NLP-82

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BEHAVIORAL AUDITORY FUNCTION AFTER TRANSECTION OF CROSSED OLIVO-COCHLEAR BUNDLE IN THE CAT

I. Pure-tone Threshold and Perceptual Signal-to-noise Ratio

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Abstract. The feline subjects were behaviorally conditioned to respond to pure tone signals at different frequencies based upon the avoidance conditioning procedure. After the transection of crossed olivo-cochlear bundle, the pure tone threshold (250–14 000 Hz) was not altered. Neither was any alteration found in the measurement of the perceptual signal-to-noise ratio at the levels of 30, 50, and 70 dB above the subjects' pure tone thresholds. Morphological confirmation of the brain stem and cochlear end organs demonstrated that proper surgical lesions had been made and there had been subsequent degeneration of the efferent nerve endings around the outer hair cells; especially in the basal coils. It is concluded, therefore, that the absence of the crossed olivo-cochlear bundle has no effect on the behavioral measurement of pure tone thresholds and perceptual signal-to-noise ratio in the cat.

Since the neuroanatomical description of the olivo-cochlear bundle by Rasmussen (1942, 1946, 1960), the course of the bundle and the patterns of peripheral termination within the organ of Corti have been studied in different experimental animal species by many investigators (Engström et al., 1966; Kimura & Wersäll, 1962; Smith, 1967; Spoendlin & Gacek, 1963; Spoendlin, 1968). After stimulation of the efferent fibers, Galambos (1956, 1960) observed that the system suppressed auditory nerve activity. He considered the role of the entire system to be inhibitory in nature, at least in part.

Although numerous electro-physiological investigations have been conducted, only a limited number of behavioral investigations of this system have been performed previously. The study of Dewson (1968) demonstrated the effect upon stimulus discrimination in noise after cutting the olivo-cochlear bundle in the midline in four rhesus monkeys (all cortically ablated except for one subject), he found that their ability to discriminate human vowel speech sounds was impaired in the presence of noise. There was no loss in ability to discriminate the same sounds when noise was absent, or at very low intensity levels. Therefore, he considered that the deficit was related to the perceptual signal-to-noise ratio.

Capps & Ades (1967, 1968) studied auditory frequency discrimination after ablating the olivo-cochlear bundle in squirrel monkeys. A modified Wisconsin General Test Apparatus together with a food reward technique was used. Focused ultrasonic irradiation or surgical interruption of the olivo-cochlear bundle in the floor of the fourth ventricle was employed. Following the transection, all animals demonstrated a marked deficit in frequency discrimination performance at 1 000

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and 4 000 Hz. They therefore suggested that the efferent auditory system operated to sharpen the frequency resolving power of the inner ear.

Trahiotis & Elliott (1970) have recently performed behavioral studies of effects of sectioning the crossed olivo-cochlear bundle in cats. Broad band noise was used at levels of 20, 30, and 40 dB of masking effect for frequencies of 500, 1 000, and 2 000 Hz. The extent of masking effect at 1 000 Hz and 2 000 Hz was found to be increased very slightly after midline section, though the shift was not statistically significant.

The overall objective of the present experiment was to study the physiological and psychological contribution of the crossed olivo-cochlear efferent system to various aspects of systemic auditory function. The behavioral conditioning approach seemed proper for this purpose in order to measure function in living animal subjects (without anesthesia) under variable acoustic conditions. The morphological results were compared with the data obtained from behavioral conditioning.

Subject

Six adult cats, two females and four males with no otological disorder (based upon otoscopic investigation and confirmation at the time of removal of electronmicroscopic specimens) were utilized for the present investigation. Their initial body weight ranged between 6 and $10\,^1/_2$ pounds with a mean weight of $8\,^1/_2$ pounds. Each animal's health condition was also examined and there was no sign of any systemic disease.

Screening

Subjects were screened according to the three-day, 90% criterion (Igarashi & Hoyt, 1963) by avoidance conditioning methods in a cat rotating cage utilizing free field hearing conditions (in IAC 1202 chamber). Subjects were required to turn the rotating cage within 5 sec of the presentation of a 1 000 Hz, 63.5 dB (re 0.0002 dyne/cm^2) pulsed pure tone signal. The signal on–off time was 0.5 sec each. Failure to rotate the cage within 5 sec resulted in a mild electrical shock which was delivered through the cage grids with an intensity ranging between 0.5 to 40 mA and a duration of 0.05 sec. Intensity of the shock was manually controlled depending upon the subject's response, body weight and pad skin resistance, etc. A buzzer was sounded when the correct response was performed. A randomized interval program was employed with a mean inter-trial interval of 45 sec with a range of 30–60 sec.

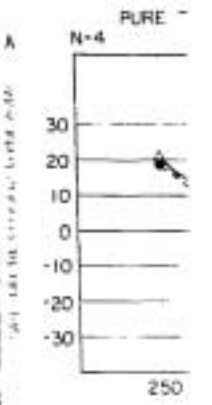
Using the above screening procedure, six subjects were selected for further training.

Testing

Pure tone threshold

Screened subjects were trained to respond to several different frequencies; namely, 250, 500, 1 000, 2 000, 4 000, 8 000 and 14 000 Hz. (14 000 Hz was selected instead of 16 000 Hz because the TV camera which was installed inside the sound proof chamber emitted a frequency of 15 750 Hz.) The absolute pure tone threshold for each frequency was determined by attenuating the signal until the animal no longer responded.

A criterion was used where three negative responses in succession were recorded as no hearing. Two positive responses out of five trials were recorded as hearing equal to the sound pressure level tested. Spontaneous activity was not scored as either positive or negative responses; however, such activity was counted and recorded. All subjects were tested five days a week, and with two neighboring frequencies a day. Since the responses ordinarily became most accurate after two or three testing days, several threshold scores were discarded for this reason. A minimum of four non-discarded scores were needed to calculate a mean threshold at each of the seven frequencies.



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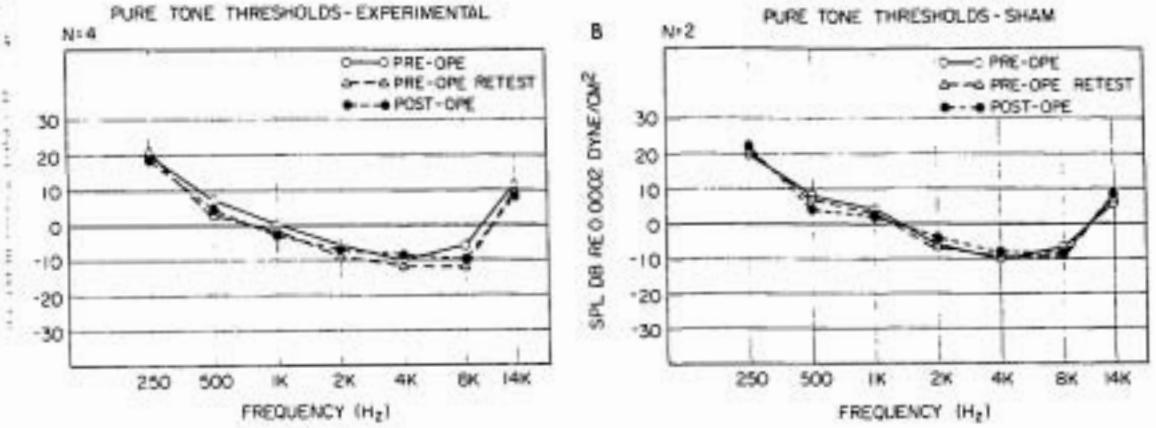

Fig. 1. (*A*, *B*) Pure tone thresholds for experimental and sham groups; pre-operative (transection of crossed olivo-cochlear bundle) testing, pre-operative retesting, and post-operative testing.

Perceptual signal-to-noise ratio

At each of the seven frequencies tested, pure tone signals with the intensity level of 30, 50 and 70 dB sound pressure level above the subject's pure tone hearing threshold were delivered. Broad band white noise (500–15 000 Hz) was then introduced and its intensity level was gradually increased until the pure tone signal was masked. Noise intensity levels were scored as previously indicated. Inasmuch as the output of the noise generator was not of a constant amplitude, the spectrum of white noise between 500 to 15 000 Hz was found to have a 13 dB increase at 14 000 Hz over the amount of white noise at 500 Hz. Since this phenomenon was not known until after the present study was terminated, the effect was not taken into account while calculating the intensity of white noise.

The measurement of perceptual signal to noise ratio consisted of subtracting the dB sound pressure level (re 0.0002 dyne/cm^2) of noise from the dB sound pressure level of the signal. The subjects almost always required a greater dB noise than the pure tone signal. Thus, the ratios were negative numbers. The more negative the perceptual signal-to-noise ratio, the better was the subject able to detect the pure tone signal in a field of white noise.

At least four readings of perceptual signal-to-noise ratio scores were obtained at each of the three intensity levels in the seven frequencies. Due to the standard established in the equipment set-up, it was not possible to produce noise sound pressure level of sufficient intensity to ordinarily mask frequencies of 50 and 70 dB above the subject's threshold at 250 and 500 Hz.

(C) *Retesting of pure tone threshold and signal-to-noise ratio*

To determine whether the pure tone thresholds had changed after long period of testing, all subjects were retested. Two of the 6 subjects had lower thresholds, one at 8 000 and 14 000 Hz, the other at 8 000 Hz only. Their signal-to-noise ratios were retested accordingly to correct for the difference. The overall pure tone thresholds for the 6 subjects did not differ more than 5 dB at each frequency.

Surgery (Transection of the crossed olivo-cochlear bundle)

Animals were anesthetized with pentobarbital (40 mg/kg body weight) intraperitoneal injection. An occipital midline incision was made and the occipital bony calvarium was removed by rongeurs to expose the posterior portion of the cerebellum and brain stem. The cerebellum was very gently retracted up-

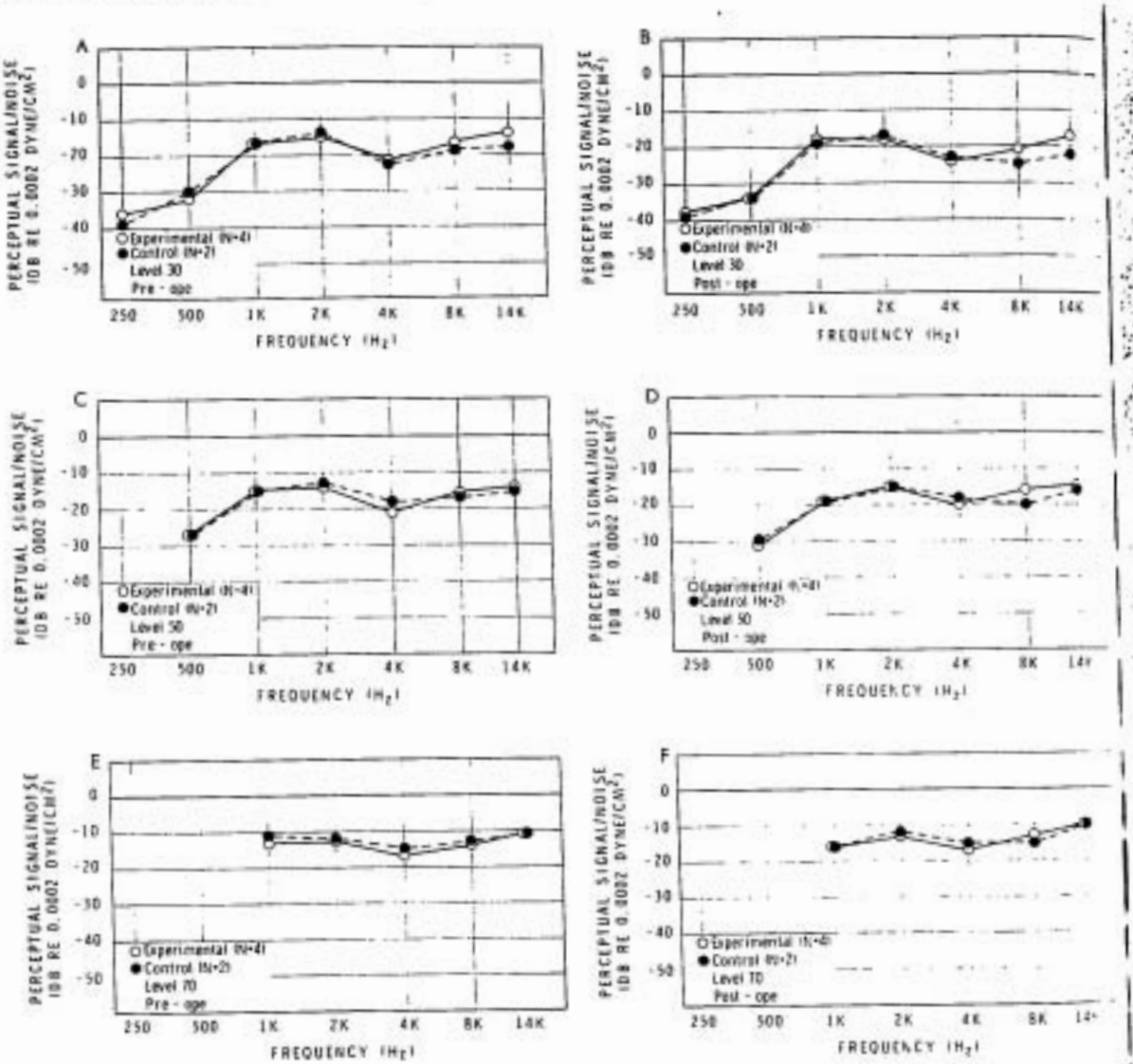

Fig. 2. (*A–F*) Perceptual signal (30, 50, 70 dB intensity levels) to noise ratios for experimental and sham groups; pre-operative (transection of crossed olivo-cochlear bundle) testing, pre-operative retesting and post-operative testing.

