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EFFERENT OLIVOCOCHLEAR BUNDLE: SOME RELATIONSHIPS TO STIMULUS DISCRIMINATION IN NOISE

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Efferent Olivocochlear Bundle: Some Relationships to Stimulus Discrimination in Noise[1]

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FROM THE RESULTS of a recent electrophysiological study (8), a function of the crossed olivocochlear bundle (OCB) was postulated, namely the improvement of signal-to-noise ratios at the receptor-element level within the cochlea. By way of recapitulation, it was shown that the equated effects upon the click-evoked eighth nerve action potential produced separately by either noise masking or electrical stimulation of the OCB did not summate when these conditions were delivered simultaneously. Further, those minor additive effects which could be measured decreased progressively as either masking or OCB stimulation was increased in intensity. Other experiments of the study lent added strength and substance to the concept that the OCB, in inhibiting receptor elements of generally lower threshold, was effectively removing them from a pool which would otherwise be available for activation by acoustic stimulation.

Such a mechanism should invariably increase signal-to-noise ratios (7) so long as the signal has access to receptor elements which (via restrictions of either intensity or frequency sensitivity) are unavailable to the influences of noise masking. The present study is a behavioral investigation, the results of which support and extend the earlier findings: monkeys, trained to discriminate between human speech sounds presented in 2,400-Hz low-pass masking noise, were found significantly impaired in their performance following surgical section of the OCB.

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METHODS

Subjects

Four adolescent rhesus monkeys (*Macaca mulatta*) whose weights averaged 3.0 kg were used. They were housed individually in a separate facility and were brought from their home cages to the laboratory for testing at the same time each day. Aside from the food received during testing (Ciba, 190-mg banana-flake pellets), they were fed 8–10 standard-size Purina monkey chow pellets per day after return to the facility, and had access to water at all times in their home cages.

Previous laboratory experience

Prior to the experiments reported here, all of the monkeys had been trained (in the same apparatus) to discriminate between the speech sounds [i] and [u] (6). Retention of this habit was measured following bilateral superficial ablations of the inferotemporal (visual "association") cortex (monkeys *263* and *265*), or superior temporal (auditory "association") cortex (monkey *261*). These animals completely reachieved their preoperative performance levels either immediately (*263* and *265*), or within 13 days of postoperative retraining (*261*). Although histology on the cortical lesions has not yet been completed, visual inspection of the fixed whole brains indicates that lesions are bilaterally symmetrical, confined solely to cortical tissue, and of the areas mentioned above. The remaining monkey of the present study (*264*), had undergone no intervening surgery.

Apparatus and measurement of discrimination

With operant-conditioning techniques, the monkeys were trained to discriminate between the human speech sounds [i] and [u] in a successive, go-left/go-right paradigm. Briefly stated, the monkey, in a special testing cage (Fig. 1), initiated a "trial" by pressing lever X (Fig. 2). This response immediately produced one of the two possible auditory stimuli (each presented 50 times in every 100 trials with neither appearing more than 4 times in succession) for which a press on lever A or lever B was correct and was reinforced with food. A press on the inappropriate panel lever was not reinforced. Any press on levers A or B in the presence of a stimulus immediately terminated that stimulus and produced a time-out of 6 sec: if correct, the houselights dimmed during this period; if incorrect, a total blackout was given. At the end of the 6-sec time-out, the houselights became bright, signaling that a press on lever X would again introduce one of the speech sounds. The basic measurement of discrimination ability was the number of correct responses in a block of 50 trials expressed as a percent.

General procedures

The monkeys were given 50–75 trials/day in a single session on consecutive days, and the noise level at which they could discriminate [i] from [u] (presented at standard and equal intensities) approximately 63.5% of the time was determined. Their ability to discriminate between the stimuli at the 90% correct response level in the absence of

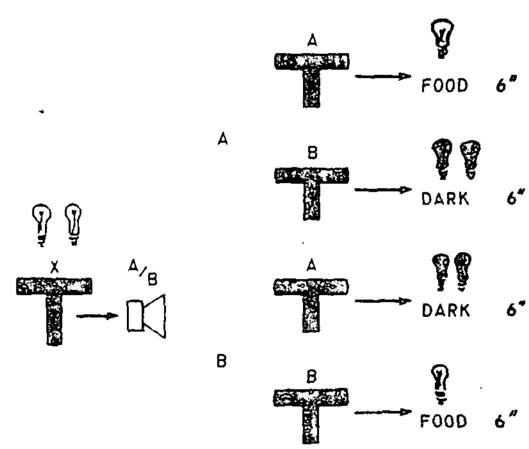

FIG. 2. Testing schedule and contingencies, showing the possibilities for any given discrimination trial. For further details, see text.

