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BLOCKAGE OF VIBRISSAE AFFERENTS: I. MOTOR EFFECTS

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INTRODUCTION

The vibrissae of rats have been regarded as a major source of sensory input because of their dense innervation and the relative size of their cortical representation. It has been calculated that each sinus hair receives over 300 afferent fibers, two-thirds of which are myelinated (30). Moreover, their cortical representation occupies more than 25% of somatosensory cortex (28). Rats typically explore environments by repetitive movements of their whiskers over the various surfaces and edges. Vibrissal functions in thigmotaxis (19, 20, 24) and tactile discrimination tasks (4, 5, 15, 27) have been extensively studied. The pioneering work of Vincent (27) concluded that the vibrissae are tactile organs with an important role in equilibrium, and locomotion. Posterior reports partially supported this conclusion. It was also postulated that vibrissae have functions in aggresive, sexual and social behavior (1, 16, 25, 26).

On the other hand, it has been proposed repeatedly over the years (2, 10, 12, 17) that sensory systems could have another role in addition to their known transductive functions. According to this view, sensory activity could help to support some kind of "central tone" in the central nervous system (CNS). As formulated by Ewald (10) and von Buddenbrock (2), this "tonic hypothesis" assumes two functions for afferent systems. The first one is the *specific sensory* function; i.e., providing reliable information about specific aspects of the environment for the formulation of discrete behavioral patterns. The second one would be the *tonic* or level-setting function, that is, providing a necessary activity background for the CNS to work. This idea implies that the background activity of afferent systems would set central excitability of large areas of the CNS, playing a role in shifting the entire organism from one behavioral state to another (6, 18). Von Buddenbrock (2) considered that the tonic role would be independent of the specific sensory functions. In spite of the many observations apparently supporting the tonic hypothesis (see ref. 18, for an historical review), as far as we know, these two postulated functions have never been experimentally dissected. On the other hand, we were unable to find publications with specific references to these ideas after the New York Academy of Sciences Symposium from 1977 (29).

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At least two conditions should be fulfilled in order to test the tonic hypothesis (3). It is necessary to show: *a)* a generalized (or non specific) loss of resposiveness to various forms of stimulations after silencing the afferent nerve; and *b)* the amelioration of these deficits by allowing the afferent nerve to continue sending impulses to the CNS, but somehow preventing it from conveying specific sensory information. The rat vibrissal system seems an ideal candidate for dissociating these two postulated roles of afferent nerves. Trimming whiskers would allow the afferent vibrissal nerve (infraorbital branch of trigeminal nerve, IO) to continue sending impulses but prevent it from carrying specific sensory information. In this way, if changes in behavior are present following IO blockage but are not observed when only the whiskers are cut, it would seem valid to propose that vibrissal afferents do play a role in maintaining a "central tonus".

The aim of the present work was to test whether the effects of vibrissal afferent blockade on certain types of motor behavior are really due to a lack of tactile information. Thus, we compare effects of trimming vibrissae with those of infraorbital nerve blockade on general locomotor activity in an open field and on a learned motor performance. These results have been partially presented elsewhere (7).

METHODS

Animals.

Adult Wistar rats (250-300 gr) were housed in an experimental room with a 12 hs light-dark cycle, (light on at 7:00 hrs), for a week prior to experiments. Behavioral observations and vibrissae manipulation (both surgical and local aneathesia procedures) were always carried out between 10:00 and 12:00 hrs.

Experimental groups.

1) Normal group: rats without any treatment.

2) Vibrissae trimming: all vibrissae on both sides were trimmed at the level of the fur, just before the start of the session. This procedure was used as a technique to assess the specific sensory role of the vibrissae in the motor tasks studied.

3) Transitory blockage of vibrissal afferents: this was produced by local anaesthesia. One cc of 0.5% procaine solution was injected subcutaneously in each vibrissal pad. Rats were tested 2 min later.

4) Control anaesthesia: to assess the possible role of systemic absorption of procaine. Similar amounts of the drug (previous group) were injected subcutaneously in the rat dorsum. The test was also carried out two min. later.

5) Permanent blockage: both IO nerves were cut under general anaesthesia (Sodium Pentobarbital 40 mg/kg, i.p.). Prior to the neurotomy 0.3 cc of 1% procaine solution was injected inside the nerve trunk. The IO was sectioned just when it emeges from the infraorbital fissure. In this case, rats were tested 24 or 48 hs after the operation (see below).

