

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

II. Conditioned Visual Performance with Intense White Noise

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(Received April 2, 1973)

Abstract. Feline subjects were trained to respond to a visual signal in the presence of distracting background white noise. The fixed "performance ratio" was measured by varying the intensity of the background white noise. The experimental results indicated that the elimination of the crossed olivo-cochlear bundle resulted in an increase in white noise distraction of the light signal detection task in the cat. Statistical analysis confirmed a significant difference between the experimental and sham groups. The electron microscopic and neurohistological investigations confirmed the disappearance of the efferent nerve endings in the cochlea and that proper midline olivo-cochlear bundle sections had been made. Probably one way in which the crossed olivo-cochlear bundle operates to inhibit acoustic processing is by the activation from a sensory system of a different modality.

Neurophysiological studies of the olivo-cochlear bundle (OCB) after electrical stimulation or interruption of it have been conducted by many investigators. After electrical stimulation of the efferent fibers, many investigators including Galambos (1956, 1960) and Fex (1962) considered the role of this system to be inhibitory in nature, or at least in part.

A study by Pfalz in 1969 on the other hand described absence of function of the crossed OCB under physiological conditions in the guinea pig. In our study (Igarashi et al., 1972)

after transection of crossed OCB, the pure tone threshold (250-14 000 Hz) was not altered, and neither was any change found in the perceptual signal/noise ratio at the levels of 30, 50, and 70 dB above the subject's pure tone threshold. Neuro-histological investigation of the brain stem confirmed that proper surgical lesions had been made in the brain stem. Also, there had been clear degeneration of the efferent nerve endings around the hair cells, especially in the basal coils (electron microscopic investigation). Irvine & Webster (1972), measuring cochlear microphonic and auditory nerve action potentials in unanesthetized cats, concluded that the OCB does not function as a peripheral gating mechanism in the auditory system.

Guzman-Flores & Alcaraz's experiments (1963) showed that lesion of the OCB abolishes the attenuation of cochlear evoked potentials during attentive behavior to a visual stimulus, which suggests that the auditory and visual systems are connected by the OCB.

The present study was conducted in order to examine whether the crossed OCB might be activated by a non-auditory stimulus (i.e., a visual signal) during exposure to intense background white noise. The hypothesis of the investigation is that the OCB plays the role of gating an irrelevant auditory signal when a more significant stimulus is presented.

The present study was supported by the National Institute of Neurological Diseases and Stroke, Grant NS-08589, NO3-NS-38619, and PO1-NS-10940.

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Subjects

Six screened cats were used for the present study. They were clean, healthy, young adult cats (with no preference as to their sex) with no otological disorders. Intact tympanic membranes were revealed by the otoscopic investigation, and also a clean middle ear was confirmed at the time of specimen removal for electron microscopy.

Preoperative procedure

Subjects were screened by an avoidance conditioning method using a cat rotating cage in a sound-proof chamber (IAC 1202). Subjects were required to turn the cage within 5 sec after the presentation of the flashing light signal. A light box was made of plexiglass covered with black paper. The size was 7 cu. inch. A small circular hole (1/2" in diameter) in the front was the only opening of this box not covered with black paper. The box was suspended about 30" from the subject (in the cage) at his head level. The speaker which delivered white noise was installed at a higher level so that the box would not interfere with the noise presentation. White noise (15 dB above 0.0002 dyne/cm²) was constantly used to mask a faint "click" produced by the light. The ambient light intensity of the IAC testing chamber approximated the level of lighting outside the chamber so that light adaptation was not a factor.

The subjects were further trained to rotate the cage while the light signal was on, to a 90% correct response criterion. The training was continued for one week. Then, the intensity of the light was gradually (step-wise) decreased to reach the subjects' positive response thresholds (dimmed light detection threshold). This particular procedure required 2 to 3 weeks. Thereafter, the light intensity was increased up to the 80% correct response level and stabilized at that level which was specific for each subject. Background white noise (500–15 000 Hz) was then introduced and was gradually increased in 5 dB steps until the intensity of white noise was reached at which the subjects responded to the light at only a 50% correct performance ratio

(distraction level). At least six preoperative measurements were obtained.

