STIMULUS CONTROL AND AUDITORY DISCRIMINATION LEARNING SETS IN THE BOTTLENOSE DOLPHIN¹

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The learning efficiency of an Atlantic bottlenose dolphin was evaluated using auditory discrimination learning-set tasks. Efficiency, as measured by the probability of a correct response on Trial 2 of a new discrete-trial, two-choice auditory discrimination problem, reached levels comparable to those attained by advanced species of nonhuman primates. Runs of errorless problems in some cases rivaled those reported for individual rhesus monkeys in visual discrimination learning-set tasks. This level of stimulus control of responses to new auditory discriminanda was attained through (a) the development of a sequential within-trial method for presentation of a pair of auditory discriminanda; (b) the extensive use of fading methods to train initial discriminations, followed by the fade-out of the use of fading; (c) the development of listening behavior through control of the animal's responses during projection of the auditory discriminanda; and (d) the use of highly discriminable auditory stimuli, by applying results of a parametric evaluation of discriminability of selected acoustic variables. Learning efficiency was tested using a cueing method on Trial 1 of each new discrimination, to allow the animal to identify the positive stimulus before its response. Efficiency was also tested with the more common blind baiting method, in which the Trial 1 response was reinforced on only a random half of the problems. Efficiency was high for both methods. The overall results were generally in keeping with expectations of learning capacity based on the large size and high degree of cortical complexity of the brain of the bottlenose dolphin.

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General Discussion

The learning efficiency of a number of mammalian species has been compared using discrimination learning-set (DLS) tasks (Harlow, 1949; Riopelle, 1960; Warren, 1965). A DLS task consists of a series of discrete-trial, two-choice, nonspatial discrimination problems. Learning efficiency is commonly measured as the probability of a correct response on Trial 2 of a new discrimination problem following the single prior learning trial (Trial 1).

For most mammalian species tested, the probability of a correct response rises over suc-

cessive blocks of problems, but the rate of increase and the final probability level reached vary widely among species. Average Trial 2 scores of 85 to 97% correct responses have been reported for rhesus macaque monkeys and great apes during the final block of problems given, and individual rhesus have achieved 100% correct responses for 20 to 30 consecutive problems (Harlow, 1949; Rumbaugh and McCormack, 1967). These average and individual scores considerably exceed levels reached by the more primitive primates, the New World monkeys and prosimians, and by nonprimates (Riopelle, 1960; Warren, 1965).

¹This work was supported in part by the Naval Undersea Center, Hawaii Division, by the Hawaii Institute of Marine Biology, and by a Biomedical Sciences Research Support Grant. Preparation of this paper was aided by Grant GB-32148X from the National Science Foundation. For assistance in carrying out the testing program, we thank Fred Ball, Lynn Cowan, Chris Moore, Ted Schultz, and Paul Siri. Reprints may be obtained from Louis M. Herman, Department of Psychology, University of Hawaii, Honolulu, Hawaii, 96822.

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Performance levels on DLS tasks across species are generally in keeping with an ordering based on cortical complexity (Harlow, 1959). The highly convoluted surface and large size of the brain of the Atlantic bottlenose dolphin (Flanigan, 1972; Jansen and Jansen, 1969) suggest the capacity for a high degree of learning efficiency, which might be revealed in a DLS task. Measurement of efficiency, however, must take account of (a) the considerable influence of stimulus and procedural variables on DLS performance (Devine, 1970; Kay and Oldfield-Box, 1965; Harlow, 1959; Miles, 1965; Reese, 1964; Stollnitz, 1965), and (b) the biology of the dolphin, a completely aquatic mammal with unique specializations in auditory sensory processing (*e.g.*, Norris, 1969).

An initial study of DLS in the bottlenose dolphin used geometric patterns cut from 1-ft square plywood sections as discriminanda (Herman, Beach, Pepper, and Stalling, 1969). These were discriminable potentially either visually or by use of active sonar ranging. A second DLS study used auditory discriminanda (Beach and Herman, 1972). Training and testing methods in both studies were relatively close adaptations of procedures described for DLS testing of primates (Harlow, 1949; Reese, 1964). The auditory study also examined successive reversal learning and the transfer of learning between reversal tasks and DLS tasks. A correction procedure following errors was used to guard against position responding, which had developed in the dolphin studied by Herman *et al.*, (1969).

The DLS results of both studies were that as the trials per problem were reduced in number over successive problems, as is usual in a DLS task, the per cent correct responses of the dolphins tested decreased to near chance levels. Discrimination of many of the pairs of plywood forms appeared difficult in the study of Herman *et al.*, (1969) as did many of the simultaneously presented sound pairs in the study of Beach and Herman (1972). In the successive auditory reversal task of Beach and Herman, however, there was a progressive reduction of errors over successive reversals, probably because the use of a constant auditory pair for all reversals facilitated the formation of a discrimination. There was also some evidence of positive transfer between DLS and successive reversal tasks, an effect noted previously for rhesus monkeys but not for cats

(Warren, 1966). Hence, there was suggestive evidence that the DLS capability of the dolphin may have been underestimated. In general, in the DLS portion of the study of Beach and Herman (1972), as well as in the DLS study of Herman *et al.*, (1969), control of responses by relevant stimulus dimensions did not appear well developed and alternate methods of stimulus control were not investigated.