6) Facial nerve section: Local anaesthesia blocks both afferent and efferent vibrissal innervation. Furthermore, vibrissal pad movements remain unchanged after cutting the whiskers. Thus, to evaluate the importance of the motor supply to the vibrissae, both buccal and upper divisions of the marginal mandibular branches of the facial nerve responsible for the motor innervation of vibrissae (9, 23), were bilaterally cut under general anaesthesia (Pentobarbital 40 mg/kg, i.p.). Section of these facial nerve branches was made 1-2 mm rostral to the extraorbital lacrimal gland in the rat's face. Rats were also tested 24 or 48 hs later (see below).

7) Sham group: same procedures as in groups 5 and 6, but without nerve section. Sham surgery for group 5 (IO nerve section) included troncular anaesthesia. All rats in this group were also tested 24 or 48 hs later (see below).

The sensibility loss was routinely tested in both vibrissal blockage groups (local anesthesia and IO nerve section) by means of the lack of response to either blunt or sharp pinch in the vibrissal pads. In the local anestesia group there was a further complete loss of vibrissal movements.

Rats in the IO and facial nerve sectioned groups were killed by decapitation, under ether general anaesthesia after the experiments were done in order to check for the completness of nerve section. Animals with any intact nerve fibers were not considered in the final analysis of the results.

Apparatus and procedure.

The first experiment was conducted in a wooden open field apparatus (1 1 0.50 m). The floor and walls were black, and the floor was divided into 20x20cm sections by 0.5 cm broad lines of white paint. Rats were individually placed in the central square of the open field and behavior was scored by two independent observers. The trial lasted 5min, after which the rat was returned to its home cage. The floor and walls were carefully wiped with soap and water between each trial. Two types of behavior were studied by direct observation: locomotor activity (number of field sections entered with all four paws) and rearing activity (time spent in rearing, with or without placing the front paws on the walls of the open field).

In this experiment, because sham surgery significativly decreses activity in open field 24 hs post-operation, observations were carried out 48-50 hs after surgical operation on the neurotomized (both IO and facial nerve) and sham groups. On the other hand, since there are well known differences between male and female behavior in open field, only male rats were used in this experiment.

For the second experiment adult male and female rats were used. Animals were individually housed with water available ad libitum, whereas food access was restricted in order to maintain rats at 85% of their free-feeding body weights. Since statistical differences between groups were sought across time increments produced by vibrissae manipulations (see results), the normal group (without treatment) was not needed in this case.

An apparatus with two platforms, A and B (both 20 30 cm, elevated 60 cm off the floor) connected by a rope (0.7 cm diameter and 34 cm length) was constructed in our Lab, for the second experiment. Rats were placed on platform A and trained to cross to platform B, where food had been placed. Two time intervals were scored by direct observation: 1) *Waiting time*: measured from the time the rat was placed on platform A until the animal had placed all legs on the rope to start going over it; and 2) *Crossing time*: counted from the end of waiting time until the moment the whole body of the rat (with or without tail) rested on platform B. Animals were trained twice a day with a 4-5 min interval between each trial and scored in both waiting and crossing time with the mean value of these two measures. Learning criterion was established as a waiting time score $\leq$ 30 sec. on five consecutive days. This criterion was reached by the 30th to the 35th training day.

All mathematical and statistical procedures (for both experiments) were carried out using the SigmaStat software (v 2.0, ® SPSS).

RESULTS

Experiment one: Open field behavior.

We observed striking changes in rat aspect and behavior after vibrissal pad anaesthesia. A generalized loss in muscle tone was apparent 1-2 minutes after procaine injections in the pads: the animal posture shifted down so that the entire body was flattened and rested upon the ground. The head, normally raised, fell down and the