Surgery

Animals were anesthetized with sodium pentobarbital (30–40 mg/kg body weight). An occipital midline incision was made to expose the posterior portions of the cerebellum and brain stem. The cerebellum was gently displaced upward by a malleable metal retractor. The crossed OCE was cut in the floor of the fourth ventricle with a fine pick. The incision was extended about 2–3 mm, both rostrally and caudally from the 11 mm point anterior to the obex. Three cats were assigned to the transection of the crossed OCB while the other three were randomly used for the sham control operation; exposing the region, retracting the cerebellum, but not sectioning the crossed OCB.

Postoperative procedure

A two-week period was allowed for each subject to recuperate from surgery. Immediately after this period, the dimmed flashing light detection threshold for each subject (experimental and sham) was remeasured. After the animals were able to respond at a mean rate of 80% or greater for four trial days at the initial 80% correct performance rate intensity, the background white noise was introduced. The distraction level was measured according to a method identical to that used preoperatively.

After obtaining sufficient postoperative data, all subjects were sacrificed for the purpose of morphological investigation. After local perfusion with 2% osmium tetroxide solution (Millonig), cochlear specimens were removed and processed according to the standard procedure. Specimens were embedded in Epon and ultrathin sections were cut with a Porter-Blum ultramicrotome. Ultrathin sections were stained with uranyl acetate and lead hydroxide and were studied under a JEM-7 electron microscope. Sections obtained from at least five different areas (from basal and middle turns) of each cochlea were studied.

The surgical area of the brain stem was pre-

pared separately. The serial cross sections of the brain stem were studied after cresylecht-violet, gallocyanine or methylene-blue staining. By this procedure, the depth and extent of the surgical lesions were confirmed.

RESULTS

After the two-week recuperation period, the dimmed flashing light detection threshold for each subject (both in experimental and in sham groups) was remeasured and no change in it was observed. The light intensity level of postoperative 80% correct response for each subject also remained the same. The sham controls required a mean of 6.0 days to reach the criterion (4 days, 80% correct response) while the experimentals, a mean of 9.6 days.

With background white noise introduction, different results were obtained between the experimental and the sham subjects. The animals which belonged to the experimental group postoperatively required less intense white noise to distract them from the 80% correct response level when compared with the preoperative state. At least 72 dB noise (re 0.0002 dyne/cm²) was required to demonstrate noticeably more distraction in experimental cats. All subjects in the sham operation group required slightly higher noise intensity to distract them from the 80% correct response level. The improvement

Table I. This table demonstrates the preoperative and postoperative distracting white noise level of the visual task

The statistically significant difference was found in the required noise level between the experimental (X) and sham (S) groups. See text

Subject	Noise level (dB re. 0.0002 dyne/cm ²)		
	Pre-Op.	Post-Op.	Difference
X	95.5	84.8	-10.7
X	89.0	84.8	-4.2
S	90.0	78.5	-11.5
X	88.0	90.8	+2.8
S	92.0	96.5	+4.5
S	89.0	92.8	+3.8

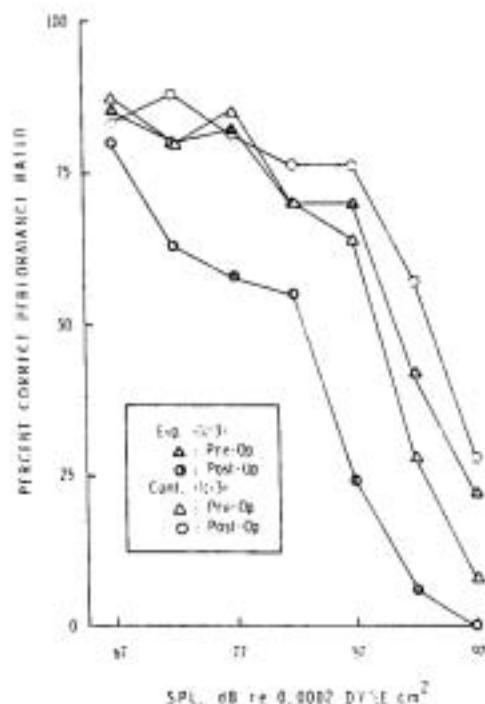


Fig. 1. This graph displays the comparison of the distracting noise level between the averages of experimentals and shams.

in the performance of the sham animals is considered to be due to a training effect.

Table I summarizes the pre- and postoperative results of functional testings. Statistical analysis by *t*-test confirmed a significant difference between the experimental and sham groups ($t=5.30$, $p<0.005$). Therefore, it is suggested from the results that the elimination of the crossed OCB resulted in an increase of white noise distraction of the dimmed flashing light signal detection task in cats. Figure 1 graphically displays that less intense noise distracts visual performance in experimentals postoperatively.