ward so that a fine pick could be inserted between cerebellum and brain stem. The crossed olivocochlear bundle was sectioned at the level of the facial colliculi in the floor of the fourth ventricle. The sectioning point was calculated by the distance (11 mm) from the obex. A fine hook (2 mm cutting edge) was used to make the lesion. The incision was usually extended about 3 mm both rostrally and caudally from this calculated point; however, in some cases it was intentionally prolonged. Care was taken not to retract the cerebellum too much. All bleeding spots were controlled and the area was covered by a piece of gelfoam. The wound was closed. Two out of 6 cats served as sham operated animals in which the identical surgical procedure was performed except for actual mid-line cutting.

Fig. 3. (*A–B*) Photo tical lesions (*arrow*

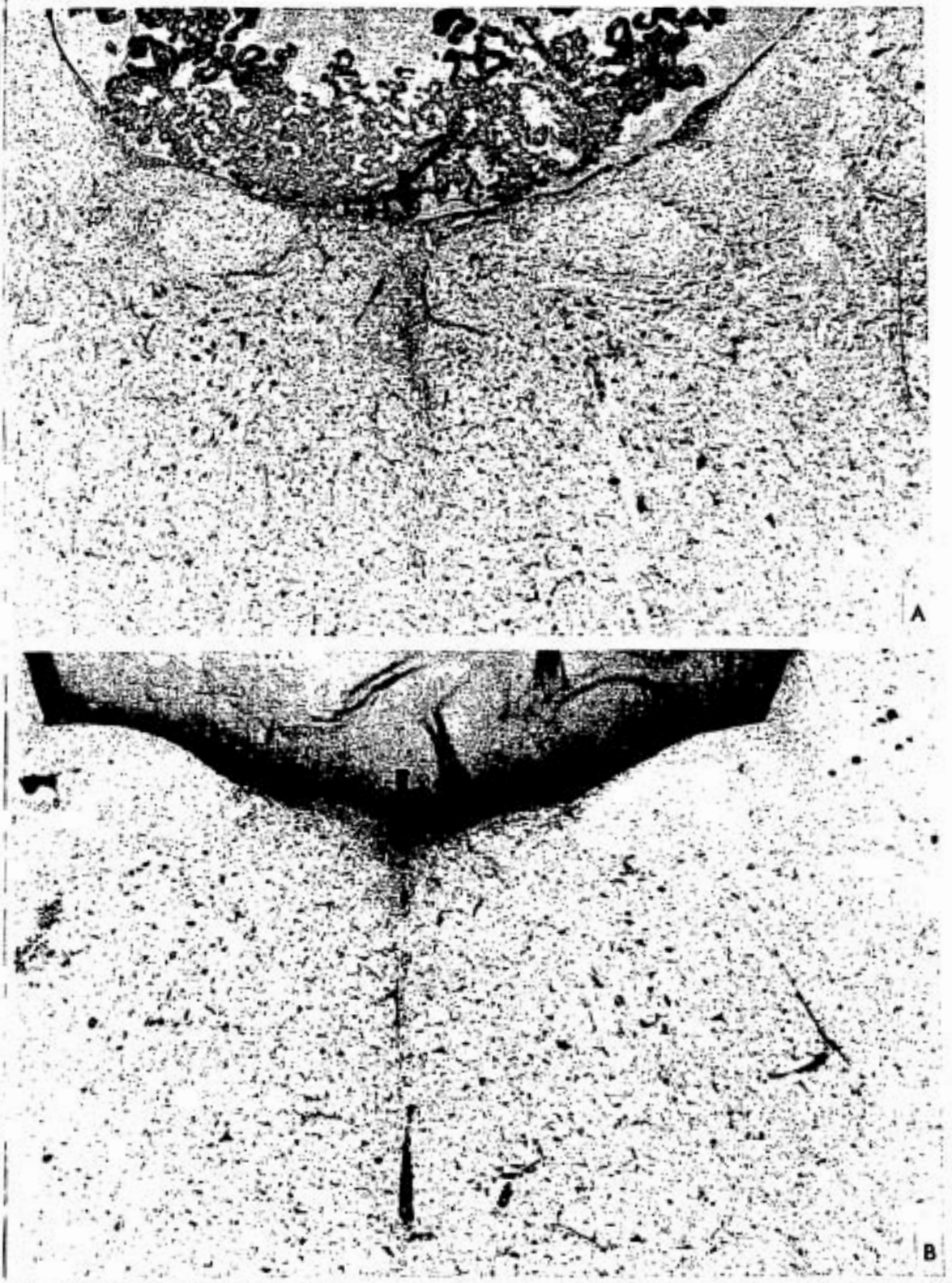

Fig. 3. (*A–B*) Photomicrographs demonstrate the surgical lesions (*arrows*) at the floor of fourth ventricle from two representative (experimental) subjects. × 30 (Gallocyanin staining).

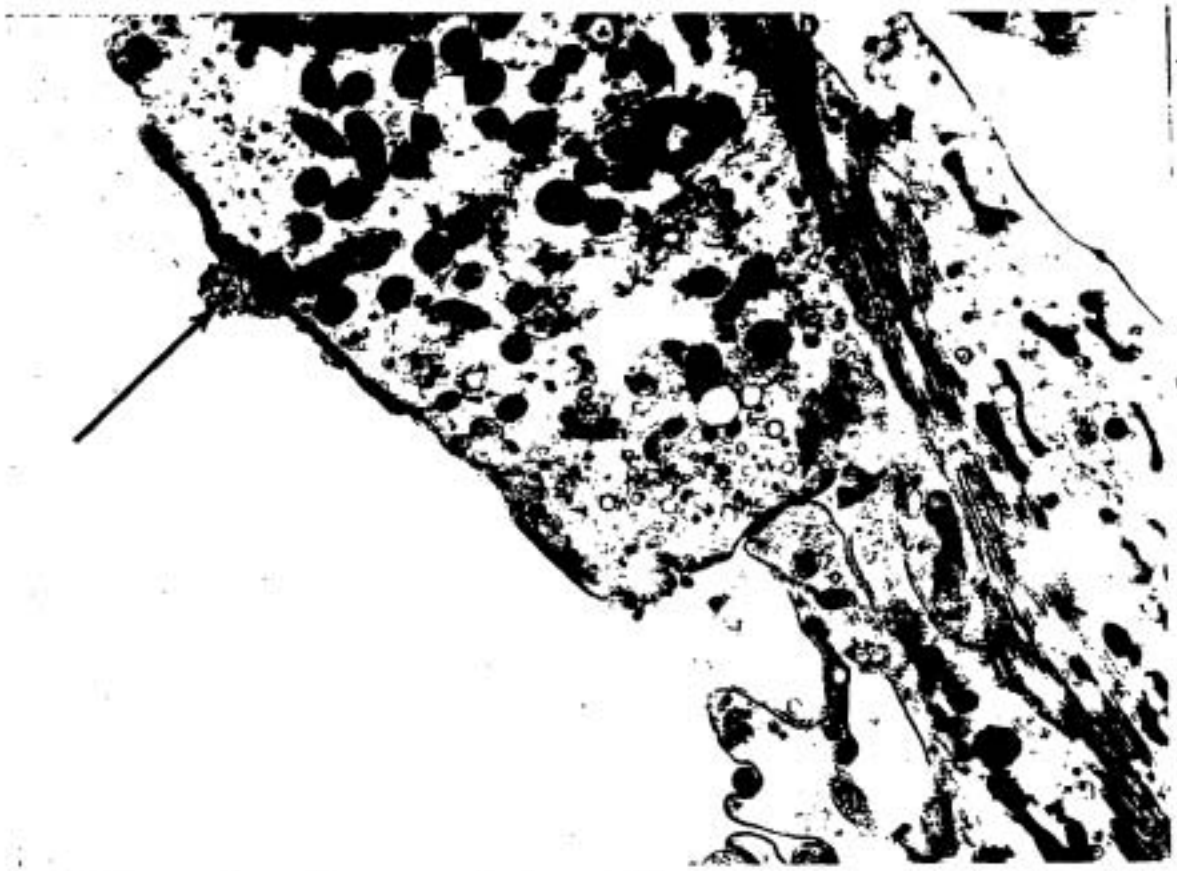

Fig. 4. Electronmicrograph demonstrates the lower portion of first row outer hair cell from the basal turn (about 8 mm from the basal end; chronic cat). Efferent nerve endings are entirely disintegrated and only some cell debris is present (*arrow*). × 14 550.

Fig. 5. Electronmicrogra of first row outer hair about 17 mm from the

Post-operative testings

All subjects survived the surgical procedure. There was not sign of post-operative infection. Subjects were retested starting about 7 days post-operatively and all were able to rotate the cage competently although some subjects exhibited slight dysequilibrium at the time. The animals were first retested for pure tone threshold, and thereafter for perceptual signal-to-noise ratio, in exactly the same fashion as was done in pre-operative testings.

Morphology

After acquiring sufficient post-operative data, all subjects were sacrificed for morphological investigations. The animals were deeply anesthetized and intravital cardiac perfusion with 2% gluraraldehyde solution, preceded by physiological saline solution, was performed. Cochleas were removed and processed according to the routine procedure of electronmicroscopic preparation. Specimens were embedded in Epon and ultrathin sections were cut by a Porter-Blum MT-2 ultramicrotome. Sections were stained with uranyl acetate and lead hydroxide, and were studied under JEM-7 electron microscope. Specimens from at least four different areas of each cochlea were investigated.

The serial cross sections (20 μm) of the brain stem (Gallocyanin staining) were also prepared for neurohistological confirmation of the depth and extent of the surgical lesions.

