Auditory Discrimination and Recall in Monkeys

Abstract. *The first auditory recall functions have been derived for monkeys; the same animals also demonstrate perceptual abilities closely approximating those of man. An efficient, powerful psychophysical technique is used to specify and force predicted levels of difficulty of task performance across time, animals, and problems.*

The study of animal memory has been bound necessarily by experiments that test recognition. Yet, most of our knowledge of memory processes has been gained through investigations in humans which must allow, because of man's linguistic capabilities, some degree of recollection. The use of monkeys as presumed surrogates for man in neurobehavioral research ideally should entail examination of behaviors as similar as possible to those of humans. Because of recent widespread interest in hearing, brain, and language, we attempted to specify some heretofore unmeasured auditory cognitive capacities of nonhuman primates. We present data from ten monkeys on two auditory behavioral problems which can be solved only by long-term, stable performance of a bisensory delayed conditional discrimination habit. The first problem shows their ability to discriminate between acoustic events of very brief duration; and the second, their capacity for recollection of a given auditory stimulus of 0.5-second duration. In both instances, the testing method is response-determined titration (*1*) which allows us to equate the difficulty of various problems for different subjects and, for the same subject, at different times and experimental conditions.

To measure recall capacity in animals that possess no language, we have trained monkeys (*Macaca fascicularis*) to press, through the bars of their cage, either a red-illuminated panel after hearing a 0.5-second, 1000-hertz tone or a green-illuminated panel after hearing a 0.5-second burst of "white" noise. The acoustic stimuli were chosen for their perceptual distinctiveness at suprathreshold listening levels and are delivered through a loudspeaker mounted behind the testing array, at 72 db sound pressure level (SPL) (tone) and 65 db SPL (noise) with gated rise/decay times of 10 μsec. The two translucent plastic response panels, 3.2 cm in diameter and spaced 6.4 cm apart, are vertically oriented above a food well where pellet reinforcements are given after each correct response; the response panels are backlit simultaneously at the appropriate time during the trial sequence to indicate to the monkey that a single discriminative response can be made. This response terminates the trial. When a third panel, 12.7 cm above the upper response panel, is lit, an "observing response" (a single press) made by the monkey at that panel initiates each trial by causing the auditory stimulus to be presented. A testing session—completed in about 20 minutes—typically involves 200 self-paced trials in which the tone and the noise are each presented randomly approximately 100 times. Likewise, either the red-above-green or the green-above-red response panel cues are programmed separately to appear at random for each trial. Thus we obtain demonstrations of pure auditory recall uncontaminated by any possible use of invariant spatial cues by the monkeys.

Although straightforward in conception, this task takes both time and effort to teach (approximately 18 weeks per animal) particularly because it involves a highly demanding auditory-governed discrimination; such problems are difficult for monkeys (*2*). The chief advantage of this task is that it sets firmly a baseline habit through which many derivative problems, perceptual and cognitive, may be solved. Performance functions then can be obtained, for instance, before and after restricted unilateral lesions of the cortex of the temporal lobe. These lesions spare the animals' ability to do the basic task yet cause definitive changes in performance on certain dependent problems (*3*).

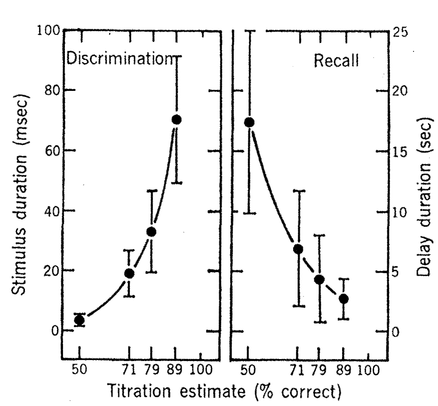

Fig. 1. Tone versus noise discrimination and recall functions for ten monkeys. Each point and its vertical bar represents the group mean ± 1 standard deviation.

With our method of stimulus titration, we specify beforehand the level of performance to be attained by the monkey during the test. Step changes of equal magnitude along a critical experimental dimension (in the present studies, duration of either the acoustic stimulus or the poststimulus delay interval) are made contingent upon the animal's preceding response (or responses) according to predetermined schedules of control (*4*). For example, to establish the 50 percent correct response threshold for a two-alternative forced-choice task, the magnitude of the critical variable is adjusted one step in the direction of greater difficulty of discrimination after each correct response, and one step in the direction of greater ease after each incorrect response. Schedules that establish performance at levels above 50 percent correct have more stringent response requirements but are no less efficient in their outcomes; for instance, to force the 89 percent correct response level, we demand six consecutive correct responses before moving one step toward greater difficulty, and a single incorrect response to move toward greater ease of discrimination. The factor of different reinforcement densities at peak titrated performance levels does not appear to us to affect the monkeys' commitment to the tasks during testing. We believe this can be accounted for by (i) extreme prior overtraining on the basic task, (ii) frequent untitrated "control" sessions given during the course of the experiments, and (iii) the nearly 100 percent reinforcement density attainable during the initial portions of every titration session regardless of its ultimate demanded level.

