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Lateralization Performance of Squirrel Monkey (*Samiri sciureus*) to Binaural Click Signals

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AN IMPORTANT FUNCTION of the auditory system is to determine the locus of a sound source. Two of the primary acoustic cues for localization are the interaural time difference (Δt) and the interaural intensity difference (ΔI). In man, the presentation through paired earphones of dichotic stimuli having interaural time separations of less than 1 or 2 msec gives rise to a unitary acoustic image localized someplace "within the head." Under these experimental conditions, the assessment of the intracranial position of the acoustic image is a process often referred to as "lateralization" (3). In lateralization experiments, in contrast to localization, it is possible to vary the two interaural cues independently. However, the neural processes involved both in the localization of an external sound source and in the lateralization of an internal image are thought to be similar. Lateralization has been well studied psychophysically in humans (4, 5, 7-10, 13, 18, 19, 21, 23, 27, 30) and neurophysiologically in cats (11, 20, 22, 24), and attempts to correlate the two types of data have been made (11, 22). To avoid such generic differences there is a need for the collection of psychophysical data from animals amenable to neurophysiological study. In the present paper we describe results of psychophysical lateralization experiments in squirrel monkeys using dichotic clicks that can be compared with a companion paper (25) in which single-unit response to the same click signals was obtained in another group of monkeys.

METHODS

Training regimen

Subjects for the study were three male and one female adult squirrel monkeys weighing

500-800 g. Their hearing, as judged from their ability to orient toward low-level sound stimuli in their environment, was apparently normal. Each was trained in the click-lateralization task as follows (details of the training procedure can be obtained from ref 6):

1) The monkeys were habituated to sitting and eating in a restraining chair inside an acoustically sound-treated room and were never fed elsewhere.

2) They were trained to press either the right or left of two levers (Fig. 1) in order to receive a small (0.19 g) banana-flavored food pellet. Each monkey consumed approximately 100 of these nutritionally balanced pellets per day, an amount which adequately supplied his caloric needs.

3) Once lever-trained, each animal, under anesthesia, received a head mount attached to the frontal bone of the skull with dental acrylic. A central screw in this device, when bolted to a frame-supported crossbar on the restraining chair (Fig. 1), restricted movements and allowed reproducible placement of earphones.

4) Each animal was then habituated to pressing the levers and eating while his head was bolted to the crossbar.

5) Each monkey was then taught to press only one lever during the monaural presentation of a train of clicks, and to achieve 85% correct responses in three consecutive sessions. Each session consisted of at least 100 trials. The lever to be pressed was on the same side as the earphone through which the click train was presented. The right-left sequence of stimulus presentation was randomly determined. The correct-lever response terminated the train of clicks and provided a food pellet. An incorrect response turned off the lights in the sound room for 10 sec.

6) Trains of binaural clicks were then presented with varying interaural time and intensity differences. The monkeys' task was to press the lever on the same side to which the earlier or more intense click of the binaural pair was presented. As in the monaural experiment, a correct response provided a food pellet and an incorrect response turned off the sound-