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Fig. 1 (*A* and *B*) d pure tone threshold and 2 sham subjects quencies, including operative retesting, testing. The data i tween the pre-oper live testing sessions sham controls did operated cats. On t cies except for 250 improved between pre-operative rete This slight differe to a further prac

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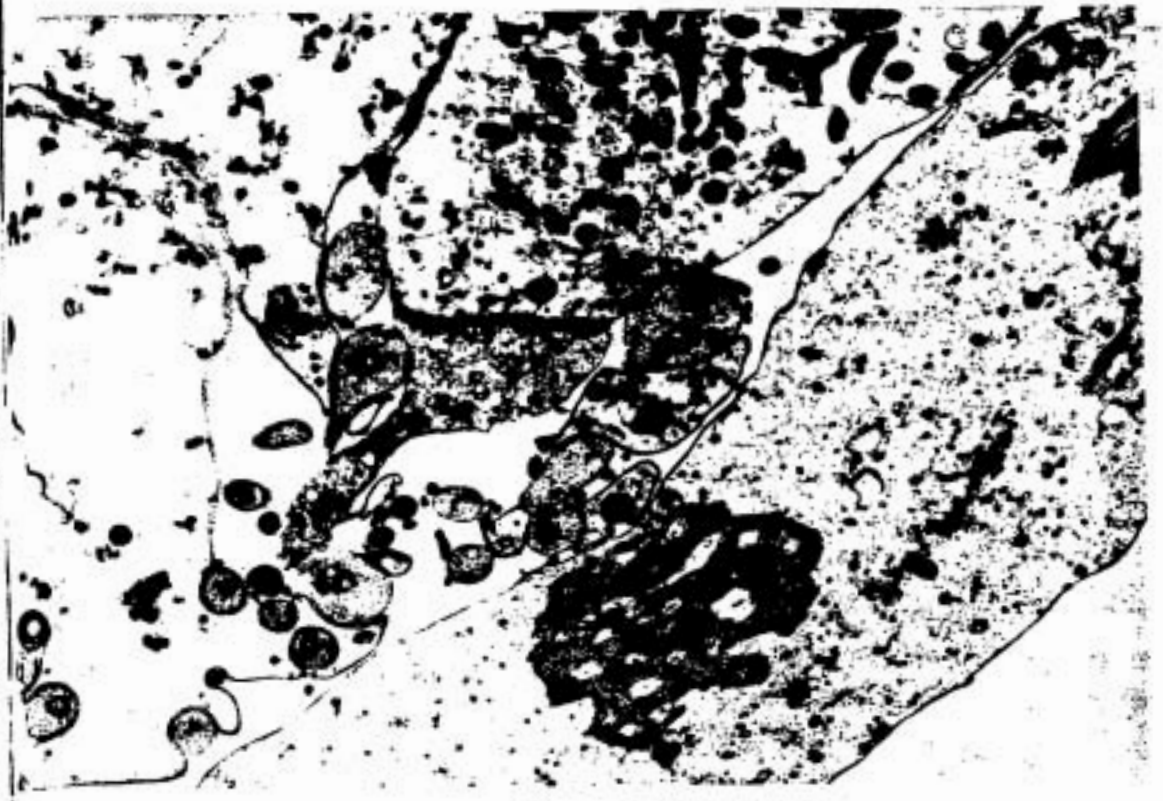

Fig. 5. Electronmicrograph shows the lower portion
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RESULTS

A) *Pure tone thresholds*

Fig. 1 (*A* and *B*) demonstrates the averaged
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nd 2 sham subjects at each of the seven fre-
uencies, including pre-operative testing, pre-
perative retesting, and the post-operative
esting. The data indicate no difference be-
ween the pre-operative and the post-opera-
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ham controls did not differ from those of
perated cats. On the other hand, all frequen-
es except for 250 and 14 000 Hz were slightly
nproved between pre-operative testing and
re-operative retesting of their thresholds.
This slight difference is most probably due
o a further practice or training effect. No
post-operative effect occurred at the high frequencies such as 4 000, 8 000 and 14 000 Hz, which locate the basal turns.

(B) *Perceptual signal-to-noise ratio*

By comparing experimental and sham groups, no significant difference could be determined between pre-operative and post-operative perceptual signal-to-noise ratios at different frequencies and intensity levels (Fig. 2*A–F*). As a trend, the post-operative scores were slightly in the direction of better discrimination; namely, perceptual signal-to-noise ratios were more negative. Again, the possible existence of the training or practice effect should be considered in this regard.

Relatively high negative perceptual signal-to-noise ratios were present at 250 and 500

Fig. 6. This electronmicrograph is from the lower portion of second row outer hair cell of the basal turn (about 11 mm from the basal end) from a sham control subject. Normal efferent and afferent nerve endings are seen. Outer spiral fibers (afferent) between Deiters' cells are also normal. × 16 000.

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(C) *Morphology*

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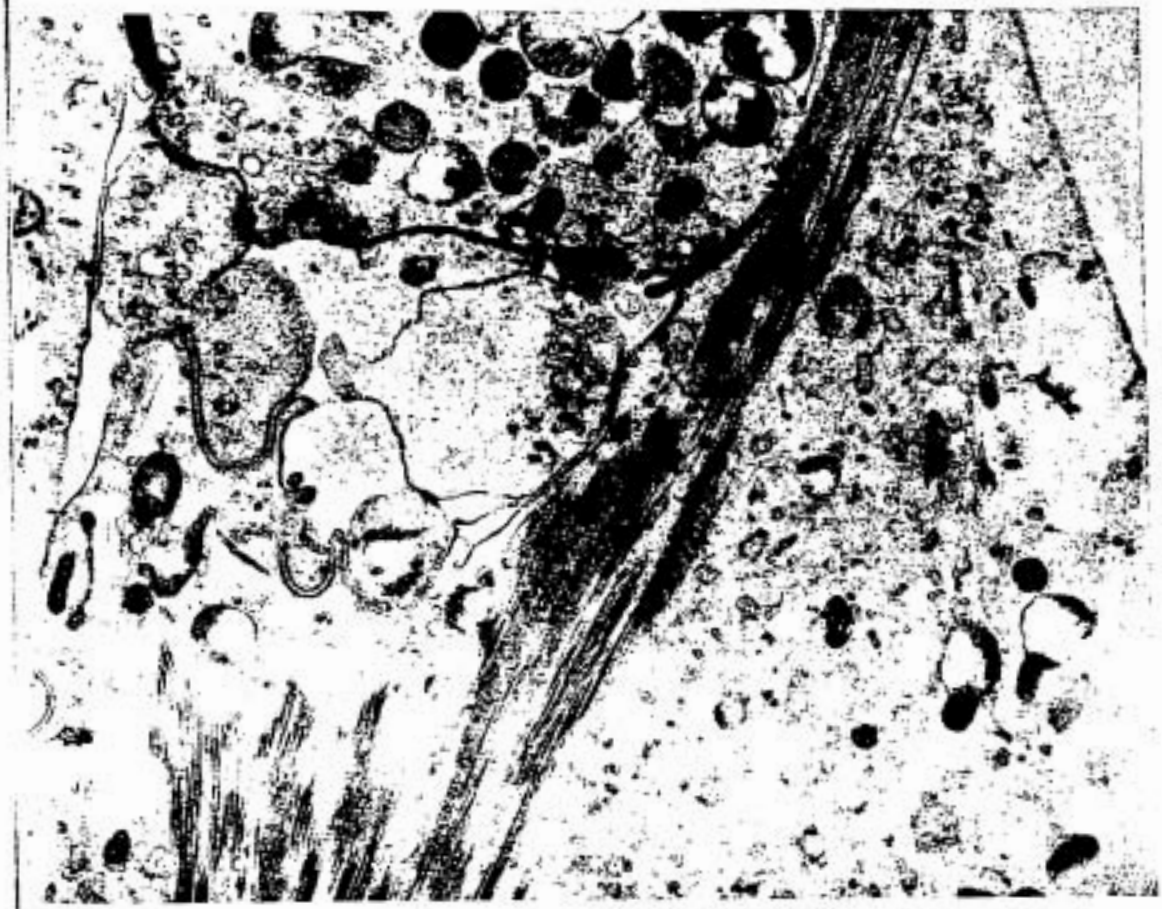

Fig. 7. Electronmicrograph shows the lower portion of second row outer hair cells from lower basal turn (about 5 mm from the basal end; 13 days post-operative). Degenerated efferent nerve ending can be seen although afferent nerve ending looks normal. Mitochondria have disappeared but some of synaptic vesicles still remain. Subsynaptic cisterna has partly disappeared. × 15 390.

Hz because white noise was not present below 500 Hz. In other words, the masking effect of white noise was more pronounced at higher frequencies above 500 Hz.

C) *Morphology*

The cross serial sections of the brain stem from 4 animals which belong to the experimental group confirmed that both depth and extent (rostral and caudal) of the surgical lesions were proper to eliminate the crossed olivo-cochlear bundle, although the lesions were not clearly distinguishable in these chronic animals (Fig. 3*A–B*) when compared with those in acute animals. The rostro-caudal extension of the surgical lesion was found to be 1.0–2.0 mm from the edge of facial genu, (average 2.7 mm from the 11.0 mm point rostral to the obex). The measurements were based upon 15–20% correction which occurs due to nerve tissue shrinkage.

From the electronmicroscopic investigation, it was confirmed that many of the efferent terminals to the outer hair cells were eliminated, especially in basal coils (Fig. 4). However, rudimentary efferent endings were observed in middle coils and higher (Fig. 5). Sham control subjects did not have any efferent terminal degeneration (Fig. 6). Additional electronmicrographs obtained from

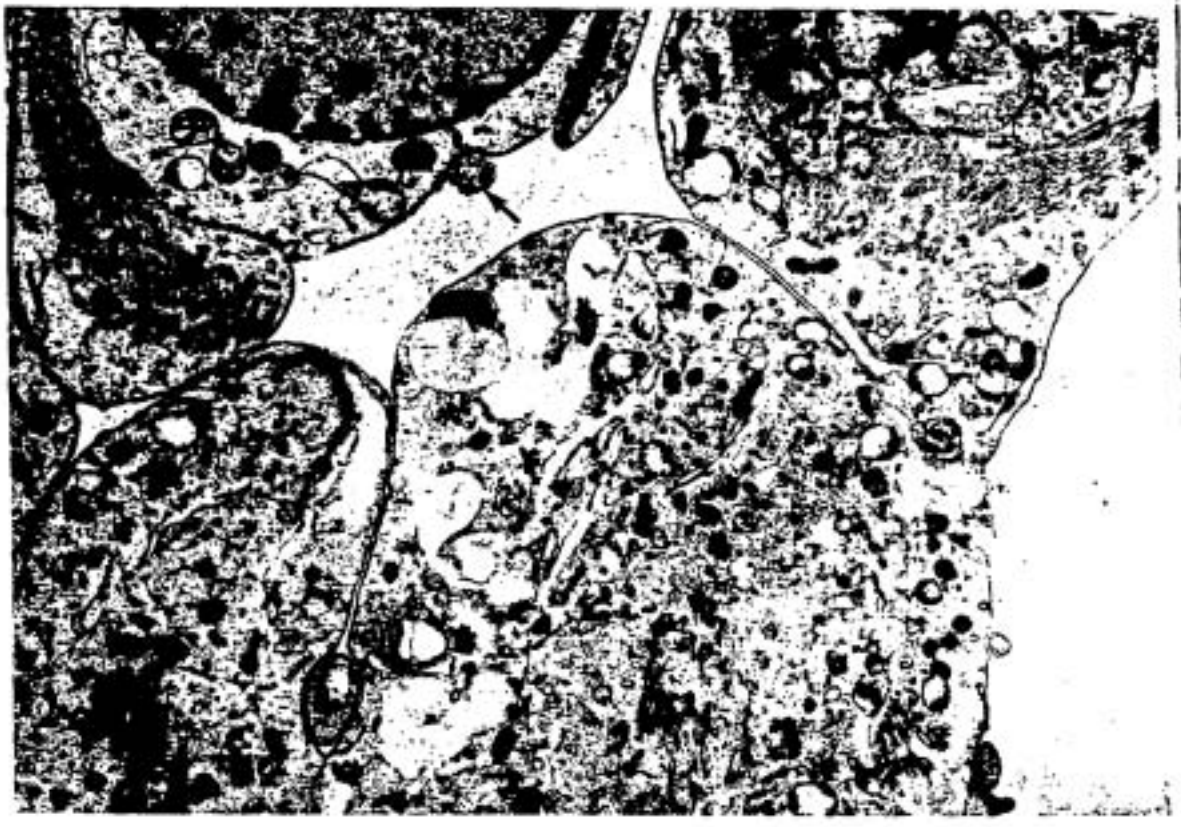

Fig. 8. This electronmicrograph is of the first and second row outer hair cells from lower basal turn (about 5 mm from the basal end; 13 days post-operative). There are three normal-looking afferent nerve endings below the first row outer hair cell. The efferent nerve ending below the second row outer hair cell is entirely disintegrated and only some cytological debris is still present (*arrow*); however, the subsynaptic cisterna along the hair cell membrane appears to be normal. × 11 400.