Reported here are further DLS studies of the bottlenose dolphin in which a search for more optimal conditions of testing was made. Under the procedures developed, the error probability was reduced to near zero during the acquisition of new two-choice auditory discriminations, even when the trials per problem were decreased in number. The procedures included a new within-trial sequential method for presentation of a pair of auditory stimuli, the development of stimulus control of listening behavior, the scaling of auditory stimuli for ease of discriminability and the subsequent use of acoustic variables having maximum within-pair discriminability, and the extensive employment of progressive training (fading) methods.

The information characteristics of the first learning trial of each problem were also varied. A cued method (*e.g.*, Riopelle and Chinn, 1961) for identification of the positive (S+) and negative (S-) stimuli on Trial 1 of a problem was used in Experiments 3 and 4. The cue was absent on subsequent trials. Experiment 5 used the more common blind baiting DLS method (Harlow, 1949; Reese, 1964). The Trial 1 response was reinforced on a random half of the problems and not reinforced on the remaining problems. The stimulus associated with reinforcement (S+) remained S+ on subsequent trials, and that associated with non-reinforcement (S-) remained S-.

An error correction procedure was used in Experiments 1 to 4. Since this procedure was incompatible with correct responding following a response to S- on Trial 1 of the blind baiting method, it was deleted in Experiment 5.

GENERAL METHOD

Subject

An adult female Atlantic bottlenose dolphin, *Tursiops truncatus* (Montagu), named Keakiko, 7 to 8 yr old, 2.4 m in length and

weighing 140 kg, was maintained on 7 kg of fish (smelt or mackerel) daily. This is the approximate quantity normally given captive adult bottlenose dolphins. Most of the ration was given during testing, carried out six days per week, up to 8 hr per day or for a maximum of 200 trials. The animal had been in captivity approximately 18 months at the start of the study and was one of two subjects used by Beach and Herman (1972).

Apparatus

Testing was in the animal's home tank, a circular concrete enclosure of 15.2 m (50.0 ft) diameter and depth of approximately 1.5 m (5 ft), located at the University of Hawaii. The apparatus, schematized elsewhere (Herman and Arbeit, *in press*), was contained within a portion of one quadrant of this tank. Two stimulus speakers (Chesapeake J9 underwater sound projectors) were suspended 2.6 m (8.5 ft) apart at 0.5 m (1.6 ft) depth. The speakers projected the S+ and S− sounds of a two-choice discrimination problem, and adjacent to each was a response paddle. A lateral press of a paddle activated a microswitch.

A listening area of 0.8 sq m (8.64 sq ft), the corners defined by four ropes suspended vertically underwater, was located 1 m (3.3 ft) back from a point midway between the speakers. At 0.9 m (2.9 ft) in front of the listening area, at 0.6 m (1.9 ft) depth, was a target paddle. A forward push of this paddle activated a magnetic switch. Two filament lamps, set to flash on and off asynchronously, were displayed 2 m (6.5 ft.) in front of the start paddle at 0.7 m (2.3 ft.) depth, and to their right was a control speaker (University MM-2PPS), used to project sounds *other* than S+ and S−.

Stimuli Used in Auditory Discriminations

A total of 372 two-choice auditory discrimination problems were given over the five experiments. Problems consisted of two electronically generated sounds constructed from both between and within pairings of the following six sound classes: (a) unmodulated pure tones (F); (b) pulse modulated tones (FP); (c) frequency modulated tones (FM); (d) mixtures of two pure tones (FF); (e) mixtures of a pulse modulated tone and a pure tone (FPF); and (f) mixtures of a frequency modulated tone and a pure tone (FMF).

The frequency values of the pure tones, the center (average) frequency of the FM tones, and the pure tone component being pulsed in the FP tones were variables ranging from 1 to 42 kHz. The percentage frequency deviation of the FM tones around their center was held constant at $\pm 25\%$, but the rate of frequency deviation varied from 1 to 40 Hz. Similarly, the ratio of the duration of pulse-on to duration of pulse-off in the FP tones was held constant at 1.0, but the pulse rate varied from 1 to 40 Hz.

The particular pairing of sound classes, together with the particular acoustic variables differing across the pair members, defined a *sound pair type*. Table 1 gives the symbolic code for the 28 sound pair types used across the five experiments. As examples, three sound pair types were F_1M_1 vs F_1M_2 , F_1M_1 vs F_2M_1 , and $F_1P_1F_3$ vs $F_2M_1F_4$ (types 8, 27, and 12), where different subscripts denote different values for the frequency variable (F), or different rates for the frequency deviation (M) or pulse rate (P) variables. In the first type, the center frequencies of the two FM tones were the same ($F_1 = F_1$) but the rate of frequency deviation differed ($M_1 \neq M_2$), while in the second type, the reverse conditions held. In the third type, the pure tone component of the FP sound and the center frequency of the FM sound differed ($F_1 \neq F_2$), but the pulse rate and rate of frequency deviation were the same ($P_1 = M_1$). In addition, the pure tone frequencies F_3 and F_4 added to the FP and FM sounds, respectively, differed from each other as well as from the previous pure tone components F_1 and F_2 .

To construct one of the 372 problems, one of the pair types of Table 1 was used and the specific value of at least one of the variables in that pair type made different from values in any previous uses of that type. Sound pair types 17 to 28 were developed from the results of a parametric analysis of discriminability of selected acoustic variables made in Experiment 4A, and were used only in the following experiments. On the basis of these same results, types 2, 6, 8, and 10 were not used beyond Experiment 4A.