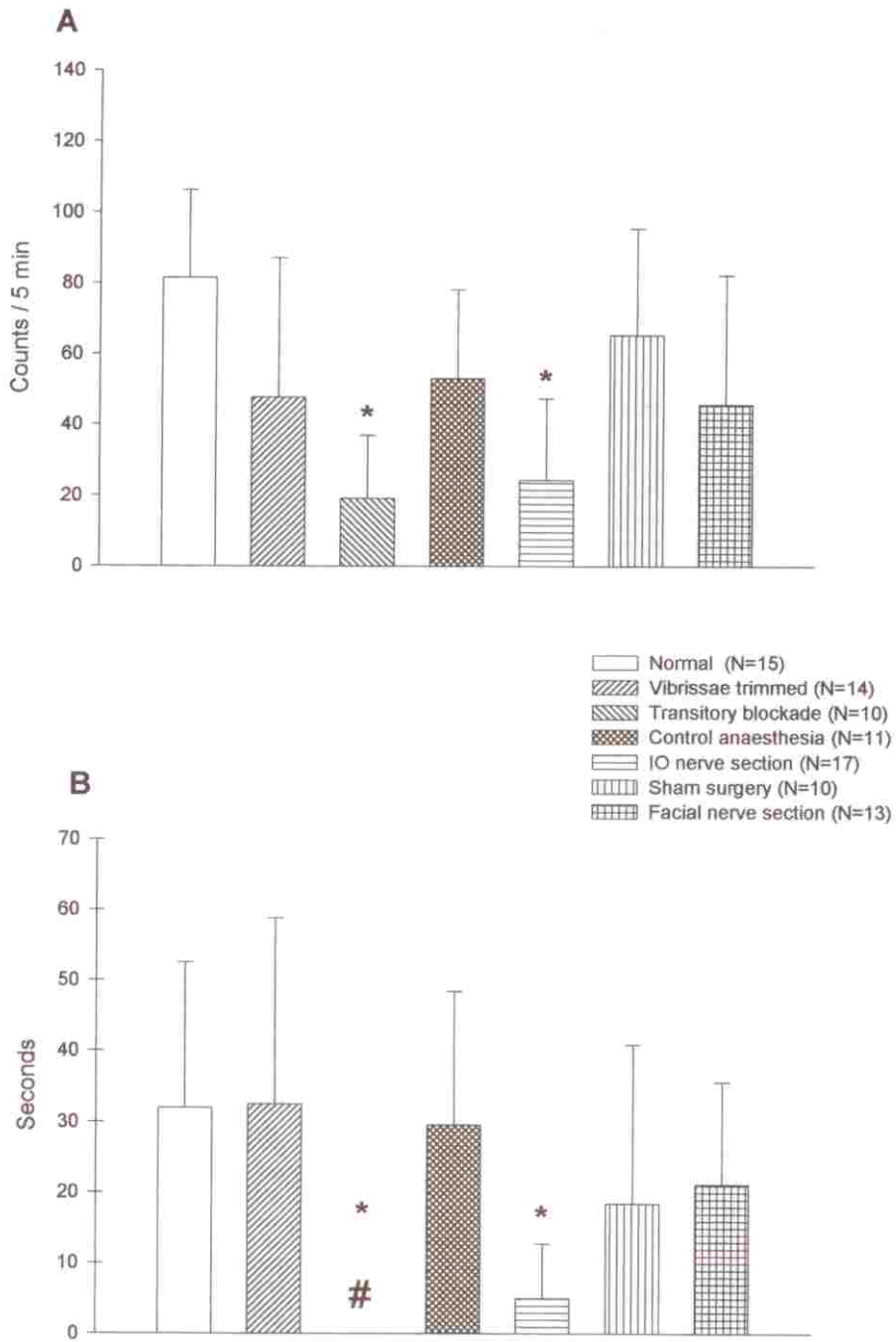

Fig. 1. - *Open field behavior.* A Locomotor activity; B Rearing activity.
* $p < 0.01$
# rearing activity was null in transitory blockade group.

chin remained against the floor, even when the rat was walking. All movements were slowed and less coordinated than normal. Another interesting fact was that these animals did not seem to recognize the borders, e.g. if the rat was walking on a table it did not stop until its head, or forelimbs, had no more support, often falling to the floor. When the rat did not fall it could remain immobile for a long time (5-10 min) with its head over the side (as if it were looking at the floor). The rats with anaesthetized vibrissae behaved in only two ways in the open field: either standing motionless in the central square for the five minutes or walking (always with the chin against the floor) a few squares until reaching a corner and ramaining immobile there. Rearing behavior was null in this group.

The same changes, although somewhat less pronounced, can be observed during the first two or three days after bilateral section of IO nerves: body flattened and lengthened, poor coordination and slowed movements, head rarely raised, often falling from the table or hanging over the side, etc. In the open field, both locomotor and rearing behavior were dramatically reduced in rats with IO nerves severed. Locomotion was very slow and poorly coordinated, and the rats remained motionless most of the time. The small quantity of rearing activity observed in this group always occurred with forepaws against the wall. It seemed as if they were incapable of standing up by themselves; their behavior was more like "climbing" the wall than standing.

