0)	13.6 (2.0-44.0)	1.05 (1.0-1.2)	1.0 (0.0-1.0)	0.81 (0.5-1.5)	0.19 (0.0-0.19)
III	22.5 (2.0-48.0)	28.0 (4.0-58.0)	1.5 (1.0-2.0)	1.21 (0.0-1.21)	0.67 (0.333-1.0)	0.23 (0.0-0.23)

excitatory and inhibitory responses was markedly diminished in most cases.

In only 9 neurons it was possible to examine the convergence of all the four kinds of input described above; that is, presence or absence of phasic change in discharge rate during *i*) EMG, *ii*) S-P, *iii*) REM, and *iv*) MRF as denoted in Table II.

TABLE IV. – *Degree of convergence onto single neurons of four kinds of input; namely, EMG, S-P, REM and MRF (for abbreviation refer to Table II).*

Degree of convergence	No. of neurons	No. of inputs tested	Group			Subtotal
			I	II	III	
100% positive in all cases tested	23	4	1	1	0	2
		3	3	2	1	6
		2	1	1	2	4
		1	4	1	6	11
intermediate positive for certain test (s) and negative for other (s)	30	4	1	0	6	7
		3	3	1	8	12
		2	3	5	3	11
0% negative in all cases tested	11	4	0	0	0	0
		3	0	0	2	2
		2	0	0	2	2
		1	4	0	3	7
Total	64		20	11	33	64

However, it was noticeable that more than two kinds of input were converging onto all of them, and in 2 neurons all the four kinds of input were converging (Table IV). In Table IV, the examination on the multi-input convergence is extended to include other neurons where not all four kinds of measurement could be done. In groups I and II, especially in the latter group, there was more tendency toward multiple convergence than the absence of it. There seemed

to be no obvious tendency of coupled convergence of particular kinds of input onto a particular group of neurons, except that neurons which responded to electrical stimulation of the MRF often showed an alteration in discharge rate concomitantly with the occurrence of REMs, while non-responding neurons tended to show no alteration in discharge rate during REM burst.

The neurons which showed a discharge time-locked to the cardiac or respiratory cycles could not be tested for all the four kinds of converging inputs, but only for one to 3 kinds of them. However, the test was always negative, suggesting a very poor convergence onto these kinds of neurons.

Discussion

The observation that a considerable number of neurons in the region of NTS was more active during SS than W (group I neurons), supports the hypothesis that this region plays an important role in the generation of SS. However, the behavior of these group I neurons did not provide any suggestion about the triggering mechanism of SS, because the increase in discharge rate during SS in these neurons lagged always behind the development of the EEG slow waves.

During motor activation in W, more than half of the neurons examined showed an augmentation or a suppression of firing. Most group II neurons, which had higher discharge rate during W than during SS, responded with excitation. These group II neurons, therefore, seem to be similar to the cells studied by Siegel *et al.* (34, 35).

It has been repeatedly documented that many neurons in the lower brain stem show a prominent increase in discharge rate during transition from SS to PS (10, 13, 19, 31, 37). In contrast, a great majority of neurons in the NTS region responded with a marked reduction in activity. This would be relevant to the disappearance of tonic vagal discharge during PS (20).

During REM bursts, there was always an increase in discharge rate, which was found in similar proportion within the three groups of neurons. Phasic excitation during REM sleep seemed to be a characteristic event common to quite many neurons in the entire neuraxis (27).

