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THE AUDITORY DISCRIMINATION BEHAVIOR OF MONKEYS: BRIDGE OR BARRIER

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Jonathan G. Wegener

Center for Neural Sciences

Indiana University

Bloomington, Indiana

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Introduction

Experimental studies of the structure and function of the auditory system have in the past usually used as the objects of investigation animal species below the level of primates. The two animals most frequently used in such studies have been the guinea pig and the domestic cat, with other species being used comparatively infrequently. Another paper read to this gathering summarizes some of the animal data which reinforce and clarify some of the clinical phenomena (7). Increasingly, primates are being used as subjects in studies of normal and impaired discrimination behavior. In the context of the data gathered from experimental studies of audition in sub-primate species, this paper will present some data gathered from the study of normal and brain damaged monkeys. This data can then be evaluated to determine whether it is at variance with data from lower species, is identical to the data from lower animals, narrows some of the gaps between existing animal experimental studies and human clinical observations, or confuses the picture by uncovering, species-specific auditory behavior.

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Naturalistic observers and experimenters agree that monkeys, and probably all primates, are predominantly visual animals. That is to say, their behavior is apparently most directly affected by visual input while input via other sense modalities serves to enhance, varify, or direct attention to sources of, visual information. Observers of primates in their natural environment have also reported on the apparently excellent auditory acuity possessed by monkeys (10). It is with considerable surprise then that the scientist wanting to study audition in primates discovers that they learn laboratory-type auditory discriminations rather slowly. This retarded rate of learning is clear if we compare the learning of visual and auditory discriminations by monkeys, or if we compare the rate of auditory discrimination learning in cats and monkeys (15).

Auditory Discrimination Behavior of Normal Monkeys

Most of the experimental studies of auditory discrimination by the cat have used electric shock reinforcement to motivate learning. There have been comparatively few studies of monkey auditory discrimination behavior using electric shock in the same manner (see 15for a summary, 1,2). Sound localizing behavior in the rat, cat, and monkey has been studied under similar (food) reinforcement conditions. It is clear from a comparison of learning rates by the three species that monkeys learn to make correct sound localizing approach responses much more slowly than cats or even rats (9, 15). It has been suggested that the slow rate of auditory discrimination learning in monkeys is related to a natural aversive reaction to unfamiliar sounds. In the native

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habitat novel sounds usually lead to flight or freezing responses by monkeys. In the usual laboratory discrimination situation the freezing response is the only one available to the animals presented with an unfamiliar sound. This natural freezing response must then be overcome before the monkey can begin performing the experimentally defined correct response to the auditory stimuli. This interpretation of the retarded rate of most auditory discrimination learning by monkeys is supported by studies of the effect of novel and familiar auditory stimuli, on activity level (3); by studies of the comparative ease with which monkeys learn a response which turns off a sound of moderate intensity (5); and the comparative rapidity with which monkeys learn a sound localizing response which requires them to move away from the sound source compared to the rate when monkeys learn to localize a sound by moving toward the sound source (15).

The electrophysiological and anatomical studies of the monkey auditory system are relatively few in number compared to those which have been made of cat (summarized in 16). Both the limits and the organization of the thalamocortical portion of the monkey auditory system are only crudely understood compared to our knowledge of the cat auditory system. However, both anatomical and electrophysiological studies of the monkey auditory system agree that a small area on the superior temporal plane of the Sylvian sulcus is clearly an important part of the cortical auditory area. The degree of involvement in the mediation of auditory input of surrounding cortical areas is not at all clear whether we look to the anatomical, electrophysiological or behavioral studies.

At a conference of this nature such considerations as the learning rate, or of our relative ignorance as just noted might seem out of place, except that we are trying to estimate the usefulness of the infrahuman primate as a subject of auditory investigations. This is not to suggest that the differences to be noted necessarily reflect any new structural or functional differences in the monkey auditory system compared to cat or human. (It has long been known that the thalamocortical portions of the carnivora auditory system are in proportion to the remainder of the thalamus and the cerebral cortex much larger than is the case in primates.) On the other hand it may mask the greater usefulness of the monkey in experimental studies aimed at a better understanding of human auditory disorders. Or it may simply reflect species-specific auditory behaviors which raise new barriers to the attempt to bridge the animal experimentation human clinical gap.

It might be interesting to a group interested in sensory capacity in normal and malfunctioning organisms to briefly summarize some of what is known concerning monkey auditory capacity A now somewhat dated summary was published in 1964 (15, 16). Studies of absolute intensity thresholds in normal monkey reported that up to about 2000 cps, thresholds for humans and monkeys are within ± 5db of each other and between 2000 and 16000 cps monkeys are inferior (9-25 db) to humans. The upper frequency limit for monkey has not been determined, but they are clearly capable of detecting sounds about 30 kc. (1, 2, 11). Apparently there have not been any studies of differential frequency or intensity thresholds in monkeys published to date. Monkeys have been trained to make frequency discriminations (15 summary, 6). Monkeys have been trained to make tonal pattern discriminations approximately as readily as cats when shock motivated (4, 8). Monkeys can also learn to make sound localizing responses in a free field situation, but their performance level at small angles has not been studied as extensively as that of cats and thus their apparently poorer performance is hard to evaluate. Other experiments have shown that monkeys can discriminate an intermittent white noise stimulus from an essentially continuous white noise stimulus (13).