Fig. 9. This electronmicrograph ...tal disappearance of tunnel ...om the lower basal turn (ab...

subjects with short-term survival (about 2 weeks) after identical transection of the crossed olivo-cochlear bundle confirmed similar findings; namely, efferent terminals to the outer hair cells in basal coils and large number of tunnel spiral fibers had disappeared (Figs. 7–9).

DISCUSSION

The testing procedure for perceptual signal-to-noise ratio is a complex one; each individual factor was therefore analysed so that no major interference could exist that would affect the experimental purpose.

The possible occurrence of a temporary threshold shift from the prolonged exposure to white noise was considered. This possibility was examined by utilizing 3 cats according to the following procedure. First, the pure tone threshold in each frequency was determined in each cat. Then the subject was exposed to white noise (which was described in the present paper) 70 dB level above his own threshold for 15 min; the severest condition of the present series of experiments. Immediately after the exposure to the white noise, the pure tone threshold acuity was measured once again at each different frequency. There was no more than 5 dB threshold change after the noise exposure; therefore, the effect from that noise exposure was considered to be negligible.

For the measurement of perceptual signal-to-noise ratio, higher frequencies were tested

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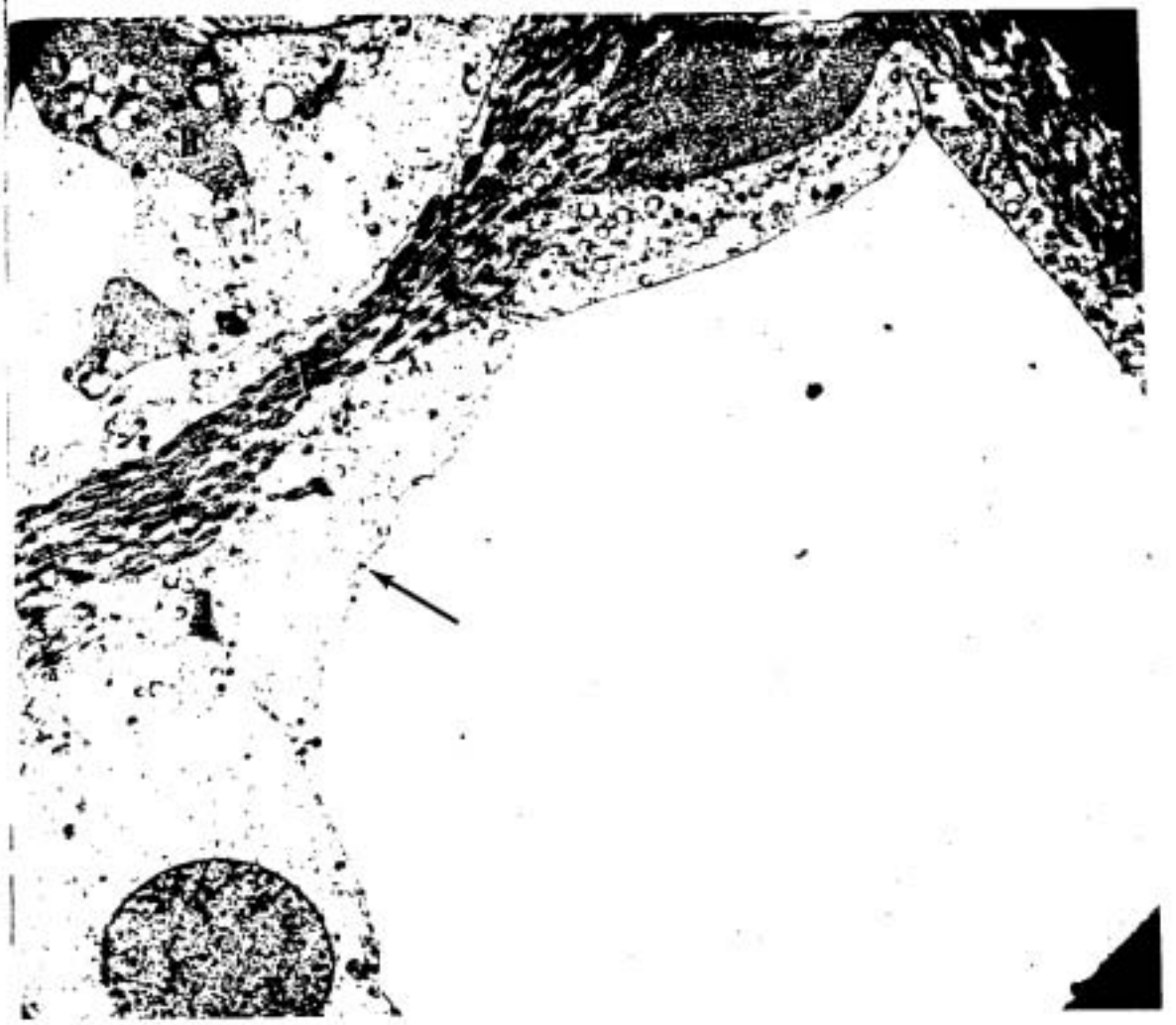

Fig. 9. This electronmicrograph demonstrates almost total disappearance of tunnel spiral fibers (arrow) from the lower basal turn (about 5 mm from the basal end; 12 days post-operative). *H* = inner hair cell. × 9 360.

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comparing to the study of Trahiotis & Elliott, with the intent to investigate the basal turn function as the crossed efferent terminals are distributed more in the basal turns. Also, higher intensities of pure tone signal and white noise were used, in order to produce more extensive end organ stimulation.

The other concern was the prolonged period of training or practice effect; therefore, before the mid-line operation, pure tone threshold was measured once again after the measurement of perceptual signal-to-noise ratio. In 2 experimental cats, a slight threshold improvement was noticed; the perceptual signal-to-noise ratio was therefore repeatedly measured based on the improved pure tone threshold.

The entire procedure required about 6 months from the initiation of the experiment; however, no cat demonstrated any deterioration in performance during this experiment.

From the present experimental results, it is evident that the morphological elimination of the crossed olivo-cochlear efferent terminals in cats has no effect on the pure tone auditory threshold or perceptual signal-to-

noise ratio. Provided that the crossed olivo-cochlear efferent system was sufficiently activated by the present experimental method, it may be concluded that transection of the crossed olivo-cochlear bundle has no effect upon these two behavioral auditory tasks. On the other hand, because pure tone detection tasks might not be so difficult for cats, the crossed olivo-cochlear efferent system might not have been sufficiently activated although the auditory end organ system was receiving quite intense white noise. Probably, in the cat, more difficult and complex tasks are needed to activate the crossed olivo-cochlear system properly, or else the translateral olivo-cochlear system has no appreciable contribution to systemic auditory function (Pfalz, 1969). In this regard, further experiments are being performed. By stepwise utilization of simple to difficult complex tasks, the ecological validity of the olivo-cochlear efferent system will be systematically investigated.

ACKNOWLEDGMENT

Appreciation is expressed to Mrs M. Lewis for her technical assistance.

ZUSAMMENFASSUNG

Die Versuchskatzen wurden so trainiert, daß sie im Vermeidungsprozeß auf reine Tonsignale von verschiedenen Frequenzen reagierten. Nach einem Querschnitt des gekreuzten Olivo-Cochlea-Bündels war der reine Ton der Hörschwelle (250–14 000 Hz) nicht verändert. Gleichfalls wurde keine Veränderung in der Bemessung vom wahrnehmbaren Signal zum Geräuschverhältnis vorgefunden bei Stufen von 30, 50 und 70 dB höher als der reine Ton der Hörschwelle der Katzen. Morphologische Bestätigung des Gehirnstammes und des Cochlea-End-Organes bewies, daß richtige chirurgische Verbindungen gemacht wurden, und man konnte die darauffolgende Degeneration der nach außen führenden Nervenenden um die äußeren Haarzellen feststellen; ganz besonders in den Grundspiralen. Es wurde daher beschlossen, daß die Abwesenheit des gekreuzten Olivo-Cochlea-Bündels keinen Einfluß hat auf das Verhalten der Katze bei reinen Ton Hörschwellen und in der Bemessung vom wahrnehmbaren Signal zum Geräuschverhältnis.

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ULTRAS

From the Otopatho

…bstract. Part 2 of an ultra… …iddle ear mucosa from patie… …edia is presented. Biopsies … …ntorial epithelium of 11 … …ne-like effusion in the mid… …th mucosa from patients … …as found that the cells pre… …nid had disappeared, whil… …lls had increased in numb… …w and the cilia often degen… …inds were demonstrated. A… …quamous metaplasia of th… …resent an early stage of a pr…

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BEHAVIORAL EFFECTS OF TELESTIMULATING HYPOTHALAMIC REINFORCEMENT SITES IN FREELY MOVING RHESUS MONKEYS

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INTRODUCTION

Many authors have related self-stimulation of various brain areas, particularly the hypothalamus, to reduction of specific physiologic drives (4,15,18,19): For instance Olds (18) reported a change of 2-30 presses per minute in self-stimulating rats when comparing the effects of no food deprivation to 24 hour deprivation for points coupled to food drive; and a change from 50 presses per minute to zero presses per minute after castration for points coupled to sex drive. Also Brady (2) reported a 20 fold increase in presses per minute in rats after 24 hours without water. However, in other experiments self-stimulation has been shown to be drive inducing, not reducing, and often it does not covary with physiologic drives at all (7,14,16). Some autnors have inferred, therefore, that emotional or motivational states are induced by the stimulation and are responsible for the self-stimulation effect (6). Others have emphasized an overriding importance of the type of goal object present for determining the behavior evoked by such stimulation (24).

This variety of observations and interpretations might become simplified if the appropriate experimental situation could be designed. In social situations physiologic drives, emotional reactions, and such motivations as dominance, are readily distinguished. Yet, there have been no studies

directly correlating stimulation of known positive self-stimulation sites with changes in social behavior in the freely moving animal. Thus, this study set out to investigate the behavioral effects of stimulating previously determined sites of self-stimulation in the freely moving monkey, while alone and in social situations.

INITIAL PROCEDURES

Surgery: Three naive subadult monkeys (Macaca mulatta), two males (L and N) and a female (T), weighing between 4.3 and 5.6 Kg, were stereotaxically implanted in standard fashion using the Horsley-Clarke system. Electrodes of teflon-coated stainless steel wire were placed bilaterally in the lateral septum, hippocampus and amygdala for EEG recording purposes.

Distal ends of the electrodes were attached to a 25-pin female Microdot connector embedded in dental acrylic directly on top of the skull. The animals were allowed a three week recovery period before any testing was done.

All three animals had had at least six months of social experience in a large colony cage. During the experimental period, however, all were individually housed and fed 25 pellets of standard laboratory chow daily, except during tests using specific deprivation periods.

Apparatus: Lever-pressing tests were carried out in a 30" x 18" x 30" box with the animal restrained in a modified Foringer chair. The stimulating cable exited through a hole in the top of the box and the monkey sat facing a lever

installed at shoulder height. Rates of lever pressing were tabulated on a Harvard cummulative recorder. Biphasic pulse trains were provided by two coupled AEL stimulators through an isolation unit. Stimulus current parameters were monitored across a 100 ohm resistor on the output.

Neurobehavioral Identification of Points: All animals were introduced to bar pressing for intracranial stimulation on a continuous reinforcement schedule without any prior training. The experimenter stood by the animals and pressed the lever in front of them four or five times rapidly, then waited five minutes before moving on to the next point. All twelve hypothalamic electrode pairs were thus tested twice in rotation at the same time each day for four days. By the third day all animals were clearly bar-pressingat some points. Lever pressing rates for these positive points were repeatedly determined by allowing the animal to bar-press 500 times followed by a ten minute extinction period.