Electron microscopic investigations confirmed the disappearance of the efferent nerve endings around the hair cells, especially the basal coils of the experimental subjects (Fig. 2). Also, the surgical lesions in the brain stems were neuro-histologically confirmed to have been properly made to interrupt the crossed OCB. The midline sections extended about 2.0 mm (both rostrally and caudally) beyond the edges of the facial colliculi (Fig. 3).



Fig. 2. The electronmicrograph demonstrates the disappearance of efferent nerve endings at the inferior portion of the outer hair cells (arrows). A, afferent nerve endings. This specimen was obtained from the upper basal turn $\times 7000$.

DISCUSSION

In 1971 Borg measured the response of the acoustic middle ear reflexes in unanesthetized and unrestrained rabbits. Chronic lesions were made to interrupt the crossed OCB. Only inhibitory influences were found. It was suggested that the inhibitory influences observed may be due mainly to tonic spontaneous activity from the efferent fibers. In an experiment of the cross-modality between middle ear muscles and the visual system, Simmons et al. (1959) trained

feline subjects to expect a loud noise when light appeared. Middle ear muscles were cut on one side. Evidence of successful training was given by demonstrating a conditioned response of the middle ear muscles on the uncut side when the light alone was presented. The experimental results demonstrated that middle ear muscle excitation can be altered by a visual stimulus.

Inasmuch as in the present study the middle ear muscles were not cut, it is not known whether the results obtained are due to the inhibitory