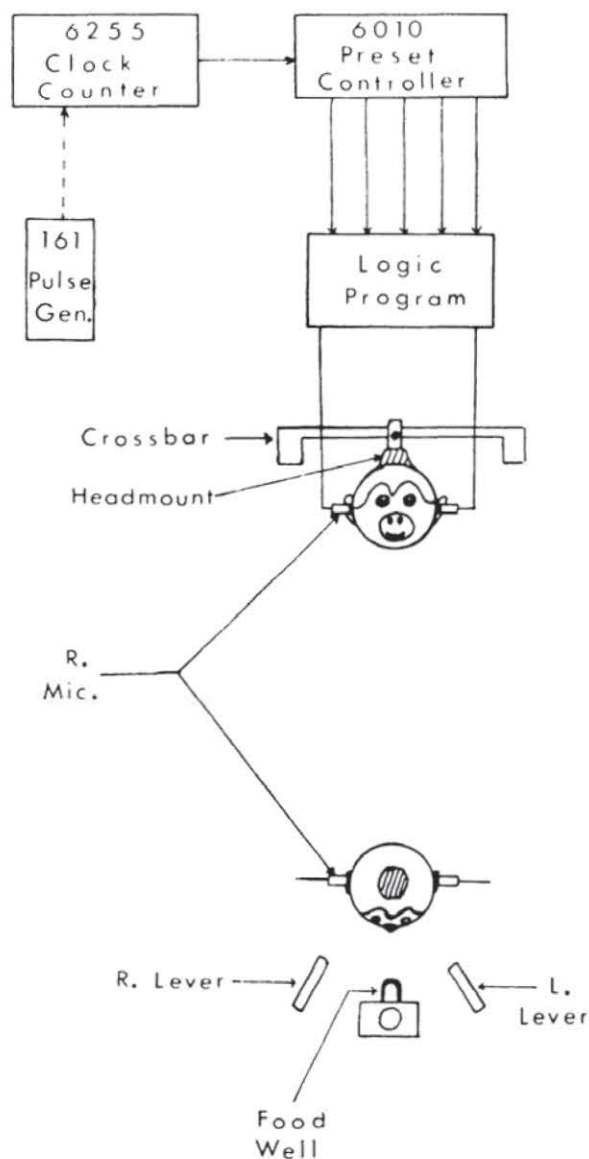


FIG. 1. Schematic drawing of apparatus for behavioral lateralization experiments.

room lights for 10 sec. In presenting these binaural stimuli, the ear that received the initial or the more intense click was randomly determined. The monkeys' response terminated the click train and the trial. In any one session, either a time or an intensity difference was imposed, but never both. Programming equipment (Iconix) was used to present the stimuli, record the responses, and provide the appropriate reinforcements.

Stimuli-control of parameters and method of presentation

The click stimuli were presented at a rate of 32/sec and were produced by applying 250- μ sec pulses to 0.5-inch Bruel and Kjaer condenser microphones (type 4134). The pulses (see Fig.

2C) were monitored on an oscilloscope to allow calibration of the pulse duration and intensity. As shown in Fig. 2, the acoustic outputs of the two microphones, as seen by a 0.25-inch condenser microphone set at a distance of 1.45 mm, are nearly identical. At the maximum applied voltage used in this study (0 dB down), the clicks were approximately 60 dB above the experimenters' threshold.

When the monkey's head was rigidly fixed, the microphones were placed so that the housings were just touching the tragus of each ear (Fig. 1). The microphone carriers were calibrated and their positions in the chair were recorded for each monkey to insure that the microphones would be placed in the same position from session to session.

Experimental procedure

Three lateralization experiments were performed on the monkeys at three intensity levels separated by 10 dB. In the first two experiments data were collected relating the percentage of correct responses to the Δt and ΔI values. In the third experiment, the end point for lateralization was investigated. The end point for