None of the above mentioned changes were observed after vibrissae trimming or facial nerve section, but the effects of these treatments showed a great variability. As matter of fact, about 75% of the rats in these two groups, performed almost normally or had somewhat greater activity (covering more squares and more rapidly than normal). Only the remaining 25% displayed a slightly diminished level of both locomotor and rearing activity. However, movements were always well coordinated.

Figure 1 illustrates the effects of different treatments, on locomotor (A) and rearing (B) activity as mean plus one standard deviation. Results were not normally distributed; thus Kruskal-Wallis one-way analysis of variance on ranks was applied to the behavior records, Dunn's method for multiple comparisons versus normal group was used in making the subsequent analysis.

Statistical analysis showed that the groups are different in locomotor activity ($H = 25{,}49$; $p < 0.001$). Post-hoc tests (Dunn's method) pointed out that only transitory ($Q = 3{,}64$, $p < 0{,}05$) and permanent ($Q = 3{,}94$; $p < 0.05$) blockade groups differ from the normal group. The control groups (anaesthesia in the back and sham surgery) do not differ from normal. Trimming vibrissae and facial nerve section groups are not statistically different from normal groups.

Similar effects of treatments were observed on rearing time. Kruskal-Wallis one way ANOVA showed that there was a statiscally significant difference in the median values among the treatments ($H = 36.7$; $p < 0.001$). The multiple comparisons versus normal group (Dunn's method) showed that only vibrissal pad anaesthesia and IO section differ from the normal group ($Q = 4.8$; $p < 0.05$ and $Q = 4.1$; $p < 0.05$, respectively).