noise was repeatedly verified throughout the entire experiment. This was done by interspersing sessions (days) among the experimental sessions in which the stimuli to be discriminated were presented without noise for 50 trials. These sessions not only preceded and followed each pre- and postoperative block of experimental sessions for each animal, they were also given at least once every 3 sessions within that block. Further, immediately prior to and following each 50-trial experimental session, each monkey was required to score either 5-in-a-row correct responses in 5 trials only, or 9 correct responses in 10 trials only (whichever occurred first), in the absence of noise. Failure to meet this particular criterion necessitated a 50-trial "control" session for that day wherein no noise was delivered.

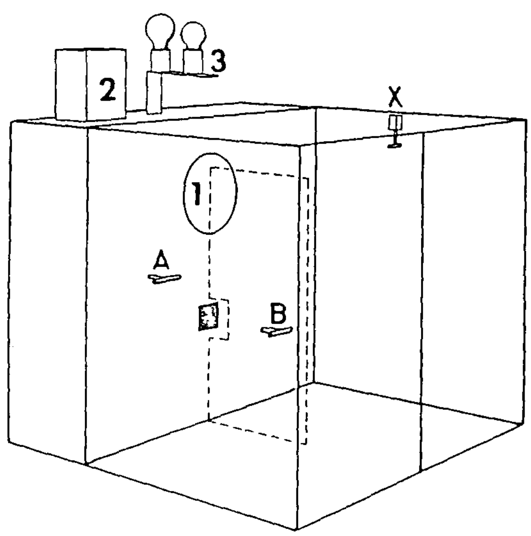

FIG. 1. Testing apparatus. This 24 x 22 x 24 inch wire-mesh cage is completely housed in a sound-shielded audiometric testing booth (Industrial Acoustics Co.). Note the center partition, jutting 12 inches out from the main panel, which gives access to the food well from either side of the cage, yet prevents the animals from pressing levers A and B simultaneously. Levers A, B, and X, loudspeaker, 1, pellet dispenser, 2, and bright and dim houselights, 3, are labeled. From ref. 9a.

Specification of stimuli and of noise

The testing equipment is illustrated by block diagram of Fig. 3. Speech sounds were recorded through separate channels on magnetic tape which was made into loops for playback. Each repetitively presented stimulus was of approximately 300 msec duration with an intervening silent interval of about 300 msec. Figure 4 presents (from one of the tapes used in these experiments) the sound spectrographs of each stimulus and shows *a*) the similar durations, *b*) the similar fundamental frequencies, and *c*) the similar acoustic intensities of each of the speech sounds. Note that the essential spectral difference between them is the region of acoustic energy reinforcement which is present at around 1,000 Hz for [u] and not present for [i].

Broad-band masking noise was produced by a Grason-Stadler noise generator and low-pass filtered at 2,400 Hz by an Allison 2BR filter. This passive network yields a cutoff slope of 30 db/octave outside the half-power point. A Hewlett-Packard 350D attenuator provided 110 db of

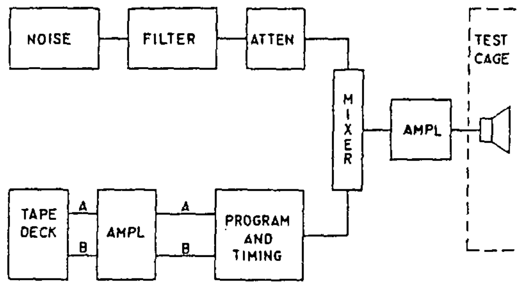

FIG. 3. Block diagram of apparatus used for stimulus discrimination testing in various levels of noise.

attenuation in steps of 1 db. Figure 5 shows the intensity function for this noise in the testing cage measured with a General Radio 1551-B sound level meter (C scale). The microphone was placed in the location normally occupied by the head of the monkey when a press on lever X was emitted. The graph shows acoustic output (ordinate) as a function of noise input determined at the attenuator (abscissa). It also illustrates the ambient noise level recorded in the quiet in the testing cage, as well as the output level of both speech signals (70 $\pm$1.5 db sound pressure level).