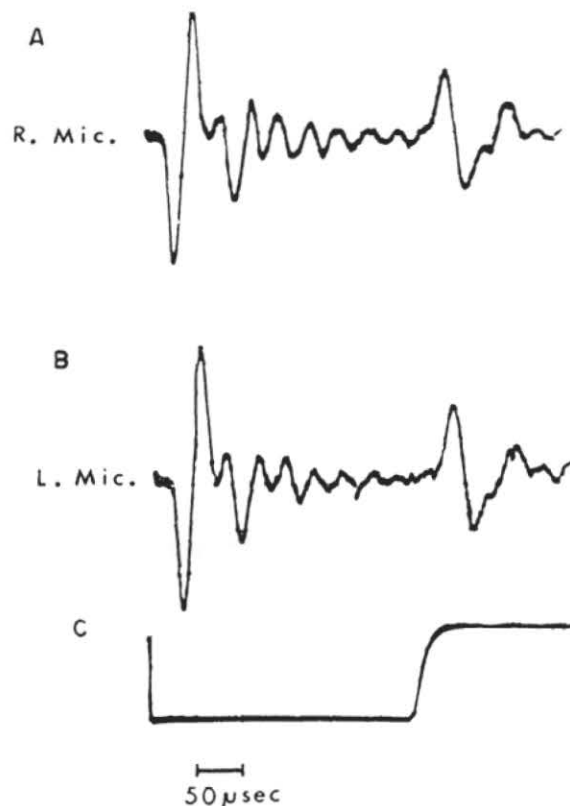


FIG. 2. Acoustic output of waveforms of the two microphones used as earphones and the voltage input waveform. A: acoustic output of right microphone; B: acoustic output of left microphone; C: voltage input waveform.

lateralization is the Δt value at which the unitary image appears to split and the click images are resolved separately in each ear.

For all three experiments, a modified version of Wetherill and Levitt's (29) block up-down method was used to determine the value of Δt and ΔI from trial to trial in each session. In this method, the Δt and ΔI values are ranked to form levels of graded difficulty. With the exception of the end-point study, it was assumed initially that the smaller the Δt and ΔI values, the more difficult it would be for the monkey to make a correct response. A block of trials was presented at the beginning of each session at some low level of difficulty (large Δt or ΔI value) and the monkey's performance over that block was recorded. If his performance exceeded, was exactly at, or was below the predesignated criterion, the succeeding block of trials was presented at a higher, the same, or a lower level of difficulty, respectively. The levels were varied in 20- μ sec, 2-dB, and 500-sec steps for the Δt , ΔI , and the end-point experiments, respectively. Blocks of three to six trials were used. The upper and lower bounds of criterion performance over a block of trials were determined by the formula given by Taylor and Creelman (26). It should be emphasized that the purpose of using a modified block up-down method was to provide a means for gradually approaching the difficult Δt and ΔI levels and not to estimate a point on the psychometric function. The psychometric function is derived by simply calculating the percentage of correct responses at each of the Δt and ΔI values.

RESULTS

Monaural task

All four monkeys learned the monaural task but each required vastly different numbers of sessions and trials (100-200 trials/session) to reach criterion performance. The quickest monkey learned the task within 8 sessions (973 trials), while the slowest monkey required 35 sessions (4,845 trials).

Δt experiments

Criterion performance of 85% correct responses on the Δt lateralization task was achieved at values ranging from 60 to 180 μ sec and varied with the monkey and the intensity level. Figure 3 is a plot of the Δt data from the monkey that performed in the most consistent manner. This monkey reached criterion performance at 60

μ sec, with the highest level of click stimulation used in this study. At a level 20 dB less intense, criterion performance required the use of a larger Δt value somewhere between 80-100 μ sec. Thus, as the overall level of stimulation was increased, the monkey's performance, in general, increased for a given Δt value. All monkeys who performed the Δt task at more than one intensity level demonstrated better performance as the intensity of the clicks was increased over the range of intensities used in this study.

Two-way analysis of variance on the last seven sessions at each intensity level indicated that varying Δt and varying the overall intensity level significantly ($\alpha = 0.05$) affected the correct-response probabilities. Moreover, it was found that 20- μ sec steps were marginal, and 40- μ sec steps were usually sufficient to significantly affect the response probabilities with cofactors being the individual monkey and the overall intensity level. It should be noted that the significant effects are restricted to Δt values, which are not in the asymptotic region of the functions. As an overall comparison, Fig. 4 is presented to show the Δt data for all four monkeys at one intensity level (0 dB down for three monkeys and -10 dB down for the fourth monkey).