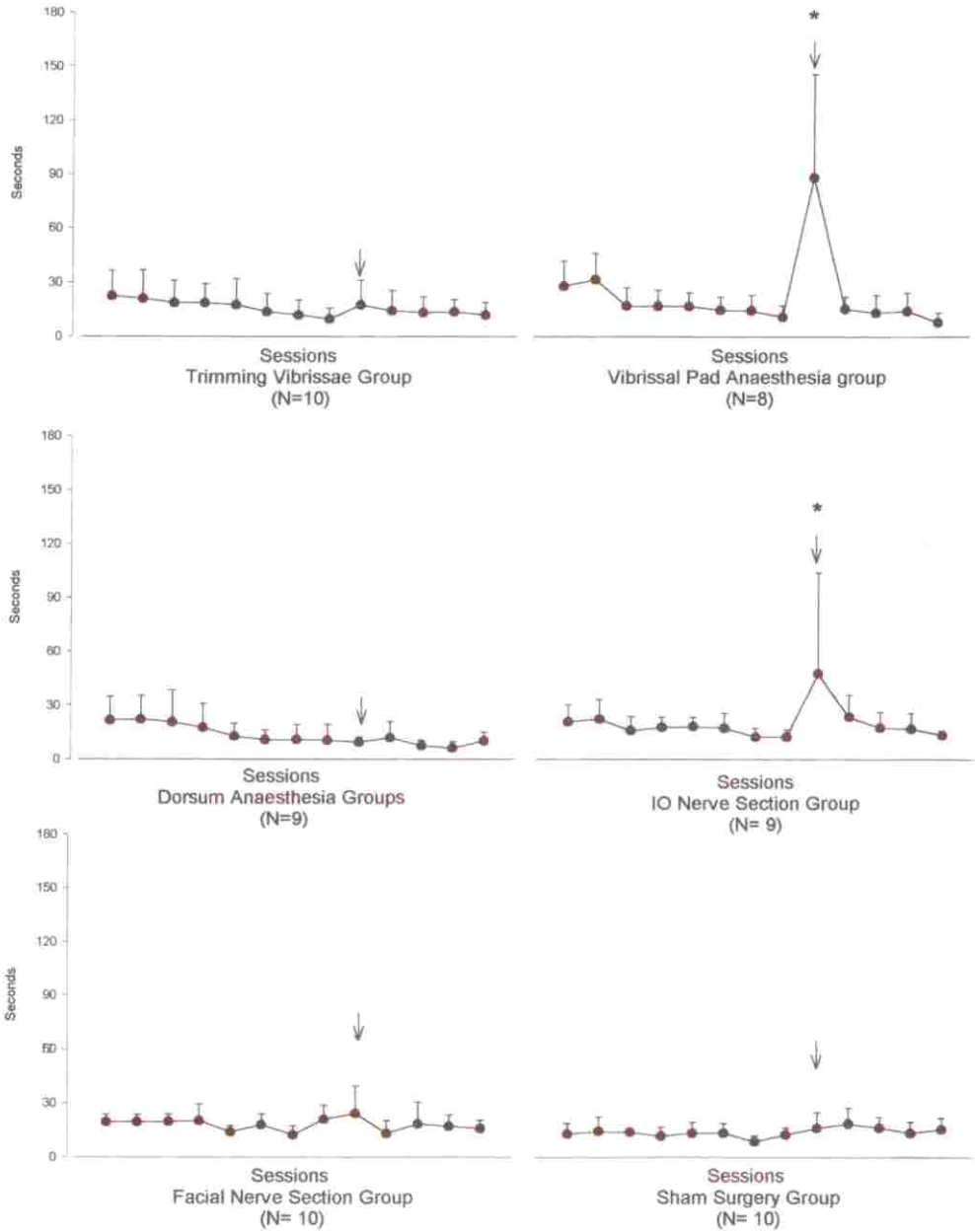

Fig. 2. - *Effects of treatments on waiting time.*

Waiting time measures of experimental groups are plotted as mean plus one standard deviation, before and after treatments (8 and 5 days respectively). Arrows indicate the session of experimental manipulations of vibrissal systems.
* $p < 0.01$