Testing method, noise masking, and data analysis

Since the monkeys had been well preconditioned to discriminate reliably at no less than the 90% correct response level, and since "chance" response level in these experiments can readily be demonstrated to be 50% correct, it was reasoned that a point on the performance function somewhere between these levels would be most sensitive in its reflection of change. Weatherill and Levitt (19) have

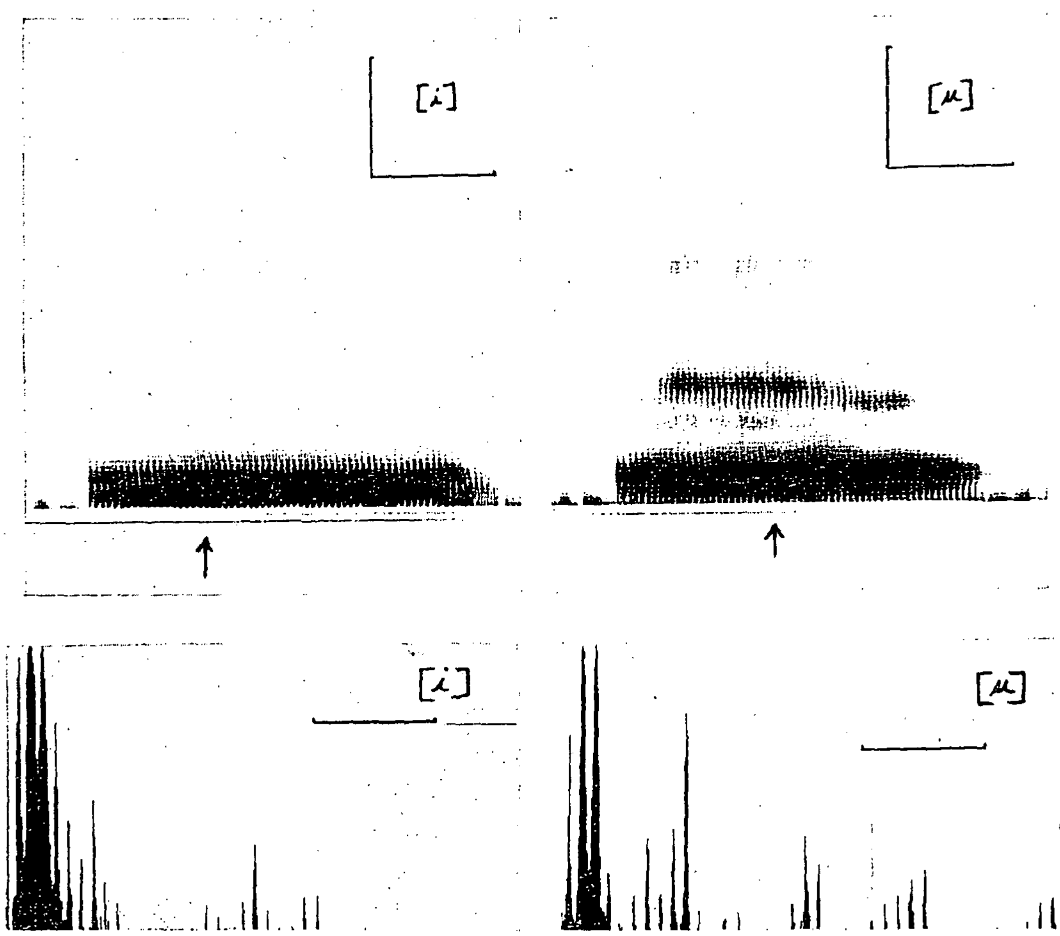

FIG. 4. Sonagrams (upper pair) and spectrographic analyses (lower pair) of the human speech sounds [i] and [u], taken from stimulus tapes used in these experiments. For the sonagrams, frequency in Hertz (44–4,400) on the ordinate, and time on the abscissa. Calibration: 1,000 Hz and 100 msec. Arrows indicate the point in time at which these sounds were spectrographically analyzed (below). For the spectrograms, relative acoustic energy in decibels on the ordinate, and frequency in Hertz (44–4,400) on the abscissa. Calibration: 1,000 Hz.