Monkeys N and T each showed one positive point, while Monkey L showed three. Rates of self-stimulation at these five points are given in Table I. Thresholds for self-

[Insert Table 1]

stimulation were at 0.25-3.0 milliamperes for a 0.5 sec. train of 1 msec. biphasic square waves given at 60 cps. Bar-pressing rates were stable from 0.5-0.9 ma; therefore

all determinations and future testing were done at an intensity of 0.7 ma. An inconsistent supressive effect was noted in Monkey L in switching abruptly from one anterior hypothalamic positive point to the ipsilateral, more posterior one. This "little pig" effect (3,12) lasted for three or four minutes, and was not seen in any other successive stimulation combination.

Control Tests: Since covariance of self-stimulation sites with physiologic drive states would confound interpretation of any results from behavioral data, animals were tested on continuous reinforcement schedules for intracranial self-stimulation, and deprived first of food, then of water for increasing deprivation intervals. In addition, after the main experiments to be reported, the two male monkeys were castrated and the female monkey ovariectomized. Bar pressing scores were obtained at 12 and 24 days post-castration. Bar pressing scores as a function of food or water deprivation and variation in sex hormone level are summarized in Table II. No animal showed a change in bar pressing rate with manipulation of these drive variables.

[Insert Table II]

The discrepancy between these results and those of previous studies (e.g. Olds (18) and Brady (2)) is not easily accounted for. Since these authors used the more sensitive fixed ratio schedule while in the present study a continuous reinforcement schedule was used, it is possible that the

lack of bar pressing change with manipulation of physiologic drives is due to reinforcement schedules. It is more likely, however, that the points studied here are simply not "drive related."

Another possibility is that self-stimulation of these points is due to subclinical seizure activity. Brady et al (5) reported that six of eight monkeys with electrodes in the hypothalamus showed spike and wave activity after the start of a 0.5 sec. train of pulses. This report led to the question of whether in the present experiments self-stimulation points, though not drive-related, were positive in part because they induced seizures.

EEG recordings were obtained in these monkeys preceding castration but following all other experiments. Recordings were taken from hypothalamic electrodes near the one being stimulated as well as from the bilateral septal, hippocampal and amygdala electrodes in Monkeys T and L. Records were obtained after 1, 2, 5, and 10 trains with the trains delivered at 0.5 sec. intervals (continuous train stimulation). Regardless of the number of trains delivered, no spike and wave activity was observed following the stimulus when it was delivered to any of the positive points. Because of stimulus artifact, however, it was not possible to rule out very brief seizures beginning and ending during the 0.5 sec. train itself.

These results are in accord with reports by a number of authors (9,17,20) who have shown that bar pressing rates actually varied inversely with seizure thresholds and who concluded that seizures were a side effect not related to "positivity" of points. It thus seems likely that results from the behavioral experiments which follow cannot be attributed to drive related phenomena, nor to disruption of mnemonic functions by seizure activity.

Histology: After completion of all experiments the monkeys were sacrificed and perfused intracardially with 0.9% saline, and 10% formalin and potassium ferrocyanide solution. One millivolt DC current was passed through positive electrode tips for five seconds. Frozen sections of the brain were cut in 50 micron slices and stained with cresylechtviolet. Relevant histologic sections are shown in Figure 1.

[Insert Figure 1]

The electrode tips for the positive point in Monkey T were just posterior and below the anterior commissure ending in the anterior hypothalamic area. This corresponded to Anterior 16.0 in Russell's Atlas (23). Electrode tips for the positive point in Monkey N were again just below the anterior commissure, ending in the anterior hypothalamic area, and corresponded to Anterior 16.5 to 16.0. Tips of the left anterior positive electrode, hereafter called L_6, in Monkey L were just posterior to the anterior commissure.

The tips were 5.5 mm lateral to the midline, placing them in the anterolateral portion of the lateral hypothalamic area. The right anterior positive point, hereafter called L_8, in Monkey L was ventral and posterior to the anterior commissure ending in the anterior hypothalamic area. The posterior positive point, hereafter called L_{12}, in Monkey L was in the coronal plane corresponding to Anterior 13.8. The tips were just lateral to descending fornix fibers, placing this point in the middle of the lateral hypothalamic area in its antero-posterior extent.

Of the five positive points then, three were in the anterior hypothalamic area and two in the lateral hypothalamic area.

EXPERIMENT I

This experiment was designed to examine the effects of self-stimulation on the behavior of individual monkeys in the physical situation to be used subsequently to test social interactions (Experiment II). Aside from the specific results obtained, therefore, Experiment I serves as a baseline for the findings obtained in the "social" experiment.

Apparatus: A 4' x 4' x 8' test cage was constructed with three walls of white painted plywood; the fourth long wall was made of one-way glass panels. Floor and ceiling were covered by 9 ga. 1 in. mesh. The floor mesh was marked off by lines in 2 ft. squares to aid in measuring locomotor activity. Interior lighting was provided by standard flourescent fixtures suspended over the ceiling mesh.

Stimulation was obtained by modifying a Heathkit 5-channel radio control model airplane system. Each receiver channel provided a 60 cps monophasic square wave output with a 1 msec. pulse duration. Two channels were used as input to a constant current stimulator. Stimulation output from the latter thus consisted of 60 cps biphasic square waves of 1.5 msec. duration in 0.5 sec. trains, and was set to deliver 0.7 milliamperes. Receiver, stimulator and batteries were housed in a standard bakelite circuit box mounted on a backpack vest modified from Cressman and Cadell (8). The collar area of the vest was soaked in 10% quinine solution to discourage the animals biting it. Stimulation was carried from the receiver via a head cable fitted with a male Microdot connector which screwed into nuts embedded in the dental cement. The entire unit weighed 510 gms.

Procedure: The cage interior was equipped with a large purse of banana pellets, a gallon can of water, an artificial "tree" and six other stimulus objects: stuffed toys, wheel castors, sponge and rattle.

Monkeys equipped with the radio-controlled receiver-stimulator backpack were introduced singly into the observation cage. Six 20 minute sessions were given on consecutive days to habituate them to the cage and transfer procedure. Testing consisted of ten 50 minute sessions given at the same time each day. On alternate days starting with day one,

the animals received no stimulation (baseline days). On stimulation days, 5 minute periods of no stimulation (running control periods), beginning with the first 5 minutes, alternated with 5 minute periods during which the animal received programmed trains of constant current stimulation once every 4 seconds. The receiver was checked before and after each session to ensure that it was working. The following behaviors were scored as to their occurrence during 15 second blocks of time:

1. Exploration: self (grooming, licking, scratching); objects (manipulated by hand); cage (picking at walls, climbing).
2. Motor Activity: stereotyped; number of squares crossed.
3. Mirror-Directed Behavior: present, grimace, threat, attack.
4. Mouth Signals: yawning, lip smacking.

Behavioral scores on monkeys alone in the observation cage were tabulated, and the five test samples for each five minute stimulation period were compared with corresponding five minute baseline period samples, using the Mann-Whitney U Test. Similarly, five samples of the alternate five minute "running" control periods in the test sessions were compared to baseline samples.

Results: Three behaviors were significantly altered by non-contingent stimulation of the positive points: exploratory activity, mirror-directed threat behavior, and locomotor activity. Figure 2 shows the mean percent decrease

[Insert Figure 2]

from baseline exploratory activity for four positive points. None of the behaviors changed significantly at the 0.05 level for the fifth point in Monkey T.

For the four positive points, the decrease in exploratory activity was significant at the 0.004 level for stimulus periods and carried over into the running control periods at $p < 0.02$ or better. Locomotor activity was similarly depressed during stimulation periods at the 0.01 level or better for three of these points. It was not significantly changed during running control periods, however. Stimulation of Monkey L at L_6 and L_8 produced a marked increase in mirror-directed threat, but not attack, behavior. Baseline levels of one or two threats per five minute period increased to 30-35 per period during stimulation. There was no increase in threats, however, during alternate running control periods.

Discussion: When monkeys are non-contingently stimulated at positive points while alone in the observation cage, stimulation produced hyperalerting and scanning of the environment while, at the same time, markedly decreasing ongoing exploratory activity. The latter behavior remained low during alternate five minute control periods as well. This long-term quieting effect produced concomittent reduction in locomotor activity. Stimulation of three of the five points produced no new behavior. Stimulation of two points in Monkey L produced a marked increase in mirror-directed threat behavior during stimulation periods, but

this did not carry over into alternate five minute control periods. Though food and water were present, no consummatory responses were elicited at any time.

EXPERIMENT II

Experiment II using the same apparatus as used in Experiment I, tested the effects of stimulating positive points when the implanted monkey was paired with a second monkey. Two normal monkeys, a low-ranking sexually mature female (A) and a subadult fairly high-ranking male (B) were paired in turn with each radio-stimulated monkey. Each pair of animals was given two 50 minute trial periods together to establish baseline dominance relationships and to habituate them to the testing procedures.

Procedure: Test sessions consisted of ten 50 minute sessions given at the same time each day. On alternate days, beginning with day one, the monkey received no stimulation (control days). On stimulation days, five minute periods of stimulation consisting of the above mentioned parameters were given every four seconds. These periods alternated with five minute periods of no stimulation beginning with the first five minutes. Animals were given a five minute "warm up" period together before each scoring session began.

After the above sessions, the monkeys were isolated from one another for 10 days, then reintroduced for one 50 minute session without stimulation. This provided a control measure on whether stimulation-induced changes in the paired

relationships were stable or would revert back to the first control session. After this single session, animal pairs were isolated for 30 days. They were then paired and behaviors again scored for ten 50 minute sessions, but the implanted animals received no stimulation at any time. This baseline measure was instituted after the initial 10 day test sessions, when it became obvious that stimulation-induced behavioral changes in the implanted monkeys were being carried over into the non-stimulation alternate control days of the first period. This baseline measure also controlled for stability of the relationship over time, and for possible behavioral changes due to crowding.

The following behaviors were scored for their occurrence in 15 second blocks of time for either animal against the other:

1. Attack: this includes a running attack whether or not contact was made with the other animal.
2. Threat Behavior: included open-mouthed, head bobbing and perch shaking threats.
3. Active Displacement: instances where the approach of one animal led to the other animal immediately moving away, either voluntarily, or as a result of being overtly threatened, pushed or bitten.
4. Dominance Mounting: mounting which did not involve usual sexual mounting procedures--mounting on the head and shoulders of the other, sitting on the prone animal, and pelvic mounting between males.

5. Sexual Mounting: assumption of full mounting position after which the pairs sat together on the same square of floor for at least 10 seconds of the 15 second period; this generally occurred as a series of 6-10 mountings.
6. Posture: this included both "dominance walking" in which the animal walked stiff-legged with arched back and raised tail (rarely seen), and "passive displacement" in which a particular cage area was rapidly moved into as the other monkey moved away. This latter differs from active displacement in that movement towards the particular area was not begun until the other animal had started to leave.
7. Ignore: ignoring specific threats by the other monkey.
8. Avoidance: looking away or moving slowly away from a threatening monkey.
9. Submissive Presenting: presentation of hind-quarters to the other animal while at a distance of more than two feet, generally combined with tail elevation. Also includes "showing neck" between two females (10).
10. Sexual Presenting: presentation of hindquarters to the other animal while less than two feet away. The tail is generally deviated laterally.

11. Grimace: fear grimace characterized by retraction of lips and cheeks exposing teeth in response to approaches, threats or attacks by the other monkey.
12. Run: rapid fleeing as a result of a threat or attack by the other animal.
13. Paralysis: this term condenses three behaviors--fear paralysis in which an attacked animal freezes and crouches, often defecating; screeches (rare) when struggling to get away ("Eee" in Altmann's terminology (1); and automasochism (shown only by Monkey B) in which the frightened animal rapidly bit his own hands and feet in alternate fashion sometimes accompanied by squeals.
14. Togetherness: the number of minutes in which two animals sat together on the same two foot square.
15. Play: inhibited biting, mouthing, hair pulling displayed only by Monkey L towards Monkey A.
16. Grooming: this and sexual mountings accounted for essentially all of the behavior between animals during periods of being "together" as defined above.