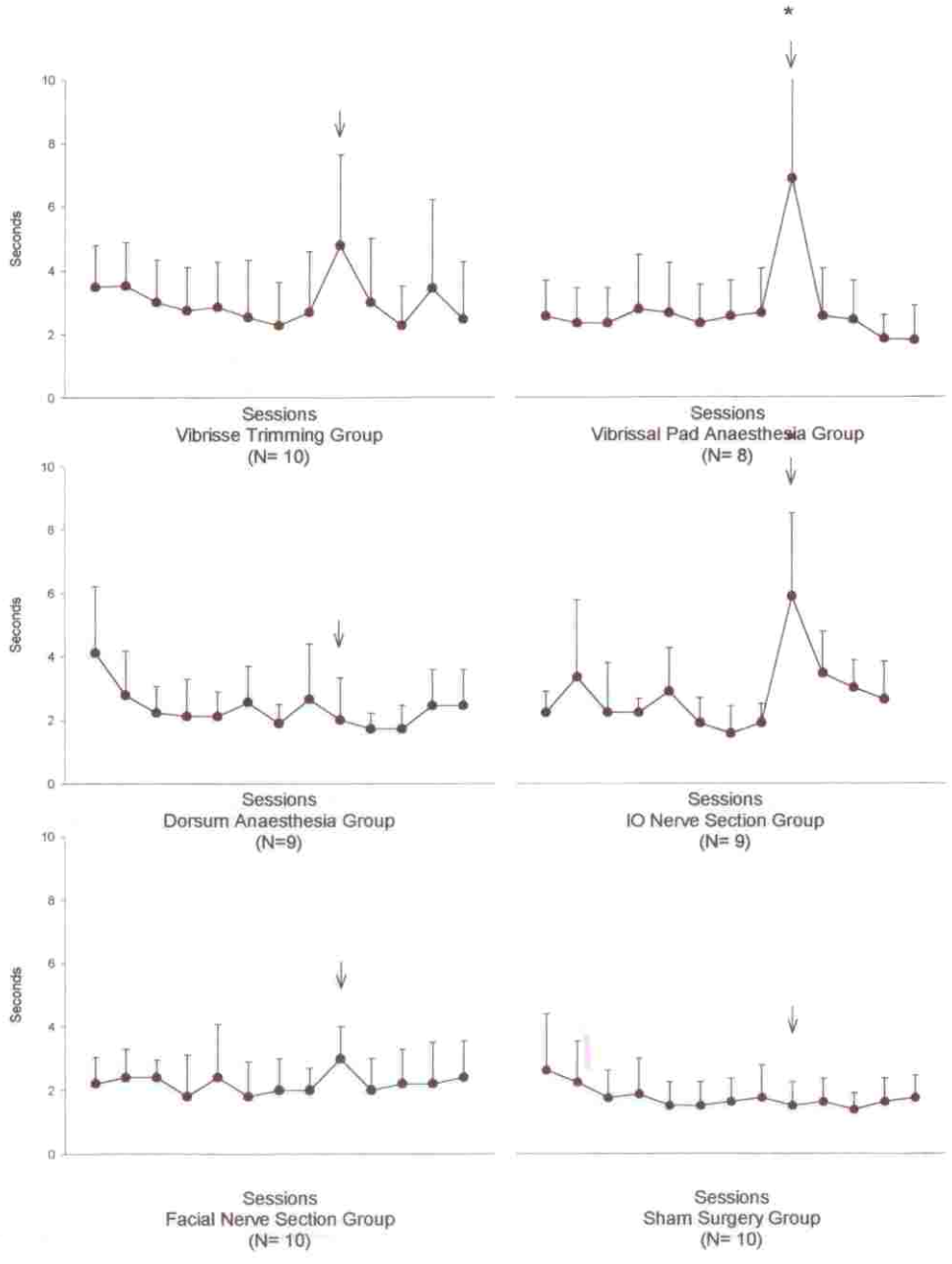

Fig. 3. - *Effects of treatments on crossing time.*

Crossing time measures of experimental groups are ploted as mean plus one standard deviation, before and after treatments (8 and 5 days respectively). Arrows indicate the session of experimental manipulations of vibrissal systems.
* $p < 0.01$

Experiment two: learned motor performance

No quantitative differences were found between male and female performances. Thus, results are shown without sex differentiation. The performance of different groups before and after treatments are shown in Figures 2 (waiting time) and 3 (crossing time), as mean plus one standard deviation.

Effects of IO nerve blockage on rat general appearance and behavior were identical to those observed in experiment one (both groups, local anaesthesia and nerve section).

In the vibrissal pad anaesthesia group, there were three rats that did not go over the rope and remained motionless for more than five minutes, with their heads hanging over the border of platform A. The other five rats in this group took a very long time before going over the rope (mean 93 sec., i.e. more than five times the 17 sec average normal waiting time period). The IO nerve section also produced a remarkable increment in the waiting time, although less pronunced than procaine injection. This lesser effect is probably related to the fact that almost 22 hs elapsed between the nerve section and the experimental trial. As is seen in Figure 2 neither vibrissae trimming nor facial nerve section had any effect on waiting time.

To walk over the rope was a more difficult task after vibrissal afferent blockage than doing the same task for the first time by a naive rat. It is a well known fact

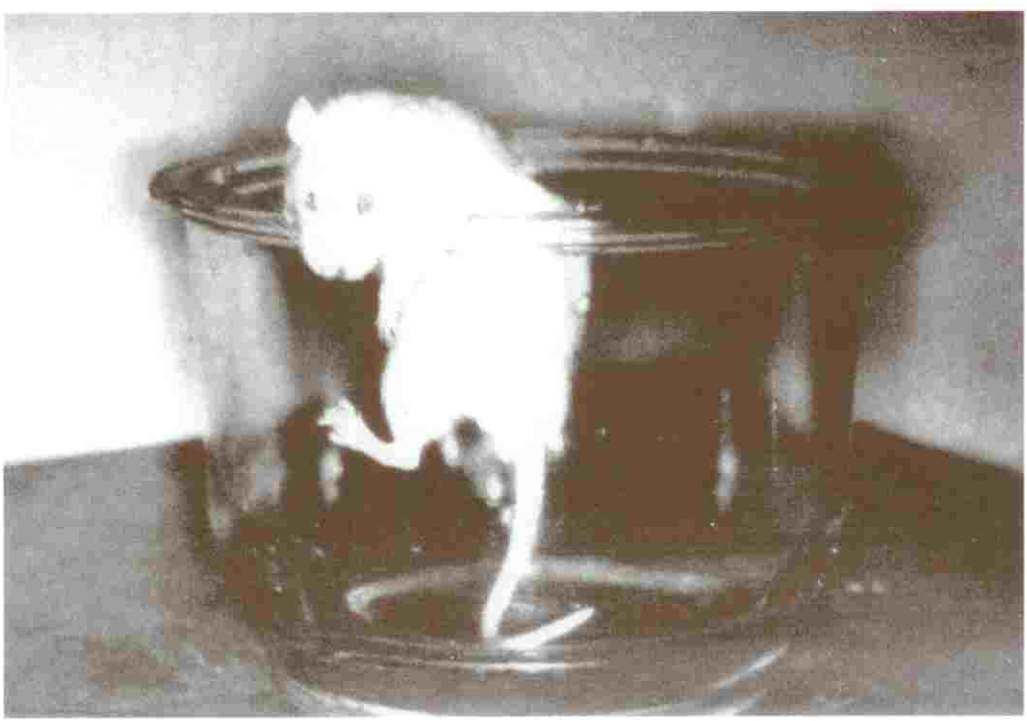

Fig. 4. - *"Cataleptic" rat.*

See text for further details.