ΔI experiments

Figure 5 is a plot of the percentage of correct lateralization as a function of ΔI and overall intensity level over the last seven sessions for the same monkey whose Δt data were presented in Fig. 3. Her per-

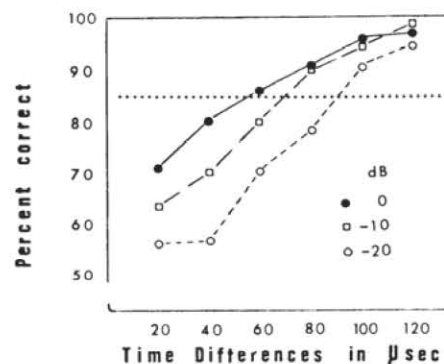


FIG. 3. Percentage correct lateral judgments as function of Δt at three intensity levels for monkey E.

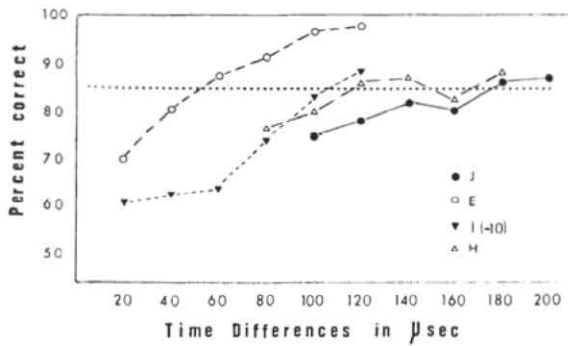


FIG. 4. Percentage correct lateral judgments as a function of Δt for the four monkeys at one intensity level (0 dB except monkey I).

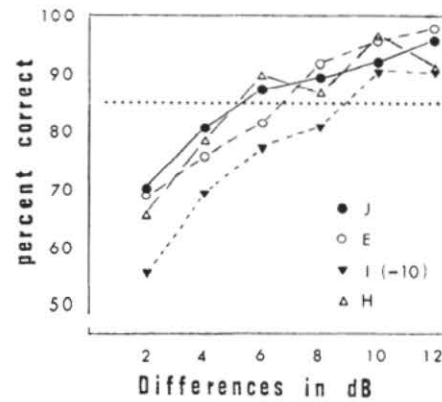


FIG. 6. Percentage correct lateral judgments as a function of ΔI for the four monkeys at one intensity (0 dB except monkey I).

formance was the best and most consistent of all the monkeys. Generally, all four monkeys reached criterion of 85% correct responses at a ΔI value between 6 and 10 dB, and 2-dB steps were sufficiently large to affect the response probabilities. Results of an analysis of variance test indicated that there was no significant effect of click intensity on lateralization performance based on ΔI . Thus, there appears to be a differential effect of changes in intensity level on lateralization performance based on interaural time as opposed to interaural intensity disparities. Figure 6 is a combined plot of the ΔI data for the four monkeys at one intensity level. In comparing Fig. 6 with Fig. 4, it would appear that performance is much more consistent for all monkeys in the ΔI than in the Δt experiments.

Trend analysis on the main effect of varying Δt or ΔI indicated that a linear component was significant, and that a linear function accounted for more than 90% of the variation.

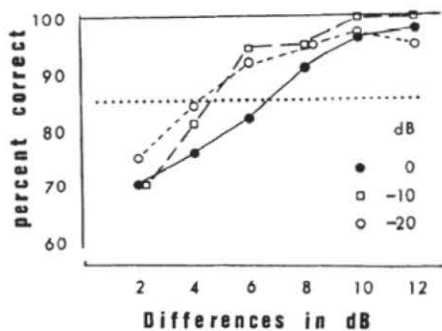


FIG. 5. Percentage correct lateral judgments as a function of ΔI at three intensity levels for monkey E.