recently described a method whereby given points on the psychometric function may be estimated. Performance at these levels can be thus "forced" upon the observer through manipulation of the test stimulus through some particular and previously determined sequence. In the present experiments noise masking was the test stimulus and it was varied in intensity, trial by trial, according to the monkeys' speech sound discrimination performance on the previous trial. In this adaptation of the up-and-down transformed response rule (UDTR) to the behavioral testing of animals, masking noise levels were determined in the following manner: *a*) if two correct responses in a row, then increase noise level by 2 db; *b*) if one correct followed by one incorrect response, then decrease noise level by 1 db; or *c*) if one incorrect response, then decrease noise level by 1 db. These three rules may be applied simultaneously for each trial if the response on the previous trial is known. It has been ascertained (19) that this sequence will estimate (or force, in the present study) the 71% point on the psychometric function, but this is true only if the "up changes" are of equal magnitude to the "down changes." In these experiments the monkeys were being pushed harder on the downside (2-db increase in noise level) than on the upside (1-db decrease in noise level), hence the point derived will be lower than 71% yet considerably above chance response level.

With no signals present the masking noise was "just detectable" to 3 human listeners with normal hearing at 80 ± 2 db on the attenuator. Since it was desirable to gather the maximum number of observations in critical noise levels per session, yet also considered less disruptive to performance to approach critical noise levels from below, large (10–25 db) increases in the noise level were made only during the first 10 trials of a session. Within these 10 trials the monkeys would typically score 2-in-a-row correct responses at each of 4 progressively increasing noise levels, e.g., 75, 55, 35, and 25 db on the attenuator (5, 25, 45, and 55 db above detection threshold) and, from that point, would be restricted to the 1- and 2-db adjustments described above for the remaining trials.

Each 50-trial experimental session was characterized by the average setting in decibels on the noise attenuator for trials 41–50. Also noted for the entire session (as well as for the final 10 trials) was the range of noise settings in decibels, and the number of correct discriminatory responses. To evaluate the effects of the lesion, the mean of the attenuator settings (for the last 10 trials) for the 5 consecutive experimental sessions immediately prior to surgery were compared with similarly derived values for the first 5 sessions following surgery.

Criteria for readiness for surgery were *a*) a spread of no more than 4 db in the levels determined over 5 consecutive sessions, *b*) indication of asymptotic

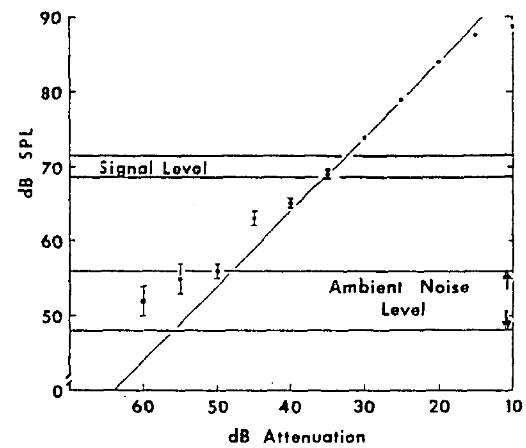

FIG. 5. Intensity function for 2,400-Hz low-pass noise. Output in the testing cage on the ordinate; input at the attenuator on the abscissa.

performance within these 5 sessions, and *c*) demonstration of stimulus discrimination ability at the 90% correct level prior to, following, and during these 5 sessions. For the results reported in this study the difference between the means of the 50 pre- and postoperative noise attenuator settings (trials 41–50, 5 sessions each) was evaluated by *t* test.

Surgery

The monkeys were anesthetized with Nembutal (36 mg/kg, iv) and positioned for surgery lying face downward with their necks flexed at approximately 45°. Approach to the fourth ventricle was made with aseptic procedures through the foramen magnum: the occipital bone was rongeured dorsally to the ventral edge of the transverse sinus, the cerebellar vermis exposed and gently retracted anterodorsally, and a longitudinal cut made on the midline of the floor of the fourth ventricle with a microsurgical scalpel. After the lesion was made, Gelfoam was placed both under and on top of the approximated dural flaps, the muscle and cutaneous layers were sutured, and the monkey allowed 4–7 days for recovery before postoperative testing.