that wild rats are very good climbers and that they are able to run along wires of 2-3 mm in diameter (11). For our inmbred white rats, running along the rope used in these experiment (7 mm in diameter) was indeed an easy task. Falling down from the rope during the early learning sessions was hardly ever observed and the crossing time reached a relatively stable value of 2-3 sec between the 5th to the 10th learning session. This crossing time increased 3-4 times after vibrissal pad anaesthesia, and 2-3 times after IO nerve section (see Figure 3). These increments may be explained by two facts: *a)* the generally slowed movements and impoverished coordination we have already observed in open field, and *b)* rats often stopped their walk along the rope, sometimes on 3-4 occasions, sometimes remained immobile for many seconds in any portion of the rope, including with the forepaws on platform B and the hindlimbs on the rope. The slower times were clearly not permanent, and even for the nerve section group, the results were normal 48 hs after the section.

Although the results of vibrissae trimming on crossing time are somewhat more pronounced than for waiting time, the differences are not significant. Animals with trimmed vibrissae displayed great variability in this aspect of the motor task. As a matter of fact, about 30% of the animals of this group were slower in their performance, while the remaining animals performed slightly faster than the controls. Considered as a single population, the results were not significant.

Increments in both waiting and crossing time were calculated (as the difference between the performance in experimental trials minus the median performance in the five previous trials), for statiscal analysis. Kruskal-Wallis tests were carried out in all cases, and Dunn's multiple comparisons method was carried out as a post-hoc test. The three rats of the transitory blockage group which did not go over the rope were scored as 180 sec for waiting time and 10 sec for crossing time (arbitrary value). The significance of the results was the same either with or without these cases.

Statistical analysis shows that groups are significantly different in waiting time ($H = 20.9$; $p < 0.001$). Post hoc tests reveal that increments in waiting time were significantly greater in permanent ($p < 0.01$) and transitory blockage ($p < 0.0001$) groups than in any of the others. Furthermore, the effect of transitory blockage was greater than that of permanent blockage ($p < 0.05$)

Kruskall-Wallis ANOVA on ranks for crossing time indicates that groups are significantly different ($H = 25.3$; $p < 0.001$). Post hoc tests reveal that increments in crossing time were significantly greater ($p < 0.005$) in permanent and transitory blockage groups than in any of the others.

We observed other changes in the rat behavior after vibrissal pad anaesthesia. Some of these animals (in both experiment one and two) showed a cataleptic like state: placed in certain awkward positions (e.g. on the border of a glass flask, Figure 4) the animal would remain immobile, in the same position for long periods of time.

DISCUSSION

Our results show that blockage of vibrissal afferents has important effects on motor activity. These data agree partially with previous reports (27) that have suggested a decrease in general activity and motivation following vibrissae trimming or infraorbital nerve section. The importance of tactile sensory information in guiding behavior (thigmotaxis) has usually been given as the mechanism behind this phenomenon. However, the statement that vibrissae trimming produces a decrease of general motor activity, as reported by Vincent (27), has been contested. Thus, Meyer and Meyer (19) did not find any decrease in locomotor activity after vibrissotomy in either open field or in an aquatic environment. Althougth about 1/3 of our animals did show a moderate effect along these lines, when the whole population was considered, the changes were not significant. We should tend to agree, then, with the conclusion of Meyer and Meyer (19).

On the other hand, in the type of motor task used in experiment two, the animals have to use their sense of equilibrium. However vibrissae trimming did not affect their performance. Thus these results would argue against Vincent´s opinion that the vibrissae play a role in equilibrium.

There are other changes in rats after vibrissal afferent blockage. In her study, Vincent (27) noted striking changes in the general aspect and behavior of rats in a maze after infraorbital nerve section: "... walks close to edge all the way; nose against floor... body much flattened and lengthened ... when resting these rats hang on by their toes ... they seemed to depend more upon their feet..." We observed the same changes in the open field test (experiment one).