In this report, four levels (50, 71, 79, and 89 percent correct discrimination) on each problem are given for each monkey. All data are derived from at least three 200-trial daily sessions for each animal under each titration condition. That multiple levels of performance can be ascertained and that a function can be plotted from these is seen to be an improvement over the more traditional all-or-none determination of a learned ability in animals. Figure 1 gives performance functions and measures of variability for the entire group. Tables 1 and 2 list individual data; each entry reflects stable performance over at least three sessions, and the accuracy is in every case within 1 percent of the designated titration estimate. These tables demonstrate that, although the values attained by the various monkeys under either monaural or binaural conditions of testing do show some differences, the shape of the individual functions is well represented by the curves of Fig. 1.

The monkeys' performance of the basic task has been stable at better than 90 percent correct for at least 1 year. Throughout the present evaluations, we interspersed 100-trial control sessions to verify each animal's ability on the basic task. These daily sessions were free of any titrated burden. Scores achieved by all monkeys leave no doubt that the underlying discrimination habit is deeply ingrained: the grand mean score for 6000 control trials (600 per monkey) is 92.6 percent, and in none of the 60 sessions was any monkey's score lower than 90 out of 100 correct. Also, we compared performance of humans and monkeys on the brief stimulus discrimination problem.

We tested six adults with normal hearing in order to determine their 50 percent discrimination threshold under conditions identical to those for the monkeys except that the humans were verbally informed of the relationships among the auditory stimuli and the required visually governed responses. The six values averaged 1.1 msec (range, 0.8 to 1.6 msec), which accords favorably with normative human psychoacoustic data derived more rigorously (*5*). This agreement could be coincidental and is a function of our particular stimulus delivery system (*6*). On the other hand, the small mean differences between man and monkey in the present results might be explained by our as yet insufficient control of absolute long-term motivational levels in these animals. Another important contributing factor could be the mnemonic burden placed upon nonverbal monkeys by the demanding cognitive aspects of the problem—particularly, the location-independent response requirement. Nonetheless, our monkeys' performance is consistently within a few milliseconds of that achieved by normal human observers on the same complex task. Because of man's verbal abilities, a similar control test for recollection by humans of a 0.5-second tone or noise stimulus is precluded.

Table 1. Tone versus noise discrimination, in milliseconds. The letters N, L, and R refer to presumed cochlear status: N, both normal; L, left cochlea destroyed; and R, right cochlea destroyed. The labyrinthectomies were performed before behavioral training.

Monkey	Titration estimate			
	50%	71%	79%	89%
Pl (N)	2.5	12	20	49
Co (L)	7.5	20	33	70
Zi (L)	3.0	21	30	55
Si (R)	3.8	9	21	65
Er (R)	3.0	13	22	48
Pi (L)	4.4	14	24	50
He (R)	2.2	17	31	69
Fe (N)	2.5	34	64	105
We (L)	4.2	23	38	90
Me (R)	4.5	26	45	100
Mean	3.8	18.9	32.8	70.1

Our results demonstrate for the first time that auditory recall functions for nonhuman primates can be derived. Only recently have initial measures been obtained for visual recall in monkeys and for auditory recall in a dolphin through the use of the delayed conditional matching paradigm (*7*). The present findings and techniques should prove valuable in a variety of experimental applications other than those in which cortical ablations are used in the study of brain-behavior relationships. Especially in the more general use of monkeys for testing memory theories (*8*) or evaluating various pharmacological agents, our methods allow the quantification of certain auditory capacities of nonhuman primates in similar fashion to that hitherto available only in man. Finally, the titration procedure circumvents a problem in evaluating performance of multiple tasks in groups of animals given different treatments. Such studies are held hostage inevitably by the question of equal difficulty of tasks over time (*9*). Adaptive psychophysical methods provide a way to hold constant at many levels the burden of a variety of demands placed upon subjects.

Table 2. Tone versus noise recall, in seconds. The notation for cochlear status is explained in the legend to Table 1.

Monkey	Titration estimate			
	50%	71%	79%	89%
Pl (N)	39.0	17.0	12.0	7.0
Co (L)	22.0	14.0	10.0	4.0
Zi (L)	14.7	6.0	4.0	3.0
Si (R)	12.0	5.0	3.5	2.5
Er (R)	17.0	8.0	2.5	2.5
Pi (L)	17.6	4.3	1.9	1.1
He (R)	13.0	4.1	2.2	1.4
Fe (N)	12.4	3.9	2.3	1.9
We (L)	17.3	4.0	3.0	1.8
Me (R)	9.3	3.0	2.3	1.6
Mean	17.4	6.9	4.4	2.7

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References and Notes

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