The responsiveness to electrical stimulation of the MRF was highest in group I neurons and lowest in group III. Taking into account the possibility that group I neurons are involved in SS mechanism, they might play an important role in the reciprocal interaction with the MRF. There was a tendency for the inhibitory responses to be attenuated during SS when compared with W. This attenuation cannot be attributed solely to depolarization of the membrane of the bulbar neurons, because the attenuation of inhibitory response was also found in neurons with lowered discharge rate; lowering in discharge rate has been shown to be usually associated with hyperpolarization (12, 15, 25). Hence, the change in the stimulated site and the conduction pathway from it has to be considered. During PS, both excitatory and inhibitory responses were strongly depressed. As the impairment of signal trasmission during PS has been reported for many other structures (30, 31, 33), it seems that during PS some powerful and widely distributed system is operating to interfere with information transfer through the neuronal network in the brain stem. It has been reported that during PS the potassium ion activity is enhanced in the reticular formation (32). An ionic alteration in the microenviroment of neurons would lead to a change in synaptic transmission and might be responsible in part for the reduction in signal transmission observed in the present experiment.

Absence of convergent input was much less frequently observed than the presence of it. There was found no group I neuron which was negative for more than two kinds of examination in the convergence. It seems, therefore, that neurons which are specifically activated only during SS without any detectable convergent input would be quite few in number. The tendency to multiple convergence seemed to be more apparent in groups I and II than in group III which has similar discharge rate during W and SS. It might be postulated that the group III neurons are related more to the functions which require steady firing, whereas the groups I and II tend to perform multiple functions by being involved in different kinds of subsystem which would be called into action at appropriate moments during sleep-wakefulness cycle.

Summary

Neurons in the region of cat's solitary tract nucleus were classified into three groups on the basis of their spontaneous discharge rate during slow wave sleep (SS) as compared with wakefulness (W): group I: SS > W; group II: SS < W; and group III: SS ≒ W. These three groups were further examined with regard to the modulation of discharge rate *i*) during motor activity in W, *ii*) at the transitional phase from SS to paradoxical sleep (PS), *iii*) during rapid eye movements (REMs) in PS, and *iv*) following electrical stimulation of the midbrain reticular formation (MRF). During motor activity in W, increase in unit discharge was frequently observed in group II, while groups I and III were often associated with suppression. At the transitional phase from SS to PS many neurons showed a reduction in discharge rate. During REMs in PS, about a half of the neurons of each group responded with burst discharge. The responsiveness to electrical stimulation of the MFR was highest for the group I neurons and the lowest for the group III. The inhibitory responses tended to be smaller in magnitude during SS than during W. During PS, both excitatory and inhibitory responses were, in general, markedly diminished. The analysis of the results has suggested that groups I and II neurons may be involved in more multiple functions than group III neurons which have a tendency to maintain steady discharge rate.

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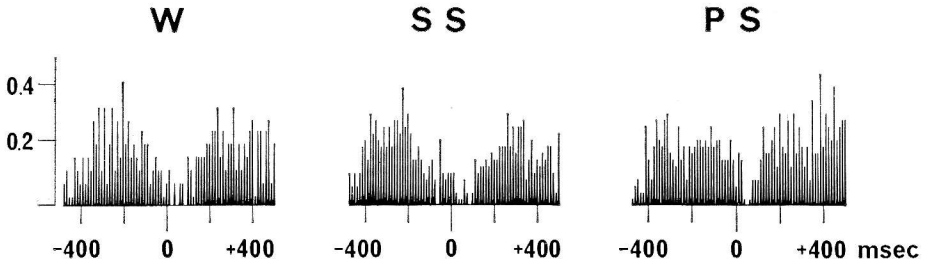

Fig. 3. – *Cross-correlation of neuronal discharge with the QRS complex in the electrocardiogram occurring at time 0 in the abscissa.*

Ordinate: spikes/QRS complex.

were facilitated and 12 were suppressed during phasic burst of the neck EMG (Fig. 4*a*, *b*). The remaining 20 neurons did not show an appreciable change. Suppression of firing was more often encountered in group I neurons, while in group II all the change, if any, was facilitatory.

TABLE II. – *Responsiveness to different kinds of convergent input.*

EMG: motor activity during W. S-P: transitional phase from SS to PS. REM: burst of REM. MRF: presence(yes) or absence(no) of excitatory(+), inhibitory(—), or both excitatory and inhibitory(±) responses to electrical stimulation of MRF. ↑ and ↓; increase and decrease in discharge rate. →; no change.