Categories 1-13, with the exception of numbers 5 and 10 (sexual mounting and presenting), comprise an ordinal ranking scale of most dominant to most submissive behavior, with "ignore" (no. 7) being a point of neutrality. The scale condenses one empirically derived by Altmann (1) but contains two items, active and passive displacement taken from Kaufmann's field study (11) of social relations among rhesus males.

Behavioral categories of sexual mounting and presenting, togetherness, and play were considered as indicators of social affinity. The behavioral categories thus represent two multiply-measured dimensions: aggression-fear, and social closeness-distance.

Behavioral scores for each animal in a pair were plotted on the ordinal "aggression-fear" scale, and then analyzed in two ways: for shift in behaviors demonstrated, or for a change in the frequency of given behaviors.

Results: Stimulation at all positive points produced increases in dominance behavior by all three implanted monkeys, irrespective of whether they were paired with an initially more dominant male or submissive female. The increase in dominance was much more marked, however, for pairings with the dominant male, i.e. when the stimulated animal was initially submissive.

In initial pairings with dominant male Monkey B, Monkey T was slightly submissive; Monkey L, moderately submissive; and Monkey N, extremely submissive. Irrespective of this initial degree of submission, stimulation at all positive points led to shifts to dominance behaviors by these animals, and the shifts were all significant at the 0.001 level or better. This was accompanied by significant increases in frequency of behaviors at the dominance end of the scale. When retested 10 days later all relationships had reverted to baseline levels.

Figure 3 shows the analysis for the pairing of Monkey L when stimulated at L_6, with Monkey B. This analysis was

[Insert Figure 3]

carried out for each of the 10 pair relationships. As can be seen from the baseline graph (Figure 3A) Monkey L started out submissive to Monkey B and during the 10 days there was neither a significant shift in distribution of behaviors shown, nor significant increase in their frequency by either animal.

The effect of stimulation on Monkey L over the 10 day test session was to markedly increase his dominance behavior. This is seen in the first three graphs of Figure 3B in which data for the pair are plotted for the first, third and fifth stimulation and alternate control days. Stimulation-induced dominance behavior by Monkey L led to an initial reciprocal increase in frequency of Monkey B's dominance behavior; then after much fighting, Monkey B showed a shift downward into submission. This is shown in two ways. First, when frequency scores for attack and threat behaviors by Monkey L, during either stimulation or alternate control days, were compared against baseline days, using the Mann-Whitney U test, they were significantly increased at $p = 0.05$ or better. Correspondingly, Monkey B showed a significant increase in the more submissive behaviors of ignoring, avoiding, and presenting ($p = 0.05$ or better). Secondly, a shift

in distribution of demonstrated behaviors was analyzed using the 2XC contingency test. This special case of the chi square test shows the significance of category shift over time expressed as z scores. Figure 3C shows that the shift to less fearful (more dominant) behaviors by Monkey L over the ten days was highly significant ($z = 10.52$, $p << 0.0001$), and to submissive behavior by Monkey B, after an initial increase in his dominant behavior ($p < 0.001$). The fourth graph of Figure 3B shows that 10 days later the relationship between this pair had reverted back to baseline. These points are also plotted on Figure 3C.

In initial pairings with female Monkey A, all three implanted monkeys were dominant. Although stimulation at four of the five points produced significant increases ($p = 0.05$ or better) in <u>frequency</u> of threats directed at submissive female A, in these already dominant monkeys stimulation failed to produce significant <u>shifts</u> to more dominant behaviors (e.g. attacks). Furthermore, threat behavior towards the female did not increase during alternate control days, and only in the pairing with female T did the submissive female herself shift to more submissive behavior.

In two of the other four pairings Monkey A actually shifted significantly to less submissive behaviors. Figure 4 graphically summarizes mean behavioral shifts for all

[Insert Figure 4]

five points when the implanted monkeys were paired with a

more dominant or more submissive animal. This graph demonstrates the major finding noted above: expression of dominance behavior induced by stimulation was much more prominent in relationships where the implanted animal was initially submissive.

Baseline social affinity as measured by time together, grooming and sexual mounting, was very infrequent for all pairings of implanted monkeys with male Monkey B, except between Monkey B and female Monkey T. In the latter pairing, as Monkey T evidenced increased dominance behavior with stimulation, the mean time spent grooming with Monkey B decreased from a baseline of 20 minutes per session to six minutes. Sexual mountings by Monkey B decreased from a mean of 12 per session to four.

Of pairings between the three implanted monkeys and female Monkey A, only that of Monkeys L and A produced high baseline sexual mounting and "together" scores. Stimulation of Monkey L at L_6, decreased the mean time spent grooming with Monkey A from 47 minutes to 22 minutes during stimulation sessions only. The mean rate of 33 sexual mountings per session was unchanged. When stimulated at L_8, mean time spent grooming decreased from 43 minutes to 14 minutes per stimulation session and sexual mountings dropped from 32 to three per session. Stimulation at L_{12} again produced a 30% drop in grooming time and 50% decrease in sexual mountings during stimulation sessions only.

Stimulation at all three positive points in Monkey L increased "play" episodes from 0-1 per baseline session to 5-8 per session during both stimulation and alternate control sessions.

In all pairings these social affinity changes were at baseline levels when retested 10 days later.

Discussion: In contrast to the results of Experiment I, when the same monkeys were paired in social relationships, stimulation at all five points appeared to induce a "bias" towards expressing dominant behavior. This was true whether or not the stimulated monkey started out being dominant, slightly submissive, or very submissive to his pair mate. However, expression of dominance was much more marked in relationships where the stimulated monkey was initially subordinate in rank. The decrease in expression of dominance behavior in pairings with a submissive, sexually receptive female tends to go along with the conclusion of Valenstein et al (24) of the "plasticity" of stimulation-induced responses and the idea of Roberts and Carey (21) that the stimulation effect produced a "readiness" or "propensity" to respond which required an appropriate object for its expression. The inhibited aggression or "play" behavior by Monkey L when paired with Monkey A might be considered as occurring because the "stimulus object," Monkey A, was not an appropriate one to aggress against.

Stimulation of these positive points failed to indicate any association between "positivity" and induction of physiological sexual drive. In those pairings where baseline sexual activity was high, stimulation led to a decrease in activity.

Figure 4 should not be construed as strictly representative of the data as z scores are only approximately additive across animals. However, the differential expression of dominance induced by non-contingent stimulation of these points as demonstrated by the difference in pair results, implies that the primary stimulation effect was not induction of aggression. As Altmann (1) has noted, the behavioral rating scale used here clearly contains fearful behaviors at one extreme and aggressive behaviors at the other. However, the series of behaviors from "threat" through "presenting," while containing levels of both fear and aggression, additionally serve as "signal markers" which are used more to communicate the understood relationship to the other animal than to simply express emotion. An hypothesis that the primary effect of stimulation was fear-reduction, not induction of aggression, best fits the fact that an initially very submissive monkey, such as Monkey N, when stimulated and paired with Monkey B, could show a marked shift towards dominance behavior, yet never overtly attack Monkey B.

A number of behavioral observations which do not show in the presented data indicate that the expression of

clearly aggressive behavior appeared to be in response to a dominance "challenge" by the other animal. It was soon evident that, for all animals, the act of sitting on the single elevated perch in the observation cage was an assumption of dominance. Threats to female Monkey A occurred most often when she jumped up on the perch to rest beside the stimulated monkey. Monkey L, no matter which point was stimulated, rarely attacked Monkey B unless the latter was on the perch. Female Monkey T's dominance behavior to Monkey B occurred mainly in two contexts: when Monkey B was on the perch and she was trying to get on it, and just before and after she presented to him, and he sexually mounted her.

EXPERIMENT III

To further study the fear reduction effect noted above, the implanted monkeys were tested in an avoidance conflict paradigm. All three monkeys showed fear when a snake was held near them, as evidencedby a fear grimace, defecation and attempts to flee. This experiment studied possible reduction of this fear by non-contingent stimulation of the positive points.

Apparatus: Test box, restraining chair and stimulation were provided as described in the initial preparation. A 12" x 8" x 5" deep clear plastic box was mounted on a wooden platform and placed in front of the seated monkey. He was able to see the contents of the box and reach into it over the edge, which was at chest level.

Procedure: In the first control condition, the plastic box contained several hundred commercial banana pellets. A test trial consisted of the observer removing the lid for 15 seconds and counting the number of times the monkey reached into the box to obtain pellets, after which the observer replaced the lid for a 15 second interval. Fifteen trials were given in each session. Animals were tested at 2, 24, 48, and 60 hours after eating.

In the second condition exactly the same procedure was used except that for five minutes preceding each test session, the monkey was given brain stimulation at a positive point while he sat in the apparatus. Stimulation consisted of the same 0.5 sec. trains of 60 cps biphasic square wave pulses, each of 1 msec. duration given at 0.7 ma. Scores were obtained at the same deprivation intervals.

In the third condition, no stimulation was given but a 2-1/2 foot California King snake was contained in the plastic box with the banana pellets.

In the last condition brain stimulation, as described above, was given for five minutes preceding each test session, while the monkey sat facing the box containing banana pellets and King snake. Scores were obtained for food deprivation of 2, 24, and 48 hours. At 60 hours, no stimulation was given so as to test for long term effects of fear reduction.

To save wear and tear on the monkeys, the first two test sessions without the snake were done at the same time, in sequence, for each deprivation interval. After a five day reconditioning interval, monkeys were again deprived and tested for the third and fourth conditions with the snake. This was done three times for Monkey L to test his three positive points, and they were tested in the order L_6, L_{12}, L_8.

Results: Table II shows that scores obtained without the snake were not significantly different whether the subject was stimulated or not. However, with the snake

[Insert Table III]

present, condition 3, monkeys rarely reached into the box, often refused to look at it, and struggled to push it away while showing a fear grimace and defecating if the snake moved slightly. Here stimulation produced a slight decrement in avoidance at 24 hours deprivation (condition 4). At 48 hours deprivation, the breakdown of avoidance was complete: for stimulation at all points but L_{12}, "reaching" scores were at the same level as when no snake was present. As a control procedure the monkeys were tested 12 hours later (60 hours) without stimulation; Monkey L continued to show avoidance reduction, the other monkeys did not.

Discussion: The results from this experiment confirm the hypothesis drawn from Experiments I and II, that stimulation of these points was fear-reducing. As noted in the

described procedure, scoring was of number of reaches, not number of pellets consumed. This meant that in control conditions 1 and 2, score values reflected individual "reaching technique" (irrespective of whether a monkey habitually grabbed a few or many pellets at once) and thus were quite insensitive to increasing deprivation conditions. Additionally, scores in condition 2 tended to be lower than in condition 1, since these were done sequentially and the monkey was somewhat sated when the second condition was begun. Lack of results following stimulation at L_{12} may have been due to a technical failure as the cable for this point was later found to be faulty. This could not be retested as the test sequence was L_6, L_{12}, and L_8. Following stimulation at L_8, Monkey L was no longer afraid of the snake. The results show that stimulation was not absolutely fear-reducing since monkeys would not reach into the box unless this stimulation was coupled with some degree of hunger. This would seem to be evidence in favor of the view that stimulation at these points was not itself coupled to specific drives.

CONCLUSION

The experimental results reported here appear to indicate that the positive effects of some hypothalamic points of self-stimulation are involved in the mediation of fear or tension-reduction and not in specific behaviors resulting from physiological drives.

A number of recent studies on the hypothalamus indicate that there are sites which, when stimulated, "bias" various behaviors selectively, and possess many of the motivational properties of physiological drives, yet are not dependent on them. Among these behaviors are eating (13), mating (25), attack (26), and gnawing (21). Stimulation at these points causes the animal to wander aimlessly about unless the appropriate response object is present. Given the appropriate response object, such stimulation can be shown to have motivational properties (13,25). These behaviors are not tied to induction of a specific drive (22), however, and may even compete with it (21).