Sound Generation System

Each of the two sound classes within a sound pair type was generated by an independent sound system, except for a common final

Table 1

Symbolic description of the sound pair types constructed and the experiments in which each type was used at least once. Each type was a pairing between or within the six sound classes: F, FP, FM, FF, FPF, and FMF (see text). Within a pair type, different subscripts for the frequency variable (F) denote different frequencies, and different subscripts for pulse rates (P) and/or frequency modulation rates (M) denote different rates for these variables.

Pair Type		Experiment							Pair Type					Experiment							
No.	Symbol	1A	1B	2	3A	3B	4A	4B	5A	5B	No.	Symbol	1A	1B	2	3A	3B	4A	4B	5A	5B
1	$F_1 - F_2$	X	X	X		X	X	X		X	15	$F_1P_1 - F_2P_2F_3$			X					X	
2	$F_1 - F_1P_1$			X	X	X	X	X			16	$F_1M_1 - F_2M_2F_3$			X						
3	$F_1 - F_2P_1$			X		X	X	X	X	X	17	$F_1 - F_2F_3$							X	X	X
4	$F_1 - F_1M_1$			X	X	X	X	X	X	X	18	$F_1 - F_1P_1F_2$							X	X	X
5	$F_1 - F_2M_1$			X	X	X	X	X	X	X	19	$F_1P_1 - F_1M_2$							X	X	X
6	$F_1P_1 - F_1P_2$			X	X	X	X	X			20	$F_1M_1 - F_1P_1F_2$							X	X	X
7	$F_1P_1 - F_2P_2$			X	X	X	X	X	X	X	21	$F_1P_1 - F_1M_1F_2$							X	X	X
8	$F_1M_1 - F_1M_2$			X	X	X	X	X			22	$F_1P_1 - F_1P_2F_2$							X	X	X
9	$F_1M_1 - F_2M_2$		X	X	X	X	X	X	X	X	23	$F_1P_1 - F_1F_2$							X	X	X
10	$F_1P_1 - F_1M_1$			X	X	X	X	X			24	$F_1P_1 - F_2F_3$								X	
11	$F_1P_1 - F_2M_1$			X	X	X	X	X	X	X	25	$F_1 - F_2P_1F_3$								X	X
12	$F_1P_1F_3 - F_2M_1F_4$				X	X	X	X	X	X	26	$F_1P_1 - F_2P_1$								X	X
13	$F_1P_1F_3 - F_2M_2F_4$					X	X				27	$F_1M_1 - F_2M_1$								X	X
14	$F_1P_1 - F_2M_2$			X				X	X	X	28	$F_1M_1 - F_1M_2F_2$									X

amplification stage. For each problem, the S+ sound was randomly assigned to one system and the S- sound to the other.

In each system, a voltage controlled oscillator (Wavetek 112) produced the pure tone (F) sound class, or else the FM sound class if driven by a sine wave function from an EICO 378 generator. For the FP sound class, the pure tone output of the Wavetek was passed through a follower and pulse sharper unit. The follower provided pulsed pure tones with pulse widths and pulse repetition periods replicating those of a square wave signal from the EICO 378. The sharper modified the pulses for relatively slow rise and fall times, to avoid acoustic transients. For the FF, FPF, or FMF sound classes, the sine wave output from an EICO 377 generator was added to the F, FP, or FM sounds before the amplification stage through a mixer circuit.

Voltage levels applied to the two stimulus speakers determined the sound pressure level in water and were controlled by an EICO 1171 step attenuator and Harmon-Kardon Citation II amplifier. Voltage levels were calibrated by an oscilloscope, which also provided a check on waveform, and pure tone frequencies were calibrated by an electronic counter.

A signal selection network controlled the sequential order of occurrence of sounds from the two sound systems and delay generators controlled the duration of the sounds and of the interstimulus interval. Separate electronics were used for the generation, timing, and sequencing of the variety of auditory and visual stimuli (other than S+ and S-) used to control the successive responses of the animal during each trial.

Procedure

Figure 1 shows the chain developed during Experiments 1 and 2 and used in all of the following experiments. This chain was developed primarily for stimulus control of listening (attentional) responses during the presentation of S+ and S- within each discrete trial. The stimulus speakers pointed at the listening area, making it a region of relatively high sound intensity, and a satisfactory listening response was the passive waiting (stationing) of the animal within the listening area for the entire duration of S+ and S-. An unsatisfactory listening response, or other inappropriate responding during the chain, immediately produced the intertrial interval state.

Fig. 1. The chain developed in Experiment 1 and 2, and used in all of the following experiments. Plain rectangles indicate responses and dotted rectangles indicate stimuli.

The chain began with a limited-hold (10-sec) call tone from the control speaker. In its presence, the animal entered the listening area at the end adjacent to the main area of the tank, passed through it with its head and anterior portion of its body, and pushed the target paddle with the end of its jaw. The push terminated the tone and the subsequent release initiated S+ and S-, in random sequential order. S+ was projected from one stimulus speaker, left or right, chosen randomly, and S- from the other speaker.

The flashing light stimulus began immediately after the second sound of the sequential pair, and in its presence the stationing response ended and either response paddle could be approached. A response to S+, *i.e.*, a press of the paddle adjacent to the speaker having projected S+, replayed S+ from the original stimulus speaker, followed by a 0.5-sec sound from the control speaker and then by an approximate 34 g thrown fish. A response to S- replayed S- from its original stimulus speaker, followed immediately by the intertrial interval of 7 to 10 sec in length. Playback of S+ and S- was first used in Experiment 2, and the call tone in Experiment 1B. The call tone and the 0.5-sec sound following S+ playback were complex waveforms different from each other with the fundamental frequency of each below 1 kHz.