Percentage of responses to right as a function of Δt and ΔI

The foregoing data have been presented in terms of percentage correct as a function of Δt and ΔI . The data are presented in a slightly different manner in Fig. 7

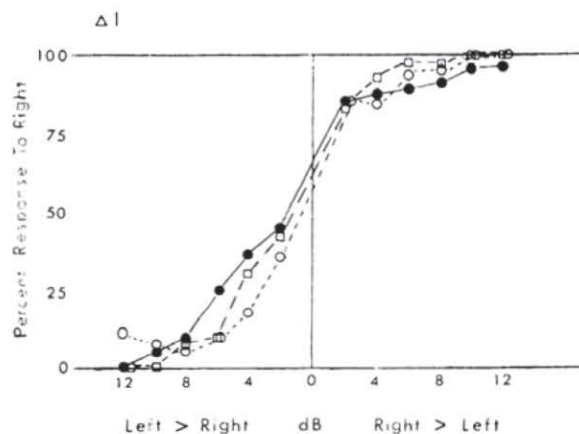
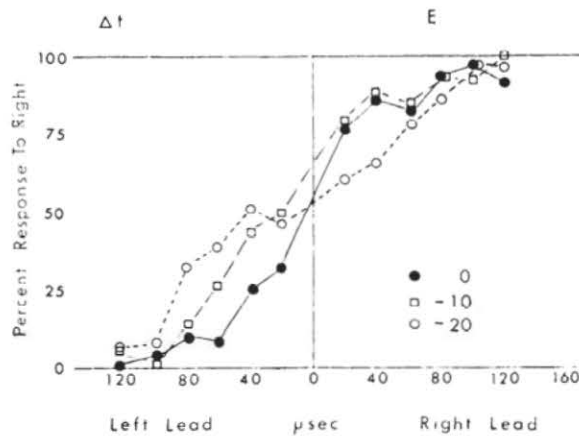


FIG. 7. Percentage responses to the right lever as a function of Δt (top) and ΔI (bottom) for monkey E at three intensity levels.

in order to reveal some characteristics about responses and errors. The upper graph is a plot of the percentage of responses to the right lever as a function of Δt , and in the lower graph as a function of ΔI . It will be noted that there is a slight bias to the right. That is, at any of the three intensity levels, there is a tendency for the monkey to make more responses to the right lever at small Δt and ΔI values, even when the click stimuli to the left ear led in time or were of greater intensity. Three of the four monkeys exhibited a right-lever bias, while the other monkey showed a left-lever bias. The response bias may be due to the fact that the monkeys actually perceived the image on the right side, or the task became difficult with the small (Δt and ΔI) values and the monkeys developed a lever preference. Our results cannot distinguish between these two possibilities. Now, as the overall level of the clicks was decreased, there was an increase in responses to the right lever for left-leading stimuli. This increase in responses to the right lever with changes in intensity was not as striking in the ΔI data. Thus, there appears to be little change in the functions when intensity level is varied for the ΔI task but marked changes for the Δt task.

Lateralization end-point experiments

The initial block of trials was presented at a Δt value of 500 μsec and if criterion performance occurred, the Δt value was increased by another 500 μsec . An example of the end-point data is shown in Fig. 8.

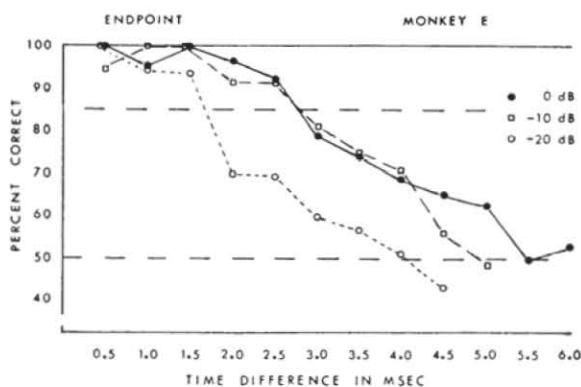


FIG. 8. Lateralization end-point experiment. Percentage correct responses as a function of Δt at three intensity levels for monkey E.