All monkeys recovered well and, after 4–7 days, were indistinguishable from normal animals with regard to motor behavior. During the postoperative recovery, however, all animals exhibited to a greater or lesser degree *a*) general postural unsteadiness, *b*) intention tremor, *c*) past-pointing, *d*) horizontal nystagmus, and *e*) vomiting. These effects were transient and were likely due to the surgical procedure itself, as they were also seen in equal magnitude in an animal whose OCB was completely spared (a sham-operate). Another note-

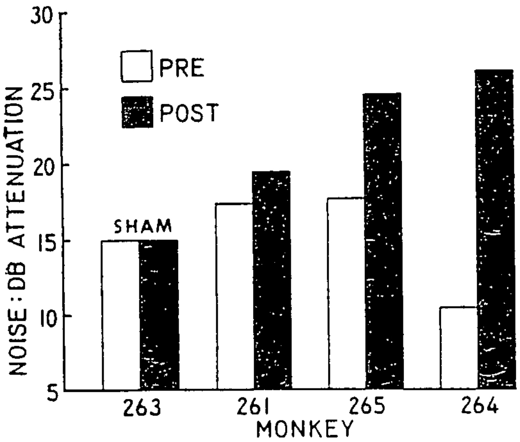

FIG. 6. Discrimination of speech sounds in noise by 3 monkeys prior to and following lesions of the OCB. Monkey *263* was a sham-operate. Most intense noise level is at 5-db attenuation on the ordinate. Height of each bar is the mean noise level attained in trials 41–50 of the five 50-trial experimental sessions given immediately prior to or immediately following surgery. Postoperative means for monkeys *261*, *265*, and *264* differ from their preoperative means at <.002 level of significance (2-tailed *t* test).

worthy, albeit transient, effect was a general bilateral facial paresis: the monkeys were unable to draw back their lips in a characteristic grimace, and the skin below the eyes showed a marked sagging. This effect, absent in the sham-operate and present in the other three monkeys, was considered to be the sign of a lesion appropriately placed in the area of the genua of the seventh cranial nerve.

Histology

The animals were deeply anesthetized and killed by cardiac perfusion with normal saline solution followed by 10% formalin. Their brain stems were coronally sectioned (frozen technique) at 50 μ, and every tenth section was stained for cells with cresyl violet. Additionally, a section immediately adjacent to these was stained for fibers by either Weil method or Sudan black.

RESULTS

Speech sound discrimination in noise

Monkeys deprived by surgical lesion of the normal activity of the OCB show highly significant deficits in their ability to discriminate between complex auditory stimuli in low signal-to-noise ratios. This finding is presented in Fig. 6 which shows the postoperative discrimination performance changes for the three monkeys whose lesions involved the crossed OCB. Figure 7 illustrates typical pre- and postoperative session records for monkey *264*.

It should be kept in mind that postoperative changes are delineated for but one point on the psychometric function, namely, the 63.5% correct response point. This point is completely dependent upon an invariant set of testing rules, must be inferred statistically, and could be specified only at the termination of the experiments. This determination was made by finding the mean percent correct responses for those 50 trials composed of trials 41–50 from the last 5 preoperative sessions for all 4 monkeys (62.5%), and averaging with the similarly derived and insignificantly different postoperative mean percent correct (64.5%).