On the other hand, it has also been reported that vibrissal anaesthesia produces a loss of sensory capacity for responding to footshock (25, 26). We also found significant increases in nociceptive thresholds (measured as responses to footshock) after transitory or permanent blockage of vibrissal inputs (7, 8). We should also mention the depressive effects of vibrissa afferent blockage upon social, aggressive and sexual behavior (see ref 1 and 16 for reviews). All these observations in the vibrissal system would seem to support the old neurophysiological idea which states that, in addition to their sensory functions, some receptors play an essential role in maintaining a central excitatory state of the CNS. The hypothesis was proposed specifically by Ewald (10) and von Buddembrok (2) in the case of invertebrates. Granit (12) reviewed some of the vertebrate data consistent with the idea of what he called the "central energizer" role of certain sensory afferents. Support for this hypothesis, but not proof, would also come from the work of Pavlov's school, which reported that increased light conditions could improve classical salivary conditioning (17). Along the same line, Ozorio de Almeida and Pieron (21) showed that complete removal of frog skin causes muscle hypotony and hypoactivity. It is remarkable that their description of frog aspect and behavior could be extended to our own observations in those rats which showed a cataleptic like state. We will discuss this phenomenon in the third paper of this series (22). There are also old observations by Gray and Lissman (13, 14) showing that spinal cord deafferentation plus bilateral

labyrinthic destruction impede swimming in the frog. Finally, Cohen (6) also reported postural changes and loss of muscular tone after the ablation of several proprioceptive receptors (myochodotonal organs) in the crab (*Cancer magister*). The loss in muscular tone was alike in operated and intact legs. However, in spite of the considerable number of observations supporting a central, nonspecific excitatory role for some sensory afferents, these two roles for sensory systems have never been differentially tested before. This has probably been due to the difficulty of experimentally dissociating the specific sensory message from any other possible role a given sensory system may have (3).

We believe that cutting the vibrissae hairs, by cancelling the exploratory tool of this sensory system, impedes a meaningful sensory message's being sent. Thus the lack of significant effects of vibrissae trimming in our experiments indicates that the sensory information provided by the intact vibrissae system was not important either for the correct performance of the motor task which the animals had previously learned nor for locomotor activity in the open field. On the other hand, the complete blockade of the vibrissal afferent IO input, either transitory or permanent, did produce a clear change (slowing) in the learned motor performance and on the open field behavior. The fact that IO section effects on motor performance were transitory should not argue against the hypothesis above mentioned, since great plasticity is a well known property of a complex nervous system. The lack of motor effect observed after sham surgery clearly indicated that the results observed after IO nerve section were not due to residual pentobarbital in blood (it is well know that barbiturates may be present up to a week after administration).

We have not tested the effects of plucking out the whiskers, a procedure commonly used in vibrissal system plasticity studies. This deafferentation technique affects follicular integrity and therefore the follicular receptors and nerve terminals. When vibrissae are trimmed both follicle and skin receptors are left intact. Thus we thought that effects of plucking out vibrissae would have effects similar to nerve section. We chose this latter procedure because it is a more standarized and controlled way of complete vibrissal pad deafferentation. Furthermore plucking out the whiskers is a painful operation that requires general anesthesia. Thus we may expect the same time course for barbiturate recovery as for IO nerve section. As we will discuss in the next work (8) it is very probable that the recovery time for general anaesthesia overlaps the time in which compensation from deafferentation occurs.

In summary, our results, by separating the two possible roles of the vibrissae, show clearly that a non specific general "energizer" role could be postulated for the rat vibrissal afferents.

SUMMARY

In the past, it has been proposed that the rat vibrissae play an important role in guiding locomotion and motor behavior, through their sensory capacity. On the

other hand, postural abnormalities, muscle tone decreases and hypomotility after sensory organ destructions were proposed as evidence supporting the "level setting" or "tonic" hypothesis. This hypothesis postulates that afferent activity, besides its well know transductive functions, sets the excitability state of the central nervous system. We thought the vibrissal system to be a good model to dissect these two postulated roles because vibrissae trimming would annul the transductive function without affecting the integrity of nerve activity. Thus we compare the effects of trimming the whiskers with blocking the vibrissal afferent nerves on two types of motor behavior: activity in an open field and walking over a rope connecting two elevated platforms. We found that only vibrissal afferent blockage (both nerve section and local anaesthesia) produced severe failures in the motor performances studied. These effects could not be fully explained by the abolition of the vibrissae as a sensory modality because cutting the whiskers did not significantly affect the motor performance. These data are discussed in reference to a tonic or general excitatory function of sensory inputs upon the central nervous system.

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