The present experimental results agree with these studies in demonstrating the biasing effect of hypothalamic stimulation on ongoing behavior. The results extend this biasing concept to include sites of self-stimulation, and indicate that anterior hypothalamic positive points are involved in the evaluation of fear-inducing situations.

SUMMARY

Five self-stimulation sites in three rhesus monkeys were found in the anterior and antero-lateral hypothalamic areas. When the monkeys received telestimulation non-contingently at these points they showed initial behavioral hyperalerting and cessation of ongoing activity, followed by post stimulation decreases in exploratory and locomotor behavior. When paired with a more dominant monkey, non-contingent stimulation caused a marked shift to dominance behavior by the initially submissive implanted monkey. When paired with a submissive monkey, non-contingent stimulation produced much less increase in dominance behavior in the implanted animal. Pairs with initial high scores of social closeness became more distant as the stimulated animal expressed more dominance behavior. Because expression of dominance behavior appeared highly context dependent, it was hypothesized that the primary stimulation effect was fear-reduction, not induction of aggression. Further evidence for this hypothesis was obtained by demonstrating that non-contingent stimulation would reduce snake-induced fear when monkeys were tested in an avoidance-conflict paradigm. Self-stimulation at these points was unchanged by manipulation of food, water, or sex hormone levels and the results reported were not due to post-stimulus seizure activity.

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FIGURE LEGENDS

Figure 1

Each "b" tracing is magnified 2x from whole section "a." Sections 1-3 from Monkeys T, N, and L, respectively, correspond to A 16.0-16.5. Section 4 from monkey L, corresponds to A 13.8. ac: ant. commissure; ah: ant. hypothalamic area; cau: caudate; gp: globus pallidus; lh: lat. hypothalamic area; ot: optic tract; put: putamen; rn: reticular nucleus; so: supraoptic nucleus; v: ventromedial hypothalamic nucleus.

Figure 2

Line graph shows mean decrease in exploratory behavior during 50 minute stimulation session for four of five positive points. Bars on abscissa indicate stimulation time blocks. Bargraph gives mean decrease for all points, all five minute time blocks: S - stimulation, C - alternate control blocks.

Figure 3

Behaviors of Monkey L are plotted in bars above the categories, and those for his pair-mate, Monkey B, in bars below the categories. A. Baseline behaviors for the first, sixth and tenth days of the baseline session. B. In the first three graphs behaviors of Monkeys L and B for a control day (clear bars) are plotted with behaviors of the two animals on the succeeding day when Monkey L was stimulated at L6 (black bars). C_1S_1, C_3S_3, etc.--

first control and stimulation days, third control and stimulation days, etc. The last graph shows the relationship after 10 days without stimulation. *p = 0.05, **p = 0.01. See text. C. Graph of the shift in behavioral categories shown by Monkeys L and B during the 10 day test session in which Monkey L was stimulated at L_6.

Figure 4

Relationship changes resulting from non-contingent positive stimulation. a. mean behavioral shifts for all points when stimulated monkeys were paired with a dominant male. b. mean behavioral shifts when same monkeys were paired with a submissive female. Bars on the abscissa indicate stimulation time blocks.

TABLE I

Monkey	Mean Stimulation Rate Presses/Minute	Range Presses/Minute	Mean Extinction Rate Presses/Minute
N	34	30-35	0.8
T	28	26-34	0.4
L_6	33	29-36	0.4
L_8	32	30-34	0.2
L_{12}	36	32-37	0.8

Mean bar pressing rates determined from eight periods during which the animal was allowed to press 500 times, alternating with eight 10 minute extinction periods.

TABLE II

a. The Effect of Food Deprivation on Positive Self-Stimulation

Monkey Point	2 hr Deprivation rate/min. Mean	Range	24 hr Deprivation rate/min. Mean	Range	48 hr Deprivation rate/min. Mean	Range
N	83	76-90	83	80-88	100	90-107
T	26	24-28	27	24-30	27	25-29
L_6	43	38-48	41	36-44	43	39-47
L_8	42	38-46	36	34-38	42	39-43
L_{12}	34	31-37	36	34-38	38	37-39

b. The Effect of Water Deprivation on Positive Self-Stimulation

Monkey Point	2 hr Deprivation rate/min. Mean	Range	24 hr Deprivation rate/min. Mean	Range	48 hr Deprivation rate/min. Mean	Range
N	96	80-117	86	80-92	84	68-116
T	26	23-28	28	25-30	25	22-28
L_6	51	44-62	48	45-56	42	38-52
L_8	44	41-46	44	42-47	45	42-48
L_{12}	43	40-45	46	43-49	45	39-59

c. The Effect of Castration on Positive Self-Stimulation

Monkey Point	Pre-Castration rate/min. Mean	Range	12 Days Post rate/min. Mean	Range	24 Days Post rate/min. Mean	Range
N	91	83-102	112	108-116	99	92-108
T	28	26-29	26	24-28	27	25-29
L_6	48	46-51	44	39-51	48	45-51
L_8	43	41-44	42	41-44	43	40-46
L_{12}	43	40-45	41	37-44	42	38-44

TABLE III

No Snake

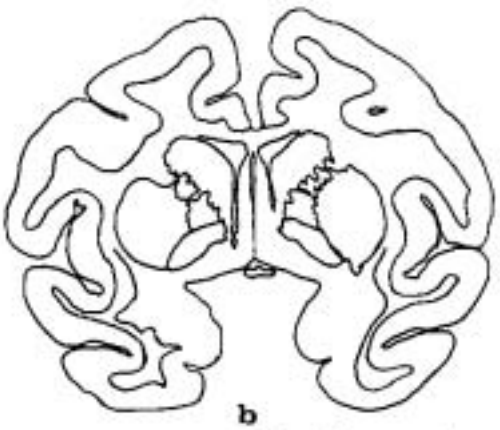
Monkey Point	Condition 1 No Stimulation Deprivation				Condition 2 After 5 Min. Stimulation Deprivation			
	2hr	24hr	48hr	60hr	2hr	24hr	48hr	60hr
T	1	47	34	50	12	40	36	42
N	44	39	36	41	40	43	34	39
L_6	73	77	72	75	68	71	73	65
L_8	71	74	62	70	64	63	60	64
L_{12}	77	76	73	75	72	70	73	73

With Snake

Monkey Point	Condition 3 No Stimulation Deprivation				Condition 4 After 5 Min. Stimulation Deprivation			
	2hr	24hr	48hr	60hr	2hr	24hr	48hr	60hr*
T	0	0	0	1	0	1	30	1
N	1	0	1	2	0	3	24	0
L_6	0	1	0	0	0	18	67	17
L_8	0	0	0	1	0	4	72	13
L_{12}	0	0	2	3	0	1	5	4

*No stimulation given. Last stimulation was at 48 hrs.

1 a



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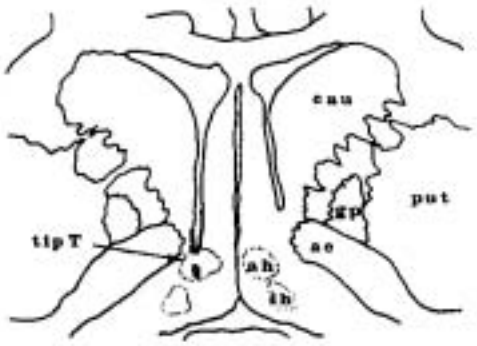

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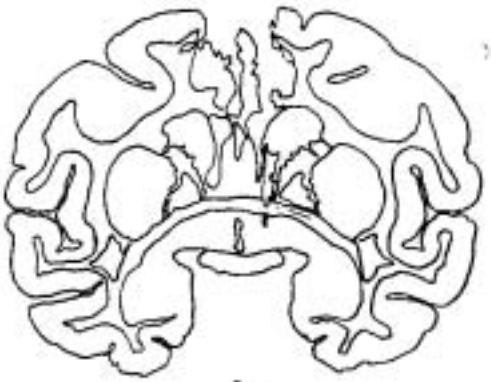

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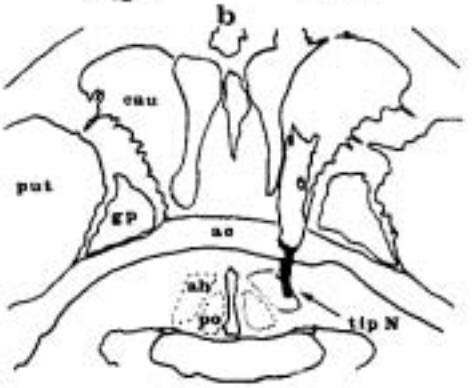

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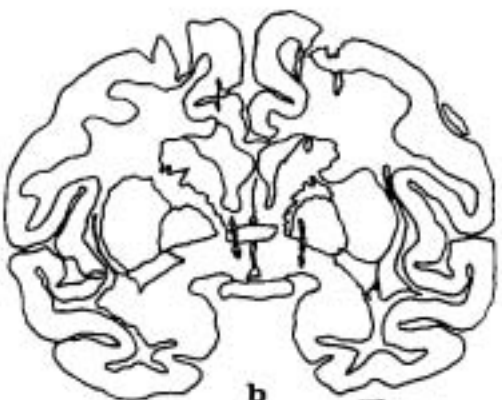

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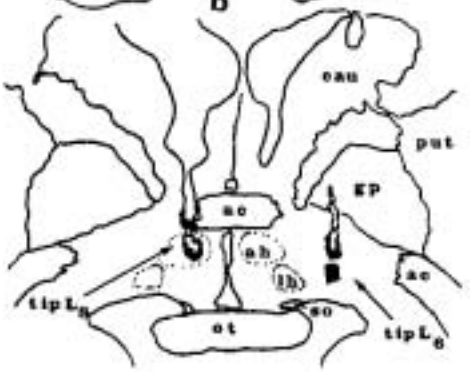

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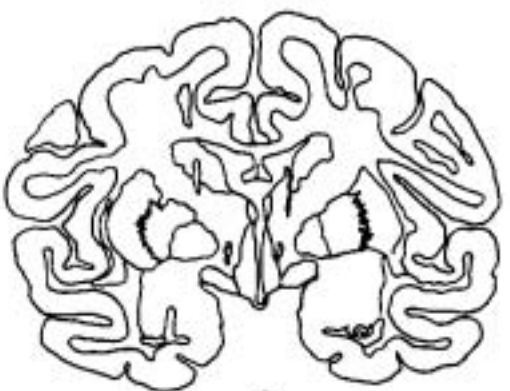

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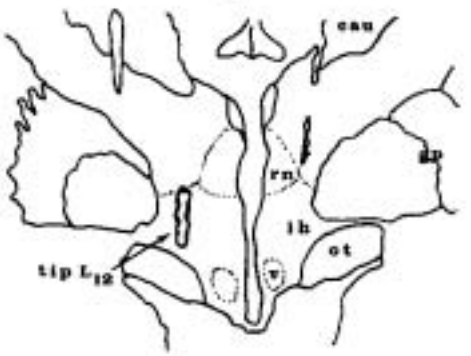
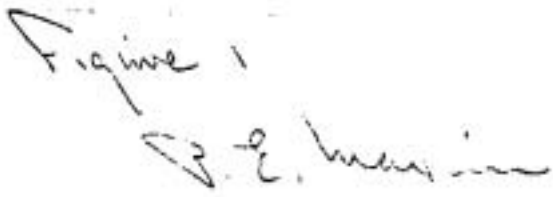