Training in the chain took place over a three-month period. New links were introduced through fading techniques, with error rates generally maintained at low levels. Most of the three-month period was used to familiarize the animal with the six sound classes and the range of variables within each class, through extended practice in paddle pressing following the playing of a sound class. The error rate in paddle pressing following a single sound projected briefly (0.5 to 5.0 sec) from one of the two stimulus speakers asymptoted relatively quickly at 0.9%. This measured the ability of the animal to localize in space the source of a sound, under the present conditions of testing.

From the results of the initial training, S+ duration in the following experiments was fixed at 2.5 sec. The final duration of S- was also 2.5 sec, but if progressively introduced into a problem its duration was increased over trials from 0.5 to 2.5 sec. The interstimulus interval was held at 0.3 sec. A fixed voltage

value (40 V peak to peak) applied to a stimulus speaker was used for S+ and for the final value of S-. During the progressive introduction of S- into a problem, its initial voltage value was 1 V. The 40-V peak-to-peak value yielded sound pressure levels in water, measured in the listening area, of from 35 to 49 dB (re one microbar), which is considerably above the threshold value of hearing for the bottlenose dolphin (Johnson, 1967). Ambient noise levels ranged from -13 to -21 dB, with the major spectral content of the noise below approximately 800 Hz.

The occurrence of S+ and S- at each stimulus speaker was balanced or near-balanced in blocks of trials for each problem. During Experiments 1B and 2, S+ more frequently occurred first in the sequence of two sounds than last, in an effort to reduce the greater error rate when first. In the remaining experiments, its order was balanced or near-balanced over blocks of trials.

A correction procedure was used in Experiments 1 through 4, and following extinction training of the correction response in Experiment 5, noncorrection was used. During correction, the error trial characteristics were repeated until the animal responded correctly, or for a maximum of five successive corrections.

EXPERIMENT 1: DEVELOPMENT OF STIMULUS CONTROL

Results for the first two-choice discrimination problem are given in Part A. In Part B, the chain was extended to control the intertrial interval and the effects tested. The large accretion of errors in both parts was analyzed in terms of the temporal effects produced by the sequential presentation of S+ and S-.

Procedure

A total of four problems were given. Sound playback was not provided following a paddle press. For each problem, the S+ was initially presented alone for a variable number of trials. The S- was then faded-in during subsequent trials, by gradually increasing its intensity and duration, alternately, until they were both equal to the values used for S+. During fade-in, increases in S- intensity or duration followed responses to S+, and decreases followed responses to S-.

In Part A, 10 sessions were given over a seven-day period, using a single discrimination problem throughout. Over succeeding sessions, the number of trials per session used for S— fade-in was generally reduced, and during Sessions 8 and 10, there was no S— fade-in. If error rates were high during any session, it was terminated early.

During an 18-day interval between Parts A and B, the limited-hold call tone was added to the chain (Figure 1) to control intertrial interval length, which in Part A was self-paced. In Part B, eight sessions were given over a four-day period, using three new discrimination problems. The first and third problems were each given for only a single session. For the second problem the number of trials per session used for S— fade-in was generally reduced with succeeding sessions, including two sessions without any S— fade-in.

RESULTS AND DISCUSSION

The lower half of Figure 2 gives the number of trials per session for Part A (no call tone) and Part B (call tone present) and the ordinal number of the trial on which S— fade-in was completed, *i.e.*, the trial number on which S— was first presented with duration and intensity equal to S+, and the animal responded to S+. Missing data points in the fade-in graph at Sessions 2, 11, and 18 signify that S— fade-in was not completed by these criteria.

The upper half of Figure 2 shows the per cent correct responses over all trials during each session. New discrimination problems were introduced at Sessions 1, 11, 12, and 18 (open circles). Progressive *decrements* in performance were found with repeated sessions with the same discrimination (Problem 1 and Problem 3). The call tone was used during Problem 3 but not during Problem 1. Hence, it did not affect positively the probability of correct responding. It did stabilize the intertrial interval length, generally resulting in shorter intervals than during the self-paced mode of Part A. It also reduced possibly disruptive behavior between trials, such as rapid swimming, leaping, tossing about of the fish reinforcer, *etc.* These positive effects were considered sufficient to warrant retaining the call tone condition.

Most of the later sessions with Problems 1 and 3 used considerably fewer S— fade-in trials than did the earlier sessions, and at some

of the later sessions, the S— was presented at full duration and intensity on Trial 1. Though this reduction in S— fade-in trials was correlated with the noted progressive performance decrements for these problems, Table 2 sug-

Fig. 2. The major conditions (lower figure) and results (upper figure) for Experiment 1, Part A (pre-call tone) and Part B (post-call tone). Open circles in the upper figure identify the session at which each of the four discrimination problems was introduced. Missing data points at Sessions 2, 11, and 18 in the Fade-In Trial No. graph in the lower figure indicate a failure to complete the fade-in of S— within the number of trials given.

Table 2

Experiment 1: Initial and repetitive error rate during Part A (no call tone) and Part B (call tone present) as a function of S+ mapped onto left or right speaker and S+ first or last in the sequence of two sounds.