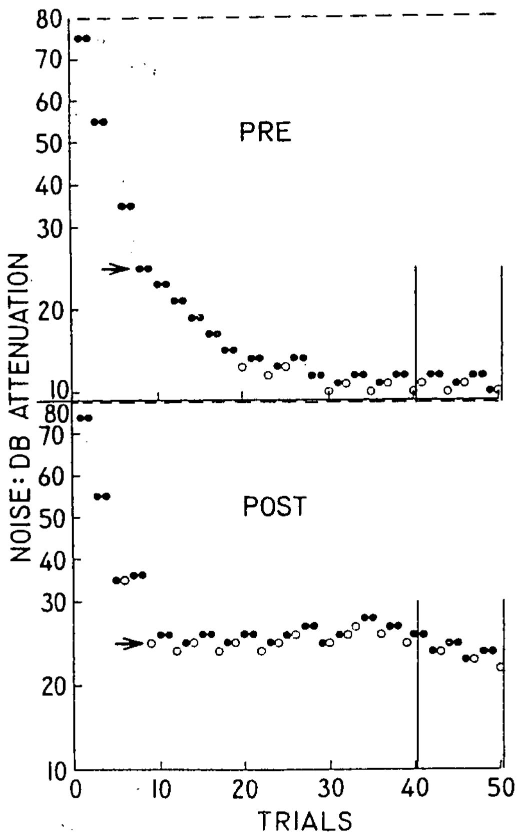

FIG. 7. Performance by monkey *264* prior to and following OCB lesion. Each 50-trial session is the third of the block of 5 sessions: arrows indicate equal starting points (in decibels) on the restricted testing schedule. Dashed lines indicate human detection threshold for the noise: noise is most intense at 10-db levels on the ordinate. *Filled circles*: correct discriminations; *open circles*: incorrect discriminations. Trials 41–50 were statistically analyzed in detail.

Speech sound discrimination without noise

The presence or absence of the OCB exerts no apparent influence on the performance of learned discriminations which involve complex auditory stimuli in high signal-to-noise ratios. Tables 1 and 2 demonstrate that the discrimination ability of all four monkeys remained essentially unchanged after surgery, provided that the stimuli were not embedded in low-pass noise. If all trials entered on both tables are summed, the percent correct response level is found to be 90.7.

Control experiments

Three human listeners with normal hearing were tested under conditions similar to those used in the animal experiments. They were instructed to discriminate (with their heads inside the testing cage) between the speech sounds in noise, using any available cues. Their performance on this task was indistinguishable from that of the animals: the established noise levels were asymptotic at 13, 16, and 17 db on the attenuator, falling easily into the range of 11–18 db determined for the monkeys prior to surgery. These 3 human listeners also served throughout the duration of the experiments as controls for such factors as changes in the fidelity of the taped speech signals; at the slightest suspicion of artifact, the magnetic tapes in use were discarded and new ones substituted. This action, however, was never found necessary during the critical 10 pre- and postoperative sessions for any of the experimental animals.

Preoperative control layoffs of 7 and 10 days (2 monkeys) demonstrated that performance change after surgery could not have been due to testing inactivity per se. Both monkeys performed insignificantly better (i.e., discriminated between stimuli in a higher level of noise) in the sessions following control layoffs.

A further control experiment (done with each of the 4 monkeys), with results more indicative than quantitative, involved pre- and postoperative sessions wherein the noise was set at their "prelevel" (that level derived from the 5 preoperative sessions) for the full 50 trials. The mean preoperative score for these runs was 69% correct, while the mean postoperative score for sessions at prelevel was 57% correct. There were no overlapping scores between these 2 categories in any of the sessions for any of the monkeys. When, following the 5 postoperative sessions, the postlevel had been established, a full session at that level was given and the mean score was 72% correct. Again, there was no overlap between the separate scores of this category with those of the postoperative sessions given at prelevel, although the overlap was extensive between preoperative/prelevel and postoperative/postlevel scores.

It might be argued that the deficit could be due to either *a*) increased distractability or *b*) general loss of motivation, in the presence of higher levels of noise. These possibilities may be ruled out by two lines of evidence. First, direct observation of the monkeys during testing revealed no changes in demeanor which could be attributed to the above behavior patterns. The time taken per session throughout the experiments was remarkably constant for each animal, and food reinforcements were treated with the same apparent relish both prior to and following surgery. Second, sessions were given postoperatively in which the standard masking noise, instead

TABLE 1. *Preoperative trials (% correct) without noise*

Monkey No.	Noise Sessions		Control Sessions (50 trials each)
	Before	After	
263	27/30 (90)	28/33 (85)	138/150 (92)
261	34/37 (92)	47/53 (90)	230/250 (92)
265	65/73 (89)	28/32 (88)	138/150 (92)
264	75/81 (93)	47/51 (92)	137/150 (91)

Numbers in parentheses indicate percent correct response.

TABLE 2. *Postoperative trials (% correct) without noise*

Monkey No.	Noise Sessions		Control Sessions (50 trials each)
	Before	After	
263	27/28 (96)	34/41 (83)	138/150 (92)
261	32/35 (92)	37/44 (84)	180/200 (90)
265	25/25 (100)	35/37 (95)	132/150 (88)
264	47/50 (94)	28/29 (97)	133/150 (89)

Numbers in parentheses indicate percent correct response.