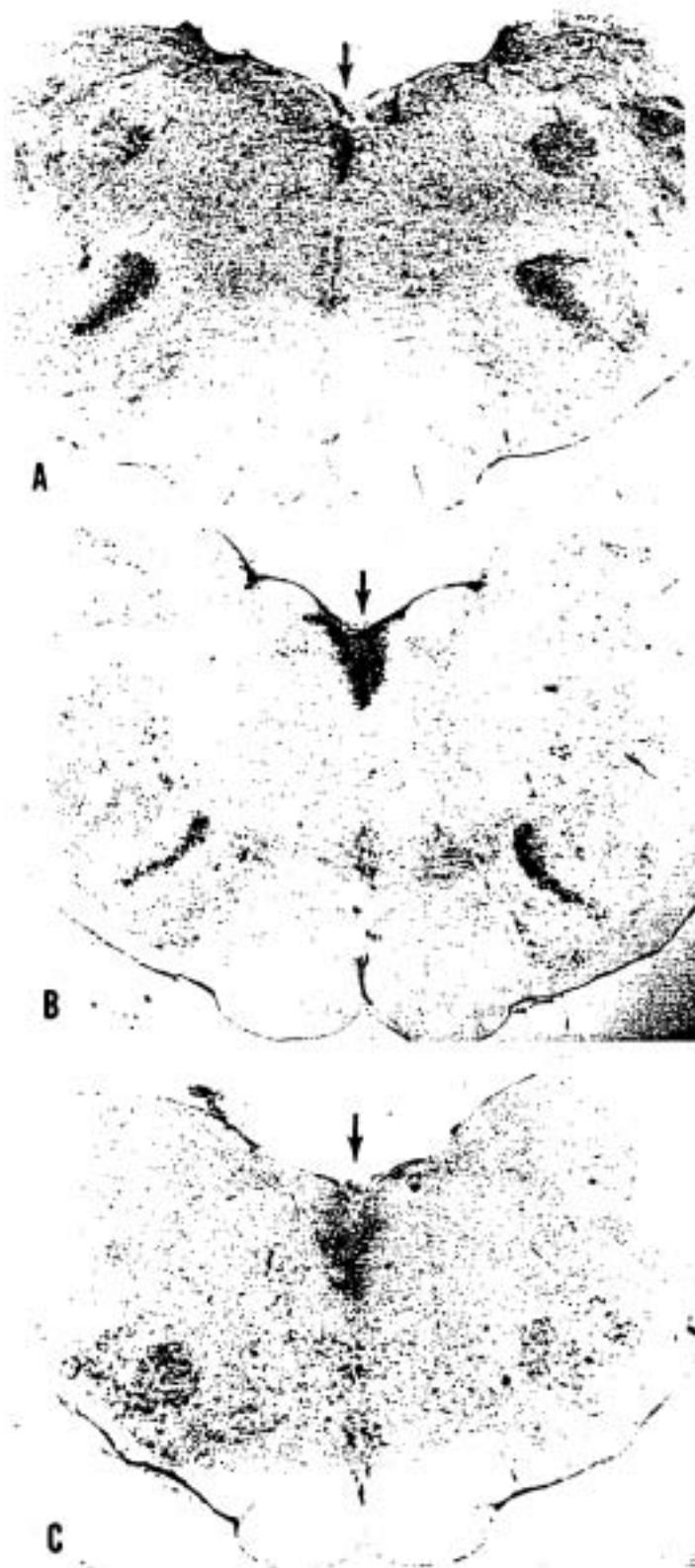


Fig. 3. Three transverse sections of the brain stem demonstrate the rostro-caudal distribution of mid-line cut lesions (arrows). A, about 2 mm rostral to the level of the facial genu. B, at the level of the facial genu. C, about 2 mm caudal to the level of the facial genu. Cresylecht-violet stain. $\times 10$.

mechanism at the peripheral end organ level, or to a functional inhibition at the level of the middle ear muscles. It is noteworthy, however, that in our previous study (Igarashi et al., 1972) with white noise of comparable intensity, no effect was noted after crossed OCB transection upon increased white noise masking. In addition, the existence of olivary complex-cochlear nucleus connections cannot be neglected. In any event, however, it was observed that the midline lesion has some effect when a subject responds to a visual stimulus under an intense background white noise, even though the lesion may affect in an unspecific way in animals' behavioral responses.

Harrison & Irving (1966), after studying the monkey, bat, dolphin, guinea pig, rat, mouse, and hedgehog, described how the medial superior olive appeared to be a part of the auditory system which was in some way related to vision. The medial superior olive was well developed in all diurnal animals and in nocturnal animals with good vision such as cats, and in animals with well developed eyes. The medial superior olive was probably not concerned with auditory localization in the psychophysical sense, but was probably concerned with the movement of the head and eyes in the direction of the sound in space. Thus, this area may be a contact between the auditory and visual systems.

In addition to subcortical connections, connections may exist between visual system and the insular temporal cortex which is suspected as an auditory (integratory) cortex (Desmedt, 1960). In regard to the corticofugal connections, according to Rasmussen (1964), two cortical fiber connections are the corticogeniculate fibers and the fibers to the nuclei of the brachium and the inferior colliculus. Some fibers from the nucleus of the inferior colliculus enter the superior olivary regions; however, the functional significance of these fibers is not known.

In 1959 Hubel and others found that while they were recording unit responses from the auditory cortex in unrestrained and unanesthetized cats, a population of cells appeared to be sensitive only when the subject paid attention

to the tone source. This experimental result very clearly indicated the importance of the functional investigation in unanesthetized subjects, and also suggested that paying attention can evoke or at least assist auditory neural function within a psychobiological unit.

It is known that in higher mammals (cats) the OCB has about 500 fibers which in turn supply 40 000 efferent nerve endings (Spoendlin, 1966). As such, it is suggested that the OCB function, if any, is probably relatively general for the inhibition of auditory input. Probably one way in which the OCB operates to inhibit acoustic processing is by the activation from a sensory system of a different modality.

ACKNOWLEDGMENT

Appreciation is expressed to Mrs M. Lewis, Mrs E. Marbley and Mrs K. Cummings for their technical assistance.

ZUSAMMENFASSUNG

Versuchskatzen wurden trainiert, auf sichtbare Signale zu reagieren, während im Hintergrund ablenkender, weisser Lärm zu hören ist. Das bestimmte Verhältnis ihres Verhaltens wurde durch die Veränderung der Intensität des weissen Lärms im Hintergrund gemessen. Die Versuchsergebnisse bewiesen, dass die Katze ohne das gekreuzte OCB [Olivo-Cochlea-Bündel] durch den weissen Lärm mehr von ihrer Aufgabe abgelenkt wird, auf die Lichtsignale zu reagieren. Eine statistische Analyse durch t-Versuch bestätigte einen bedeutenden Unterschied zwischen Versuchs- und Scheingruppen. Die elektronenmikroskopischen und neurohistologischen Versuche bestätigen das Verschwinden der austragenden Nervenenden in der Cochlea, und dass richtige, mittel-lineare OCB-Sektionen gemacht wurden. Eine Möglichkeit, in welcher das OCB so funktioniert, dass es den Hörprozess kontrolliert, besteht wahrscheinlich in der Aktivierung des OCB durch ein Empfindungssystem mittels eines anderen Verfahrens.

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