Auditory behavior in brain damaged monkeys

In presenting the data on studies of auditory discrimination in brain-damaged monkeys it is necessary to keep clearly in mind the relative nature of statements concerning capacity losses. Statements about sensory capacity losses must always be qualified by information specifying the type and extent of training. This is especially true when the damage to the sensory system is more centrally located than when peripheral structures are involved (no heart - no circulation; no inner ear - no hearing, etc., but no auditory cortex - under some conditions no normal auditory discrimination behavior).

The studies of the effect of thalamocortical auditory system lesions in monkey have involved only a limited number of auditory discrimination. The effect of temporal lobe lesions on absolute intensity thresholds in monkeys have been only incidentally reported, but point to the probable effect as being negligible (summary 16), reinforcing the data obtained from cat studies. The effect of auditory cortex lesions on tonal pattern discriminations is as severe as that reported for cats with the important qualification that the precise cortical areas responsible for the loss are not as clearly delineated for monkeys (4, 8). Monkeys with total removal of the superior temporal plane focal auditory area exhibit long-lasting deficits in the ability to make intermittent noise discriminations (13).

In the study of sound localizing behavior in the brain-damaged monkeys a number of interesting findings have resulted. (1) When the superior temporal plane focal auditory area is at least 80% removed in both hemispheres, the localization deficits is profound and lasting at angular separations of 180°, 90° 40°, 20°, 10° and 5°. This contrasts somewhat with the results reported for the cat which do not show such a profound deficit for angles larger than 40°. (2) Cortical lesions which include large areas of lateral surface cortex surrounding the Sylvian sulcus do not lead to any greater deficits than those aimed only at the superior temporal plane auditory area. Nor is the extent or density of medial geniculate body degeneration following the more inclusive lesions any greater than in animals with the smaller auditory lesion. (3) When making lesions of the superior temporal plane auditory focus it is almost impossible to do so without damaging lateral surface superior temporal gyrus cortex and/or ventral lateral surface parietal and parietal opercular cortices. When control lesions of surrounding cortex were made, sparing the superior temporal plane, the pattern of behavioral deficits was different. With only the lateral surface of the superior temporal gyrus removed monkeys showed depressed performance levels primarily at the smaller angular separations (20°, 10°, and 5°), but not the profound deficit at all angles found when auditory cortex is removed in addition. However, contrary to the case in animals with superior temporal plane removals, there was no detectable medial geniculate body degeneration. (4) When the lateral surface lesion includes, in addition to the lateral surface superior temporal gyrus, portions of all of the angular gyrus, ventral post central gyrus, marginal gyrus, and anterior superior parietal gyrus the behavioral deficit on sound localization is no greater than those cases in which just the lateral surface superior temporal gyrus was removed, even if the lesion invaded the superior temporal plane and resulted in removal of up to 25% of the focal auditory area. (5) An additional finding may come as a surprise to some, i.e., the consistent impairment of sound localizing behavior exhibited by monkeys with bilateral prefrontal lobe lesions. The frontal auditory deficit seems to be less profound than that following removal of the superior temporal plane auditory cortex. This suggestion arises from the fact that monkeys with frontal lesions show more consistent post operative improvement than do animals with auditory lesions. This improvement is most prominent for angular separations of 180°, 90° and 40° but not for smaller angles when these have been tested. It should be noted that a frontal auditory deficit has been reported for a number of types of discriminations; frequency discriminations, differentiations between chopped noise and steady noise, noise vs. tone, as well as the localization of sound sources (see 16 for review of these studies).

Barriers and Bridges

The scarcity, and comparative difficulty, of anatomical and electrophysiological studies of the monkey auditory system are a real barrier to the most effective use of monkeys as subjects in studies of auditory functioning. There are however a number of laboratories working on some of these problems. The difficulties encountered in training monkeys to make auditory discriminations can be attenuated in several ways. The use of shcok avoidance training techniques appears to speed discrimination learning without changing such critical measures as absolute intensity thresholds (2). The frontal lobe paradox may or may not be a species-specific barrier to the use of monkeys. In a preliminary study of cats trained to discriminate tonal patterns in a shock avoidance situation in our laboratory only one of four animals with bilateral frontal lobe removal showed a significant post-operative deficit. However, the use of shock, may be the significant factor in this study rather than a species difference. Symmes (14) has reported attenuation of the frontal auditory deficit in monkeys when counter shock for incorrect responses was used. The studies of Jerison (4) and Oder (8) also reported fairly rapid learning of auditory discriminations by monkeys in shock avoidance situations.

It is difficult to point to any single finding concerning the auditory discrimination behavior of brain damaged monkeys and say that the monkey findings are more analogous to the human clincial picture than the data from lower species. Symmes (13) reports that brain-damaged monkeys have deficits in the ability to differentiate chopped noise from steady noise which are similar to the results he obtained in humans (12).But this task has not been studied in lower species.

There are three types of discriminations which are clearly affected by bilateral damage to the thalamocortical auditory system of monkeys: (1) the discrimination of tonal patterns; (2) the discrimination of chopped noise from steady noise; and (3) sound localizing behavior. Under more carefully controlled stimulus involving the use of headphones, it should be possible to develop discrimination tasks of the just named type which can be used to study the effect of unilateral lesions, lesions of the inter-hemispheric commissures, and other lesions which will be more similar to the types of damage resulting in human auditory impairment (17). I suspect that monkeys can learn to perform many diagnostic tests currently used with humans - especially those used with pre- or non-languaged children. For a number of these studies we think that data from monkeys will be more useful than that from cats for the understanding of human auditory functioning. We are currently involved in such a program of research.

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