Figure 1



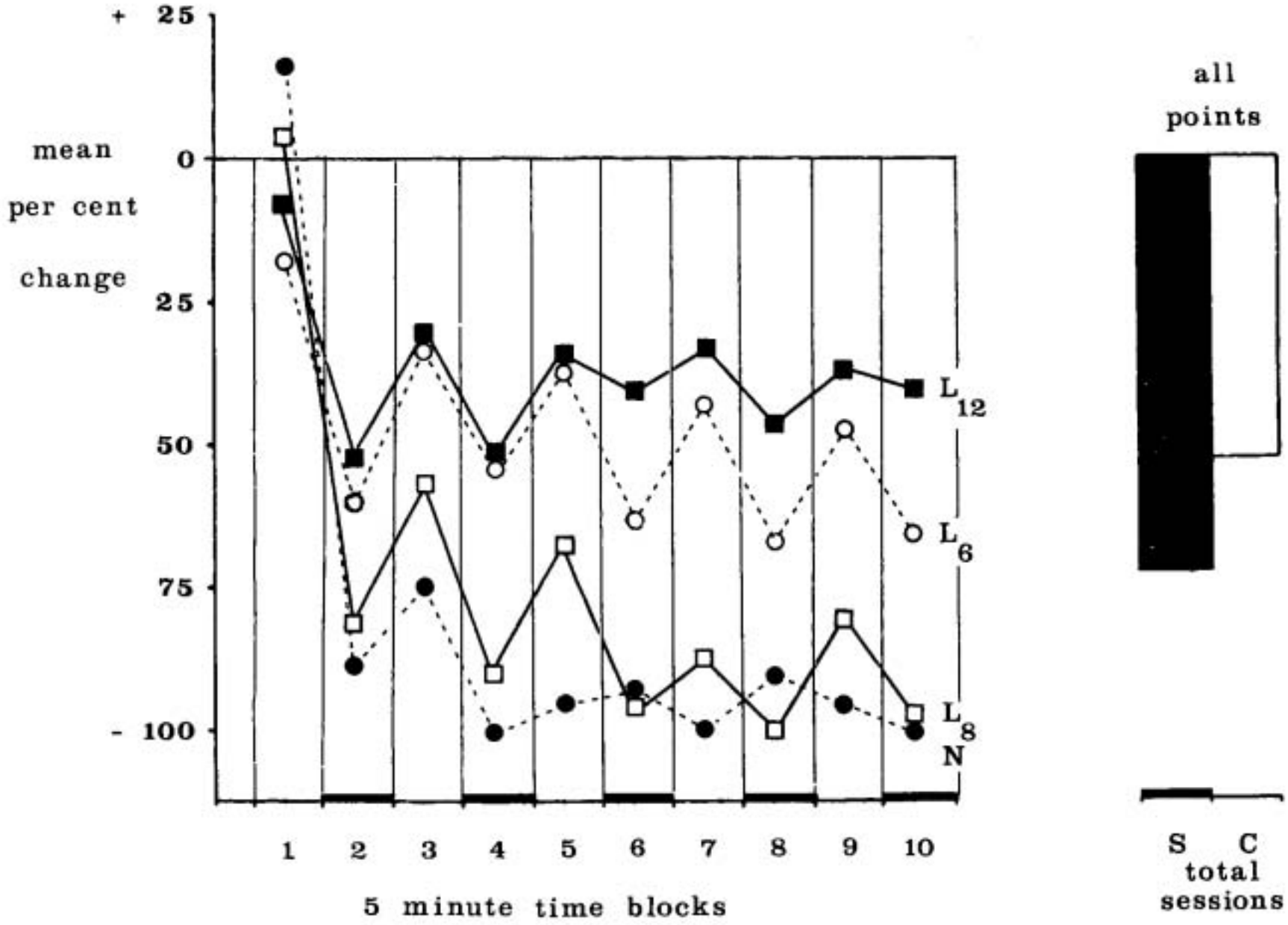
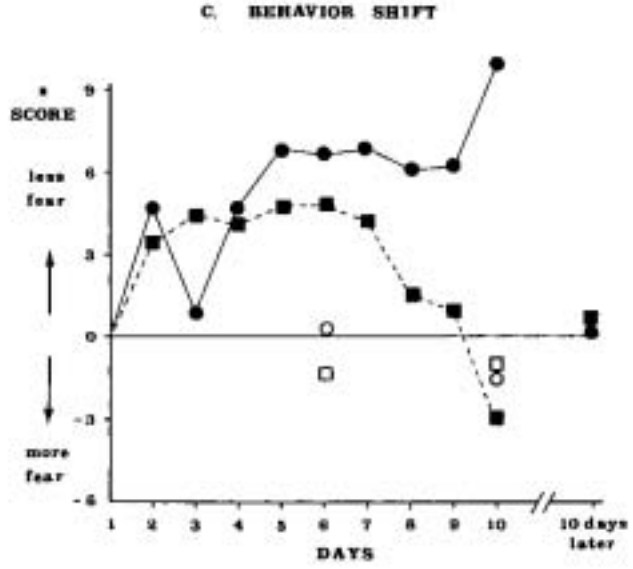

EXPLORATORY BEHAVIOR
+ 25
mean
per cent
change
0
25
50
75
- 100
L12
L6
L8
N
1 2 3 4 5 6 7 8 9 10
5 minute time blocks
all
points
S C
total
sessions

Figure 2

B.E. Maximum


A. BASELINE
attack
threat
displace
mount
posture
ignore
avoid
present
grimace
run
paralysis
L
B
Day 1
6
10


C. BEHAVIOR SHIFT
SCORE
less fear
more fear
DAYS
10 days later

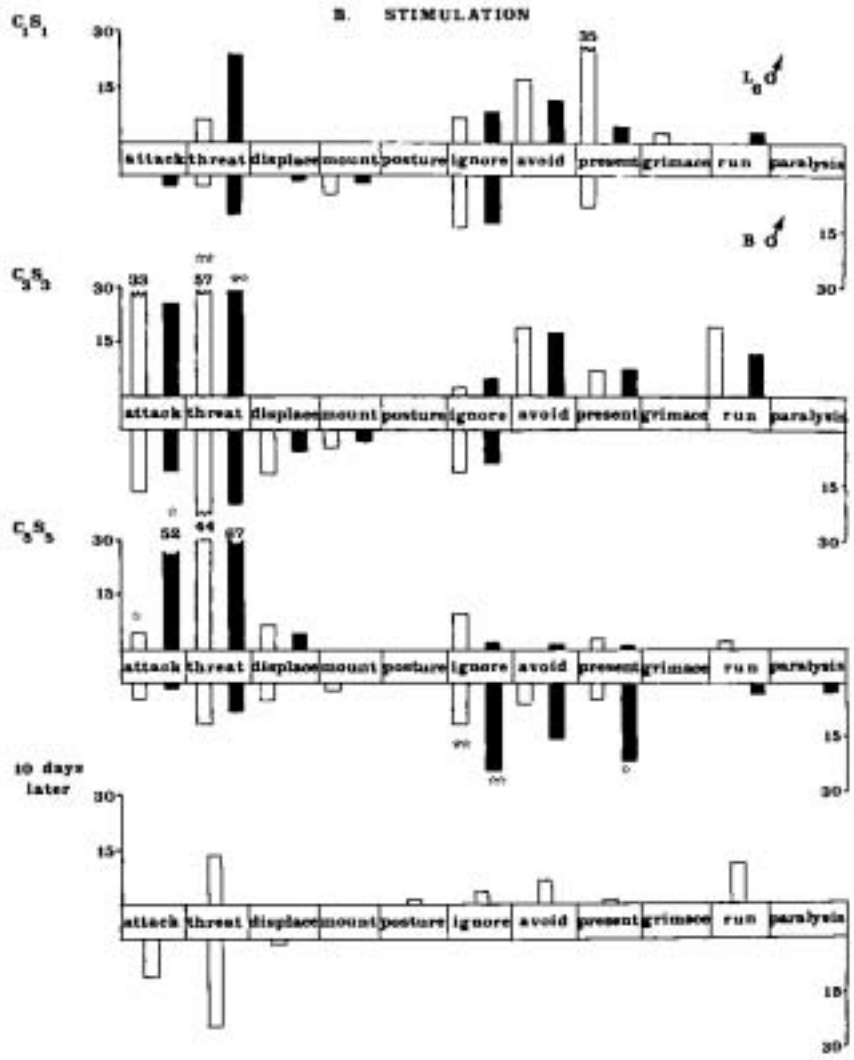

B. STIMULATION
attack
threat
displace
mount
posture
ignore
avoid
present
grimace
run
paralysis
10 days later

Figure 3

R. E. Hughes

Perhaps this should be two figures on facing pages

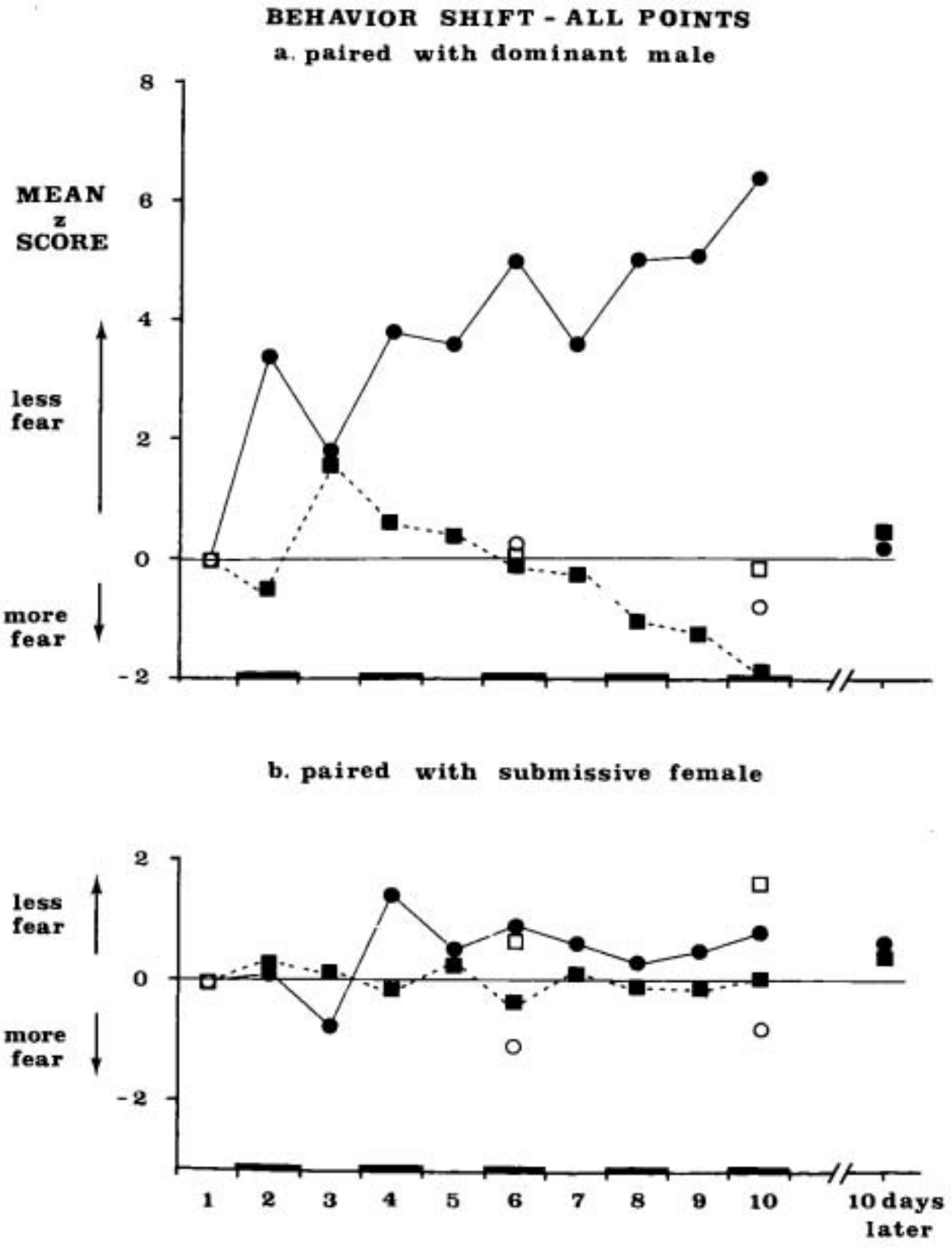

BEHAVIOR SHIFT - ALL POINTS
a. paired with dominant male
MEAN z SCORE
8
6
4
2
0
-2
less fear
more fear
b. paired with submissive female
2
0
-2
less fear
more fear
1
2
3
4
5
6
7
8
9
10
10 days later
DAYS

Figure 4

B. E. Martin