For the three monkeys who performed this end-point task, performance fell below criterion at Δt values between 2 to 3 msec. In Fig. 8 it will appear that decreasing the intensity by 10 dB had no effect on performance when compared to the 0-dB level. However, reducing the intensity another 10 dB (-20 -dB level) caused a statistically significant decrease in correct responses resulting in the end point for lateralization being reached at a smaller Δt value. Not all monkeys demonstrated a clear change in performance on the end-point lateralization task with changes in intensity.

Generalization of localizing stimuli

A basic assumption of this study is that the monkeys used the sidedness or laterality of the acoustic image as the primary cue for performance. If the assumption were correct, the monkeys should generalize to a localization task in which trains of clicks are presented free field through speakers (Altec 802D) to the right or left. A generalization test was performed on two monkeys. The speakers were placed at approximately 90° and 270° azimuths at a distance of about 50 cm. The generalization test consisted of either presenting the click stimuli through earphones at a Δt value which the monkey had performed at least at criterion or through one of the two free-field speakers. For example, for monkey E the first 10 trials were presented through the earphones at a Δt value of 120 μsec . The ear which received the earlier click was randomly determined. In trials 11 through 35 the trains of clicks were presented through one of the free-field speakers selected in random sequence. For trials 36-49 the stimuli were again presented through the earphones at a Δt value of 120 μsec , and from trials 50-62 the clicks were switched back to the speakers.

Monkey E responded correctly to every trial in the sequence. It was further noted that the response to the first trial after each of the four transitions was not abnormal with respect to response time. It appeared that this monkey generalized to the localization task very well, supporting the notion that laterality of the acoustic

stimuli was the primary cue used in the lateralization experiments. The second monkey (*monkey J*) did not generalize immediately but did learn the localization task within 50 trials. However, his data, as will be discussed later, must be interpreted with caution since he incurred an extensive neural lesion.

DISCUSSION

The present experiments show that squirrel monkeys can successfully perform a dichotic lateralization task using interaural time or intensity differences. Criterion performance (85% correct judgments) was achieved at Δt values of 60-180 μsec and ΔI values of 6-10 dB.

Lateralization experiments in nonhumans are virtually nonexistent with the exception of a series of studies in cats by Masterton and co-workers (14, 16, 17) in which lateralization and its impairment following transection or ablation of various auditory structures were investigated. The cats were taught to generalize from a monaural click train to a binaural one with a large Δt of 500 μsec . Using a shock-avoidance technique and a flexible leather helmet to house hearing-aid earphones, they found that the threshold for lateralization (above chance performance) for normals averaged less than 50 μsec . No one has reported behavioral lateralization thresholds in monkeys. In human, Walsh (28) used the same stimulus-response paradigm as in the present experiment by having his subjects indicate whether the intracranial image was to the right or to the left. He reported that normal humans could seldom achieve 75% correct at Δt values smaller than 70 μsec . However, Deatherage (4) states that humans can respond to binaural time differences of 10 μsec . Observation from pilot work of the present authors indicates that humans frequently achieve 75% correct at 20 μsec and above chance at 10 μsec , but require time separations of 30-50 μsec to achieve 85% correct. It is seen in Fig. 3 that for one intensity, criterion was achieved at less than 60 μsec . Thus, the ability of squirrel monkeys to lateralize an intracranial image is close to the performance of humans on the same task. The differences that do exist may reflect

the arduous experimental conditions to which the monkeys were exposed, the differences in one or more of the stimulus parameters (i.e., intensity level), and/or the questionable reinforcing value of the food reward employed.