		S+ First		S+ Last	
		Left	Right	Left	Right
Part A	Total Trials	145	132	142	160
	Initial Error Rate	0.21	0.21	0.04	0.04
	Repetitive Error Rate	0.11	0.15	0.01	0.01
Part B	Total Trials	188	191	115	125
	Initial Error Rate	0.23	0.30	0.10	0.02
	Repetitive Error Rate	0.17	0.13	0.21	0.00

gests that the cause of the errors lay elsewhere. Table 2 shows the initial error rate and the repetitive error rate (error rate on correction trials) for the problems in Part A and Part B as a function of the speaker from which S+ was projected, left or right, and the sequential position of S+, first sound or last. Error rates are given as the total number of errors divided by the total number of trials.

Table 2 shows no evidence of position responding, since the speaker location of S+, left or right, was unrelated to error rate. However, for both Parts A and B, substantially higher initial and repetitive error rates occurred when S+ was first in the sequence than when it was last. The initial error rates of 21 to 30% with S+ first sharply contrast with the 2 to 10% rates with S+ last.

Inspection of the trial-by-trial data indicated that errors with S+ first tended to develop during the middle and later trials of a session, generally after a period of correct responding under this condition. This development of errors might have come about from a gradual build-up of the effects of the temporal association of S- with reinforcement following correct responses with S+ first. Thus, in this sequence, S+ was heard, then S-, and following a response to S+ the 0.5-sec sound occurred and then food reinforcement. Though responses to S+ occurred during initial trials with S+ first, perhaps due to carry-over effects from highly successful responding with S+ last, through the indicated temporal arrangement S- also would become associated with reinforcement, and eventually, responding to S- begins. The following experiment tested this hypothesis by studying the effects of a rearrangement of the temporal relationships.

EXPERIMENT 2: THE ROLE OF SOUND PLAYBACK

The playback condition was added to the chain, completing it as shown in Figure 1. A paddle press produced playback of either S+ or S-. The 0.5-sec sound and a thrown fish followed S+ playback and nonreinforcement followed S- playback. Therefore, S+ always immediately preceded reinforcement, regardless of the original sequential order of S+ and S-, while S- always immediately preceded nonreinforcement.

Procedure

Training for playback took place over a five-day period using a variety of single sounds, *i.e.*, only one-choice problems were given. The playback condition was introduced by progressively increasing its duration over successive trials and sessions until a final value of 2.5 sec was reached. Some double pressing of the response paddle occurred in the presence of playback, but soon dropped out.

Following the five-day playback training period, 24 new two-choice problems were given at the rate of one to four problems per day, over a 10-day period. There were from 31 to 100 trials per problem and 12 different sound pair types were used. When a pair type was repeated, in addition to changing the values of the variables of that pair, there was counterbalancing of the pair members associated with S+ and S-, *i.e.*, if a pair type was used twice, the reinforcement values of the pair members were reversed for the second use. Playback of S+ followed correct responses and playback of S- followed incorrect re-

sponses. During S— fade-in trials, the duration and intensity of S— playback following an incorrect response were always equal to the values used for S— during the trial presentation.

RESULTS AND DISCUSSION

The results with playback, seen in Figure 3, were a marked increase in the per cent correct responses. Table 3 shows initial error rates of 4 to 12% with S+ first as compared with rates of 23 to 30% found at the end of Experiment 1 (Table 2). Similarly, repetitive error rates with S+ first declined to 3 to 4% from the 13 to 17% rates found at the end of Experiment 1.

Though there was still a greater overall error rate with S+ first than with S+ last, there was a trend toward errorless performance with S+ first (as well as with S+ last) over successive problems (Figure 3). Errorless performance occurred for eight of the 10 final problems, even though the number of trials used to fade in S— was generally fewer than for the first 10 problems. There was no apparent reason for the lapse in performance on Problem 20. The results support the hypothesis that temporal contiguity of S— and reinforcement was responsible for the poor performance observed in Experiment 1 with S+ first.

EXPERIMENT 3: FADE-OUT OF S— FADE-IN AND TRIAL 1 CUEING METHOD

Experiment 3 explored the limits of the animal's DLS skill further, retaining the playback condition. In Part A, the effects of progressively reducing the number of trials used to fade-in S— were examined, and in

Part B, performance was tested when S— fade-in occurred only on Trial 1. Part B thus provided the first measure of learning efficiency on Trial 2 of a set of new problems, when Trial 1 information was the sole basis for identification of S+ on Trial 2, *i.e.*, cueing of S+ (fade-in of S—) was absent on Trial 2 (and on subsequent trials). This method is termed Trial 1 cueing.

Procedure

The general procedures of Experiment 2 were followed. In Part A, 19 new problems were given at the rate of one to four problems per day over a nine-day period, beginning one month after Experiment 2 ended. (During the month, the animal was ill and not tested.) Each problem, except the last, was 50 trials. The trial number on which S— fade-in was completed was reduced progressively from an initial value of 29 trials to a final value of two trials. In the latter condition, S— intensity and duration values were reduced only on Trial 1. This is the Trial 1 cueing method.

For Part B, 21 problems were given, all using Trial 1 cueing. Problems were given at the rate of one to four per day, beginning the day after Part A was completed and continuing for a 12-day period. There were either 25 or 50 trials per problem.

RESULTS AND DISCUSSION

Figure 4, Part A, shows the rate of reduction of S— fade-in trials and related performance levels. One-trial fade-in, the Trial 1 cueing condition, was reached on the nineteenth problem. Over the 19 problems, no errors occurred during S— fade-in trials. On the remaining trials, there were only eight initial errors (0.9% error rate) and two repetitive errors (0.2% error rate). Errorless performance occurred on 15 of the 19 problems, including Problem 19, the first Trial 1 cueing problem.

