Effects of association area lesions on auditory frequency discrimination in cat¹

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Two groups of cats, one normal and one with prior bilateral ablation of cortical association response areas, were trained on two different types of auditory frequency discrimination. Both groups first learned an "absolute" procedure requiring response to a 250 cps tone and no response to a 2000 cps tone. They were then trained on a "repetitive" procedure where the 250 cps tone was presented as an alternation with a continuously repeated 2000 cps tone. The normal group learned both procedures equally well. The lesion group learned the absolute discrimination but were unable to learn the repetitive discrimination. This result is completely opposite to the effects of auditory cortex lesions on frequency discrimination learning.

Bilateral ablation of auditory cortex in cat results in permanent loss of frequency discrimination when the animal must respond to one stimulus complex and withhold response to another (Meyer & Woolsey, 1952; Thompson, 1960) but rapid relearning when the discrimination involves response to change from ongoing background stimulation ("repetitive" method—Butler, Diamond, & Neff, 1957; Thompson, 1960). There are at least two divergent interpretations of these results. Neff (1961) proposed that frequency discrimination is mediated by subcortical portions of the auditory system in the absence of auditory cortex when the repetitive training procedure is used. Alternatively, it has been suggested that nonauditory association response areas of the cerebral cortex may play a special role in frequency discrimination learning with the repetitive procedure (Thompson, 1964, 1965). Bilateral lesions including both auditory cortex and posterior association areas produce permanent loss of repetitive frequency discrimination (Thompson, 1964). However, interpretation of these findings is complicated by possible "mass action" effects of such large lesions. The experiment reported here tests the more specific hypothesis that ablation of association response areas of the cortex will produce selective deficits in repetitive frequency discrimination even when the auditory cortex is intact.

Method

Eight cats were used, four normals and four with bilateral ablations of all association response areas (middle suprasylvian gyrus, anterior lateral gyrus, and pericruciate area) completed at least six months prior to the experiment. Training was shock avoidance conditioning in a Brogden-Culler wheel within a sound-shielded chamber; details of conditioning procedures have been described previously (Thompson,

1960). All animals were given the preliminary training to respond to a light CS. They were then trained on an "absolute" auditory frequency discrimination, followed by training with the same tonal stimuli using the "repetitive" method of stimulus presentation. Tones were 250 cps and 2000 cps with loudness varied randomly over a 25 dB range (mean loudness 65 dB) in both procedures.

In the *absolute* procedure animals were given 10 positive stimuli (2 sec. 250 cps) and 10 negative stimuli (2 sec. 2000 cps) per day to a criterion of 90% correct in a day's session, computed as number of correct responses minus number of responses to the negative stimulus, or for 30 days. The *repetitive* procedure involved responses to two cycles of alternation of a 1 sec. 250 cps tone and a 1 sec. 2000 cps tone (positive stimulus) presented against an ongoing background of on 1 sec. off 1 sec. 2000 cps tone. Animals were given 20 trials of the positive stimulus and 20 mock trials, each consisting of four consecutive presentations of the 2000 cps tone ("negative" stimulus), per day to a criterion of 90% correct response, computed as responses to the positive stimulus minus responses during mock trials, or for 30 days. Following completion of the experiment the lesion animals were sacrificed and the brains sectioned and stained for anatomical study.

Fig. 1. Comparison of mean days and errors to criterion (or for 30 days if criterion was not reached) for normal and operated groups on the absolute and repetitive frequency discrimination procedures.

Results

The normal and operated groups are compared in terms of mean days and errors to criterion on the two auditory frequency discrimination procedures in Fig. 1. Animals that did not reach criterion were included and scored as 30 days and errors in 30 days. In the absolute procedure all normals reached criterion and three of the four operates reached criterion. The groups did not differ in terms of days or errors (days, $t < 1$; errors, $t < 1$). In the subsequent training on the repetitive procedure all normals reached criterion and none of the operates reached criterion. The two groups are thus completely differentiated in terms of the learning criterion. They also differ significantly in terms of errors ($t = 3.71$, $df = 6$, $p < .02$).

Although none of the operates learned the repetitive discrimination to criterion (or in fact came very close to criterion), all four animals performed at better than chance levels. Number of responses to the positive stimulus vs. number of responses during mock trials was compared for each of the last 10 days of training for each animal. All animals made more responses to the positive stimulus on all 10 days ($p < .001$, sign test, for each animal).

The operates failed to learn the repetitive procedure because they made too few responses to the positive stimulus rather than too many responses during mock trials. Operates and normals were compared in terms of mean number of responses per day to the positive stimulus and during mock trials for the last five days of training. Normals made significantly more responses to the positive stimulus than did operates ($\bar{X}_N = 17.4$; $\bar{X}_O = 13.3$; $t = 9.90$, $df = 6$, $p < .001$) but there was no difference in responses during mock trials ($\bar{X}_N = 4.1$; $\bar{X}_O = 4.5$; $t = 1.11$, $df = 6$, not significant).

The lesions removed most cortex of the association response fields, including the middle suprasylvian gyrus, the anterior third of the lateral gyrus, and the upper portions of both banks of the cruciate sulcus. The total amount of cortex ablated by these lesions, incidentally, is approximately the same as in large auditory cortex lesions. The greatest variability occurred at the medial and anterior margins of the pericruciate area, in the depths of the cruciate sulcus, and at the medial margin of the anterior lateral area. In three of the operates there was little undercutting of the auditory cortex and little or no degeneration in the medial geniculate body. However, the animal

who failed to reach criterion on the absolute discrimination sustained extensive undercutting of the right auditory cortex with considerable degeneration of the right medial geniculate body.

Discussion

This experiment demonstrates that cats with prior bilateral ablation of cortical association response areas are able to learn a frequency discrimination involving response to one stimulus and response inhibition to another stimulus (absolute procedure) but are unable to learn a discrimination involving the same tonal stimuli when required to respond in terms of change from ongoing background stimulation (repetitive procedure). Failure to learn the repetitive discrimination is particularly significant because the animals mastered the absolute discrimination before being trained on the repetitive procedure. These results support the view that association response areas of the cerebral cortex may play an important role in the mediation of behavioral response to stimulus change or novelty. Recent evidence (Hoelle, 1966) that lesions of inferior colliculus involving auditory projections to nonspecific systems impair response to change from ongoing background frequency but do not impair differential response to two different frequencies is consistent with this view.

References

- Butler, R. A., Diamond, I. T., & Neff, W. D. Role of auditory cortex in discrimination of changes in frequency. *J. Neurophysiol.*, 1957, 20, 108-120.
- Hoelle, D. F. Behavioral and electrophysiological effects of inferior collicular lesions in the cat. Ph.D. thesis, University of Alabama, 1966.
- Meyer, D. R., & Woolsey, C. N. Effects of localized cortical destruction on auditory discriminative conditioning in cat. *J. Neurophysiol.*, 1952, 15, 149-162.
- Neff, W. D. Neural mechanisms of auditory discrimination. In W. A. Rosenblith (Ed.), *Sensory communication*. New York: Wiley, 1961. Pp. 259-278.
- Thompson, R. F. Function of auditory cortex of cat in frequency discrimination. *J. Neurophysiol.*, 1960, 23, 321-334.
- Thompson, R. F. Role of cortical association fields in auditory frequency discrimination. *J. comp. physiol. Psychol.*, 1964, 57, 335-339.
- Thompson, R. F. The neural basis of stimulus generalization. In D. J. Mostofsky (Ed.), *Stimulus generalization*. Stanford, Calif: Stanford University Press, 1965. Pp. 154-178.

Note

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