The notion, derived from both human psychophysical (19, 30) and single-unit studies in animals (2), that interaural time and interaural intensity parameters are processed differently by the nervous system receives support from three results of the present experiments. First, the more consistent performance of monkeys presented with interaural intensity differences (see Figs. 4 and 6) may reflect the fact that interaural time differences are minimized in an animal with such a small head size, and interaural intensity differences are maximized for animals with such high-frequency sensitivity (15). Second, the fact that overall click level importantly affected lateralization judgments based on interaural time differences only (Figs. 3 and 5) is to be correlated with the single unit results described in the companion paper (see Fig. 10 in ref 25) in which click intensity affected Δt sensitivity to a much greater extent than ΔI sensitivity. And third, *monkey J*, whose left brain was atrophic at autopsy, performed the ΔI task normally and the Δt task poorly. The lesion was inadvertently produced when the head mount was implanted, and was primarily subcortical, particularly affecting the basal ganglia and internal capsule. The etiology of the lesion has not yet been established but appears compatible with a circulatory disturbance in the left hemisphere. The monkey showed the following symptoms after his lesion: 1) paralysis of the right; 2) inability to localize tactile stimuli on the right; 3) inattention to the right spatial field, and 4) localization of external sounds to the left, that is, turning to the left when attempting to orient to any intense environmental sound. Heilman et al. (12) described similar symptoms in monkeys following ablation of the temporal-parietal cortex of one side. All of these symptoms disappeared within 2 months except for a residual slight paresis on the right that affected the use of the right hand. He adapted well to the training procedure

and used his left hand to press the right and left levers. He performed poorly on the Δt lateralization task and was unable to achieve criterion performance at the two lower intensity levels when Δt values of less than 200 μ sec were employed. His performance on the ΔI task was slightly enhanced by intensity-level changes, a result not found for the other monkeys. More important, he was able to perform the ΔI task as well as any monkey at the three intensity levels. He did not generalize immediately in localizing external stimuli. It is possible, of course, that his poorer performance on the Δt task was not related to the lesion but due merely to variation in the performance ability of squirrel monkeys. However, if the lesion did reduce his ability to use time as opposed to intensity cues, this would suggest that different mechanisms are utilized in the analyses of these two parameters.

Lateralization end-point experiments

Observation from human studies (ref 1 and preliminary studies) indicates that as Δt is increased to 1.5–3.5 msec, with a consequent splitting of the fused acoustic image, the stimulus in the lagging ear is perceived to be less loud than to that in the leading ear. The time separation between the two ears must exceed by several milliseconds the Δt at which the lag click or stimulus is first detected in order for it to appear as loud as the leading stimulus. If the monkeys also perceived a loudness imbalance, they may still be able to perform well on the end-point task by utilizing the loudness differences. End point, in this case, would reflect the time separation at which the lagging click is sufficiently loud to affect the loudness judgment, and not the separation at which the image begins to split. The decreasing function in Fig. 8 would represent the effective loudness growth of the lagging click. If, on the other hand, performance begins to deteriorate as soon as the lag click is perceptible, then it appears from the data that large Δt 's are handled by both squirrel monkey and man in the same manner.

There are many variables to contend with when interpreting behavioral data

from animals. The effects of the stressful experimental test situation, of changes in motivation, and of changes in temperament on test results must be large.

An experimenter never fully appreciates his subjects' preception or their strategy in responding to the task. These problems are reduced to some extent when verbal communication with subjects exists. The lack of such communication in the present experiment with squirrel monkeys has made us cautious in interpreting the data.

SUMMARY

Four squirrel monkeys were trained to make a right- or left-lever response depending on whether clicks were presented to a right or left earphone. They were then required to do the same for clicks presented binaurally when differences in the interaural time, intensity, and overall click level were introduced. Time and intensity differences and overall click level were varied in 20- μ sec, 2-dB, and 10-dB steps, respectively. The percentage of correct lateral judgments was plotted as a function of interaural time and intensity differences for each of three click levels. Individuals achieved criterion performance (85% correct lateral judgments) at time differences ranging from 60 to 180 μ sec, and at intensity differences ranging from 6 to 10 dB. The end point for lateralization was also examined for long time differences; performance fell below the criterion at interaural separations of between 2.0 and 3.5 msec, depending on the intensity level used. Changes in signal intensity affected performance on the Δt but not the ΔI task, suggesting that the neural mechanism subserving lateralization based on interaural time is different from that in which interaural intensity cues are used.

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