In Part B, 14 of the 21 Trial 1 cueing problems were errorless, and a single error occurred on each of six of the seven remaining problems. The single error was on Trial 1 on three problems, the animal choosing S— even though its intensity and duration were reduced relative to S+. There was one error on Trial 2 over all 21 problems. The initial error rate was 1.2% over all trials (0.9% if Trial 1 errors are omitted) and the repetitive

Table 3

Experiment 2: Initial and repetitive error rate under playback condition as a function of S+ mapped onto left or right speaker and S+ first or last in the sequence of two sounds.

	S+ First		S+ Last	
	Left	Right	Left	Right
Total Trials	372	367	336	342
Initial Error Rate	0.04	0.12	0.02	0.02
Repetitive Error Rate	0.04	0.03	0.01	0.01

error rate was 0.6%. As was the case in Experiment 2, relatively poor performance occurred on one problem, without apparent reason.

Fig. 3. The major conditions (lower figure) and results (upper figure) for the 24 problems of Experiment 2. The abscissa labelling is now problem number rather than session number since a new problem was given during each session. Missing data points for Problems 10 and 20 in the Fade-In Trial No. graph in the lower figure indicate a failure to complete the fade-in of the S- within the number of trials given.

The data reveal a high degree of learning efficiency. In Part B, there was one-trial learning of most new discriminations (95.2% correct responses on Trial 2). This was a very different outcome from earlier DLS dolphin research (Beach and Herman, 1972; Herman *et al.*, 1969) in which the three animals studied, including the present animal, Kea-kiko, generally required a large number of

Fig. 4. The major conditions and results for the 19 problems of Experiment 3, Part A (fade-out of fade-in) and the 21 problems of Part B (Trial 1 cueing method).

trials to attain a successful discrimination of a new problem.

The low error rate also demonstrated that there was little tendency for the animal to generalize the properties of S+ across successive problems, since reversal of the acoustic dimensions associated with S+ and S- across successive problems, *e.g.*, in Part B, problems numbered 35-36 and 38-39 in Figure 4, did not interrupt the errorless performance of the animal.

EXPERIMENT 4: DISCRIMINABILITY AND FINAL DLS SKILL LEVEL UNDER TRIAL 1 CUEING

The occasional lapse in performance on specific problems seen in Experiments 2 and 3 might have been due in part to discrimination difficulty. In Experiment 4, Part A, a parametric evaluation was made of a subset of the sound pair types of Table 1, to identify acoustic variables associated with good and with poor auditory discrimination performance. In Part B, performance was tested on a series of new problems, all only 10 trials long, and all using acoustic variables identified through Part A as yielding easy discriminations. The Trial 1 cueing method was used for both Parts A and B.

Procedure

The 144 problems of Part A were given over a five-week period, beginning approximately one week after Experiment 4 ended. Pair types 1 to 12 (Table 1) were used. Each

type was administered once during each block of 12 problems, in an order governed by a 12 by 12 Latin square. Across the 12 administrations of a pair type, there was complete counterbalancing of the pair members associated with the S+ and also of the levels of the acoustic variables within pair members, *e.g.*, in the pair type $F_1P_1-F_1P_2$, the faster rate of pulse modulation was associated with S+ as often as was the slower rate.

The first 72 problems were 50 trials each and the remaining 72 were 20 trials each. A maximum of four problems per day were given during the 50-trial problems, and eight problems per day during the 20-trial problems.

In Part B, 25 new problems, each 10 trials long, were given over a period of three days, beginning two days after Part A ended. Sixteen problems were constructed from eight of the sound pair types found in Part A to be easy discriminations when the levels of the acoustic variables across each pair type were accounted for. For example, for pair types using the FP sound class, pulse rates of 1 to 7 Hz produced better performance than did faster rates. Hence, pulse rates in Part B were restricted to 1 to 7 Hz.

Seven additional pair types were constructed by extrapolation from the results of Part A. Generally, the number of acoustic dimensions

along which the sound pair type members differed was increased. Five of these new pair types were given once each, and two were given twice each.

RESULTS AND DISCUSSION

Table 4 gives the initial and repetitive errors on Trials 1, 2, and 2-N for Part A, for each of the 12 pair types tested. For Problems 1 to 72, N equalled 50, and for Problems 72 to 144, N equalled 20. The pair types are arranged in increasing order of performance (decreasing errors on Trials 2-N) from top to bottom. The initial and repetitive error trends were very similar, so discussion can be limited to initial errors.

Trial 1 errors, a total of 11 for the first six pair types listed and 10 for the remaining six, showed no consistent relationship to overall errors (Trials 2-N), so Trial 1 data reflect primarily the animal's skill in using the provided differential intensity-duration cues. By contrast, on Trial 2 there were 13 errors for the first six pair types and only six errors over the remaining six types. Since intensity-duration cues were not available, the overall Trial 2 performance level of 86.8% correct responses indexes the level of learning efficiency. This was below the level of 95.2% found in Experiment 3, Part B. However, some of the dis-

Table 4

Experiment 4A: Errors for each pair type ordered by obtained performance levels on Trials 2-N, with Trial 1 and Trial 2 errors also shown. For Problems 1 to 72, N equalled 50; for Problems 73 to 144, N equalled 20. Each pair type was given six times during each 72 problems.