Group	No. of neurons	EMG			S-P			REM			MRF	
		↑	↓	→	↑	↓	→	↑	↓	→	yes (+, —, ±)	no
I	20	2	6	8	2	7	2	5	0	5	7 (2, 2, 3)	0
II	11	7	0	1	2	2	0	4	0	3	5 (0, 1, 4)	2
III	33	5	6	11	3	10	0	8	0	12	11 (3, 3, 5)	11
Total	64	14	12	20	7	19	2	17	0	20	23	13

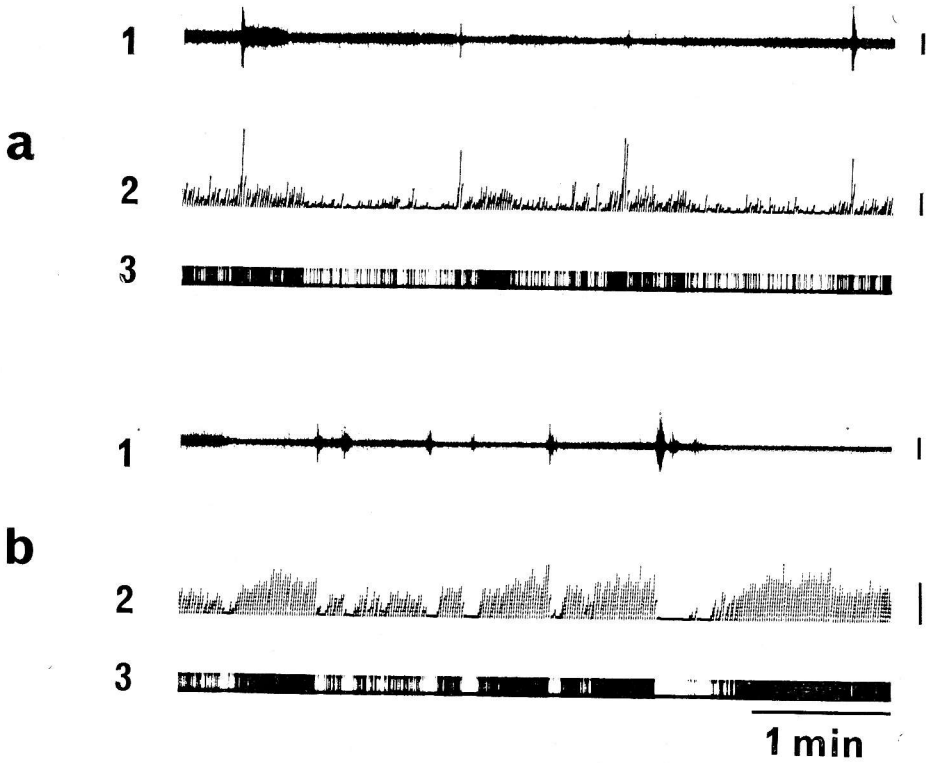

Fig. 4. – *Phasic modulation of firing during motor activity in W.*

a: facilitation (group II neuron); *b*: suppression (group I neuron). 1: neck EMG; 2 and 3: the same as in Fig. 2. Calibrations: 200 μV (1) and 10 spikes/sec (2).

During transitional phase fron SS to PS, the discharge rate was markedly altered in almost all neurons; the reduction being predominating in number over the augmentation (S-P in Table II and Fig. 5*a*).

A bursting discharge correlated with the occurrence of REMs during PS (Fig. 5*b*) was observed in about a half of neurons in every group (REM in Table II). There were no units which responded with a reduction in activity.

The effect of electrical stimulation of the MRF was studied on 36 neurons. Twenty-three neurons responded with excitation and/or inhibition (MRF in Table II). All the group I neurons responded to the stimulation, while a half of group III did not. The