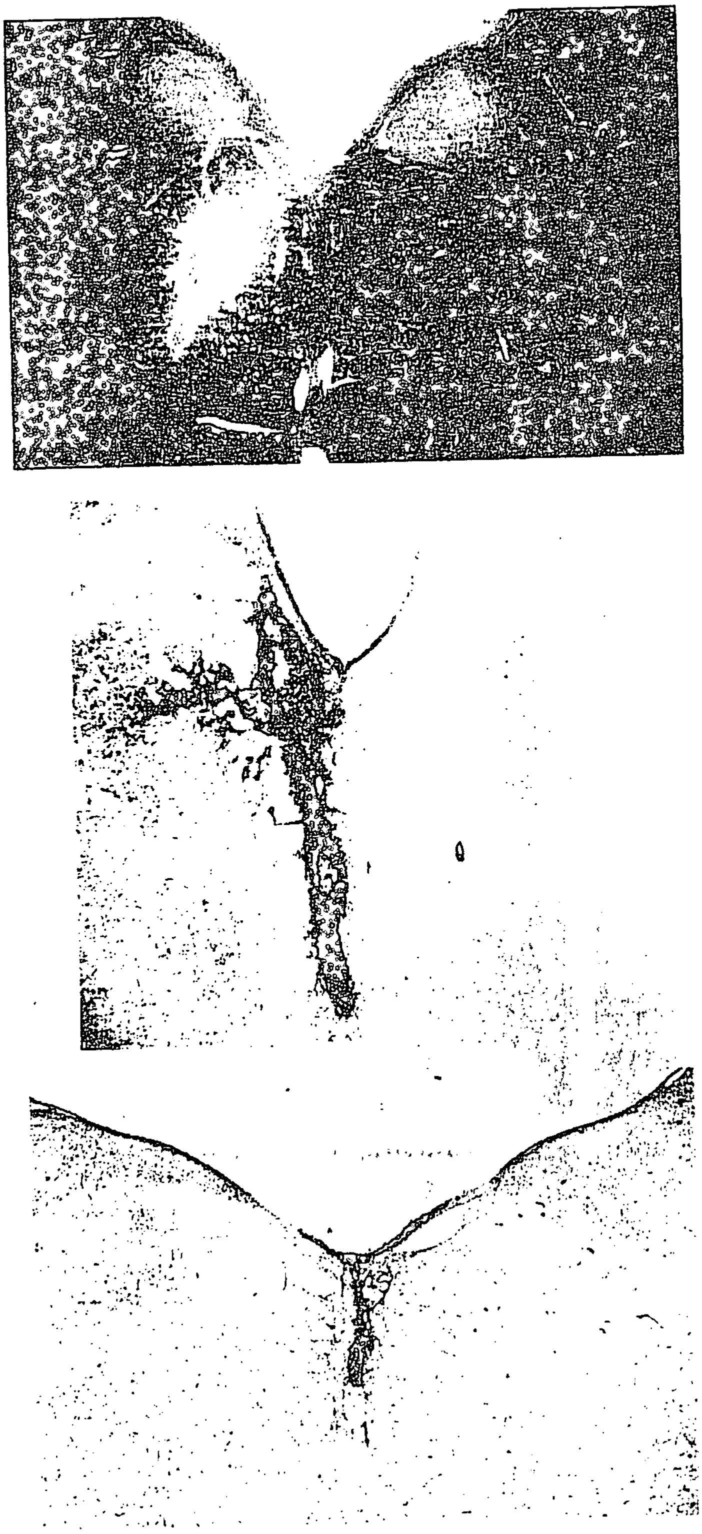

FIG. 8. Photomicrographs of three lesions taken at the level of the facial genua. *Upper*: Weil method, 33×; *middle*: cresyl violet stain, 30×; *lower*: cresyl violet stain, 35×. The animal's identification number and also the approximate A–P stereotaxic coordinate (17) of the section appears to the right of each photomicrograph.

of being low-passed at 2,400 Hz was high-passed at that frequency. The physical intensity of this noise was set equal to the low-pass masker at 83-db sound pressure level in the testing cage, and each monkey was given a full session with each of the two kinds of noise. Without exception, either within or between animals, individual scores for sessions in low-pass noise were far lower than scores for those sessions in which a high-pass masker of equal intensity was used (means: 57% correct versus 85% correct).