No.	Pair Symbol	Initial Errors			Repetitive Errors		
		Tr 1	Tr 2	Tr 2-N	Tr 1	Tr 2	Tr 2-N
6	$F_1P_1 - F_1P_2$	3	3	39	1	2	21
2	$F_1 - F_1P_1$	1	2	27	0	0	12
8	$F_1M_1 - F_1M_2$	3	4	25	1	3	10
10	$F_1P_1 - F_1M_1$	1	2	21	0	2	8
7	$F_1P_1 - F_2P_2$	2	1	13	0	1	6
1	$F_1 - F_2$	1	1	10	0	0	5
9	$F_1M_1 - F_2M_2$	2	1	9	0	0	2
4	$F_1 - F_1M_1$	2	3	5	0	1	1
3	$F_1 - F_2P_1$	1	1	4	0	0	0
11	$F_1P_1 - F_2M_1$	2	1	1	0	0	0
12	$F_1P_1F_2 - F_2M_1F_4$	2	0	0	0	0	0
5	$F_1 - F_2M_1$	1	0	0	0	0	0
Total Errors		21	19	154	2	9	65
Error Rate		0.15	0.13	0.03	0.01	0.06	0.01

criminations required in the present experiment were undoubtedly more difficult than those used in the prior experiment, in which differences in the values of the acoustic variables within a problem were made widely divergent in order to maximize the probability that the discrimination would be easy.

A detailed analysis of the relationship between the pair types studied and obtained performance levels is beyond the scope of this paper, but some broad consistent trends in Table 4 may be noted. Comparing Trials 2-N data for pair types 2 *vs* 3, 4 *vs* 5, 6 *vs* 7, 8 *vs* 9, and 10 *vs* 11 shows better performance in each case for the second listed type, for which frequency difference information was available across the pair members. Also, an increase in the number of acoustic dimensions available across the pair members resulted in improved performance, as seen by comparing results for types 1 *vs* 3, 1 *vs* 5, and 11 *vs* 12. Performance level was thus governed in part by the pair type used, and though not shown in Table 4, by the values of the acoustic variables within a pair type.

The results of Part B may be summarized simply. Over the 25 10-trial problems there were a total of three initial errors, on Trial 1 of Problem 18 and on Trials 5 and 6 of Problem 21. There were no repetitive errors. The initial error rate of 0.9% is consistent with results for Experiment 3, Part B, which used a much larger number of trials per problem, and was within the limits of localization error for a single sound for the animal, as found during the single stimulus training conducted before Experiment 1. The 100% correct level attained on Trial 2 evidences the complete mastery of an auditory discrimination learning set under the Trial 1 cueing method and favorable conditions of stimulus discriminability.

The study of Riopelle and Chinn (1961) of DLS in rhesus monkeys used a Trial 1 cueing method, and may be compared with the present experiments. On Trial 1 of each six-trial two-choice visual discrimination problem, the S+ was always presented in the same spatial position, but on Trials 2 to 6, it appeared randomly at either the left or right position. Over the 350 problems given, the monkeys progressively improved in the accuracy of response on Trial 1 and on Trial 2. For the final 35 problems, there were approximately 84% correct

Trial 1 responses and 86% correct Trial 2 responses. Under the Trial 1 cueing method of Experiments 3B, 4A, and 4B of the present study, the Trial 1 per cent correct scores for the dolphin were 85.7, 85.4, and 96.0%, respectively, and on Trial 2 the corresponding values were 95.2, 86.8, and 100% correct.

EXPERIMENT 5: DLS SKILL LEVEL UNDER THE BLIND BAITING METHOD

The prior DLS experiments used the Trial 1 cueing method with correction trials. Experiment 5 investigated DLS performance without Trial 1 cueing and without correction trials. The conditions of Experiment 5 thus follow the more common blind baiting DLS procedure (e.g., Harlow, 1949; Reese, 1964), in which the reinforcement outcome of the Trial 1 response serves as the sole cue for selection of S+ on Trial 2.

Procedure

Beginning the day after Experiment 4 was completed, three days of baseline DLS testing were given on a series of 24 new 10-trial problems. Easy discriminations were used, as identified through Experiment 4. Both sounds of a pair were presented at equal intensity and duration on Trial 1, so that intensity-duration differences no longer cued S+ on Trial 1. For a random half of the problems, the Trial 1 response was reinforced, and the sound selected remained S+. For the other problems, the Trial 1 response was not reinforced and the sound selected remained S-. If an error occurred on any trial, the predetermined trial sequence was continued without interruption.

Baseline testing was followed by six days of training to extinguish the animal's lose-shift error correction habit, with respect to speaker location of S+. Following an error, the animal had learned to respond to the opposite speaker (side) on the next trial, since S+ remained at the same speaker as on the error trial. The extinction training increased lose-stay probability by presenting S+ at the opposite speaker following errors, so that the animal now had to respond to the same speaker as on the error trial. In order to change response habits following errors, it was necessary, of course, that there be errors.

In view of the animal's capacity for near-errorless discriminations, errors were induced by conducting a series of nonspatial reversals using a fixed two-choice discrimination problem. The error occurring after each noncued reversal of reinforcement value of the sounds provided an opportunity to extinguish the prior learned lose-shift correction habit and reinforce lose-stay responding. Lose-stay training was continued, interspersed with occasional reintroduction of lose-shift training, until there was no obvious position response bias following an error. The nonspatial reversal problem favors a lose-shift response with respect to stimulus *characteristics*, but not with respect to stimulus *location*, and hence was well-suited for the type of retraining desired.