Histology

The histological material indicated that appropriately placed (14) lesions existed in monkeys *261*, *264*, and *265*. Furthermore, the brain stem cut in monkey *261* deviated slightly to the left and downward from the midline at the level of the facial genua (Fig. 8). All lesions tended to slant ventrally at their rostral extent such that the end of the scalpel track was found to be 3.5–4.0 mm below the floor of the fourth ventricle. The general spatial relationships of the lesions to the genua of the seventh cranial nerve are depicted schematically in Fig. 9.

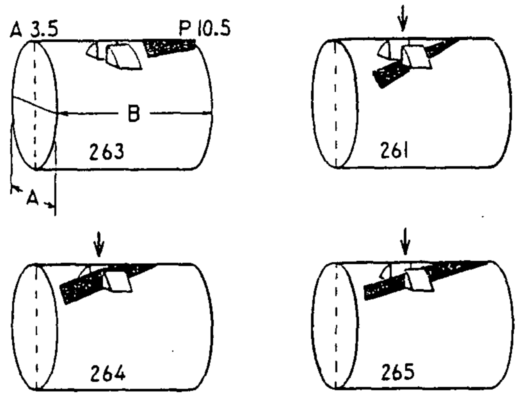

FIG. 9. Schematic diagrams of lesions reconstructed from the histological material. The facial genua, lesions (black bars), and levels at which the photomicrographs of Fig. 8 were taken (arrows), are represented on a standard cylinder whose diameter (A) is 12 mm, and whose length (B) is 14 mm. The A–P stereotaxic coordinates of the brain-stem area enclosed by this cylinder are labeled on the diagram of monkey *263* (a sham-operate).

DISCUSSION

Figure 6 shows that a wide range of values exists both for the original noise levels attained and for the magnitudes of postoperative deficit. Some mention should be made of the interesting relationships between *a*) the preoperative noise level and the fact of prior cortical ablation on the one hand and *b*) the postoperative noise level and the extent of the OCB lesion on the other.

Inspection of Fig. 6 shows that the one monkey with intact cortices (*264*) performed in a more intense preoperative noise level than did the other three animals. In fact, this monkey's level differed more from any of the other three than their levels did from one another. This observation makes it tempting to speculate that lesions of association cortex (or any cortex, for that matter) may render the discrimination of signals in noise more difficult.

A second relationship, that between postoperative level and extent of OCB lesion, may also be observed in Fig. 6. If the lesions of monkeys *264* and *265* are assumed to be complete (and their mean postoperative levels assumed to be essentially equal), then the maximum deficit obtainable under these particular conditions is the 15 db of *264*. It can therefore be further postulated that, but for the prior cortical ablations, the deficits of the other two animals with OCB lesions would have been greater by 6–7 db.

In dealing with signal-to-noise ratios in these experiments, one is bound far more by perceptual factors than by purely acoustical ones. Physically low ratios (as occasioned, for example, by the high-pass, high-intensity noise used as a control) are not necessarily disruptive to perception, regardless of the integrity of the OCB; the frequency characteristics of the stimuli vis-à-vis their noise bed must be specified. Signal-to-noise ratios, therefore, are increased by the OCB primarily when the stimulus and the noise compete for elements whose frequency sensitivities overlap.

Previously published studies of waking animals involving lesions of the OCB have yielded findings which, if not negative (11), are yet impossible to interpret (3). Reasoned speculation has, however, consistently endowed the OCB with a sensory-neural selection (or "gating") function (5, 10, 18, 20). The present study, in accordance with this viewpoint, demonstrates the process of neural sharpening (2, 12). Unlike other instances (1, 16) examined in considerable detail, this activity is probably not mediated via inhibitory mechanisms located exclusively at the periphery. Considerable evidence (4, 9, 13, 15) has accrued suggesting, rather, that it is initiated at the cortex.

SUMMARY

Monkeys, trained to discriminate between human speech sounds presented at 70 db SPL in 2,400 Hz low-pass noise of different intensities, were found significantly impaired in their performance following surgical section of the OCB. There is absolutely no loss in the ability to discriminate between the signals when noise is absent or at low intensity levels. The deficit is related to "perceptual" (as opposed to physical) signal-to-noise ratio: high intensity noise per se is insufficient to cause performance decrement if its passband provides inadequate masking of the speech stimuli (e.g., 2,400 Hz, high-pass). The magnitude of the postoperative deficit is apparently related to the extent of destruction of the fibers of the OCB.

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