Beginning the day after this training ended, and continuing for 10 days, a series of 111 new 10-trial problems were given, using the same procedures as in the baseline testing. On 55 problems the animal's Trial 1 response was reinforced, and on the remaining 56 problems it was not reinforced. A pseudo-random sequence was used to govern the successive Trial 1 reinforcement outcomes. Problems were again the easy discrimination types identified in Experiment 4.

RESULTS AND DISCUSSION

Figure 5 gives the per cent correct responses for each trial for the baseline series of 24 problems and for the 111 problems given following extinction training of the error correction habit. The per cent correct responses are shown as a function of the Trial 1 reinforcement outcome. During baseline testing, almost all of the errors occurred on Trials 2 and 3 following the nonreinforced Trial 1 response, and were caused by the animal's adherence to its prior error-correction habit. That is, the animal reliably responded to the opposite speaker position following an error, but this response was no longer necessarily appropriate because speaker location of S+ was now a random variable following an error.

Extinction of the error-correction habit considerably improved the Trial 2 and 3 performance level on the following 56 Trial 1 nonreinforced problems, without seriously affecting performance on the 55 Trial 1 reinforced problems. Performance over these final 111 problems was not quite up to the levels

demonstrated earlier using the Trial 1 cueing method with correction, but the major difference was the somewhat lowered performance level on the relatively unfamiliar nonreinforced Trial 1 problem. The results showed a continued capability for one-trial learning of new discriminations (96 of 111, or 86.5% correct Trial 2 responses) despite the elimination of Trial 1 cueing and of the correction procedure.

GENERAL DISCUSSION

The Trial 2 performance of the dolphin, 86 to 100% correct responses in Experiments 3, 4, and 5, equalled or exceeded average Trial 2 levels observed for higher primate species in visual DLS tasks (Devine, 1970; Harlow, 1949; Miles, 1965; Riopelle and Chinn, 1961; Rumbaugh and McCormack, 1967; Warren, 1965). Runs of errorless problems in some cases rivalled those reported for individual rhesus monkey subjects (Harlow, 1949). This suggests a revision to Warren's (1965) statement that "no nonprimate mammal yet tested has approached the level of one-trial learning (in DLS tasks) observed in primate species (p. 266)."

The general procedure followed in the present studies was to train initial discriminations using fading techniques, and over succeeding discriminations reduce the use of fading. When S- fade-in was reduced to the ultimate limit of a single trial, the animal remained

Fig. 5. Performance over trials for the 24 baseline problems (dashed lines) and the final 111 problems (solid lines) given following training to extinguish the correction habit, as a function of Trial 1 reinforcement outcome.

under stimulus control and performed as well as it had with a much larger number of fade-in trials. Experiment 5 demonstrated that a high level of performance could be maintained even when S— fade-in (and correction trials) was entirely deleted. Experiment 5 also showed control of Trial 2 responses primarily by the reinforcement contingency following a Trial 1 response, with the implication that the animal was attending properly to the sound quality dimensions of the sound pair on Trial 1 of each new discrimination.

A discrimination learning set can thus be acquired effectively by use of fading techniques, with very few errors made during the course of acquisition. In the traditional DLS procedure, each problem is given without fading and error rates are initially high (Harlow, 1949). With succeeding problems, error rates are generally reduced, with the final error levels dependent upon the species tested (Riopelle, 1960; Warren, 1965). Fading techniques of the type used here might result in some improvement in DLS performance for other nonprimate mammals, though the species variable is likely to remain a principal determinant of the relative level of DLS skill attained (*e.g.*, see Sutherland and Mackintosh, 1971, p. 430).

Comparatively, what is required for each species tested for DLS skill is the production of the maximum skill level achievable, and this requires favorable conditions of stimulus control. Most DLS studies have relied on procedures developed for use with rhesus monkeys (*e.g.*, Miles, 1965; Reese, 1964). The degree to which the rigid modelling of such procedures penalizes a different species undergoing DLS tests can be evaluated only by systematic exploration of alternative methods of stimulus control (*e.g.*, Devine, 1970; Kay and Oldfield-Box, 1965).

The fading techniques also were effective in guarding against undesirable emotional behavior following S— responding, as has been observed previously when fading is used in simple discrimination learning (Terrace, 1966). Emotional responses such as jaw snapping, snorting, or tail slapping were rare following errors. They occurred typically when the start of a testing session was delayed, in the presence of cues signalling that a session was in preparation. Once the session began, emotional responses ceased.

In addition to the use of fading, several other procedures probably contributed to the high level of DLS skill achieved. Auditory discriminanda had been used previously in a DLS study with the present animal, but with only limited success (Beach and Herman, 1972). The considerable improvements in the sound generation, measurement, and projection system in the present study probably permitted the dolphin to take fuller advantage of its highly developed auditory system. Also, the discriminability of pairs of sounds was measured. The use of highly discriminable pairs improved performance on specific problems, and consequently DLS performance was improved over blocks of problems. Additionally, sound pairs were presented sequentially within a trial, whereas in the earlier study they were presented simultaneously (though spatially separated). Sequential presentation likely improved discriminability by eliminating mutually interfering effects of simultaneous sounds, permitting more ready identification of sound qualities.

Playback of the selected sound following a paddle press was required for stimulus control under sequential presentation. Performance improved immediately and markedly following the insertion of playback. Playback avoided the negative effects of hearing of the nonselected sound immediately before the reinforcement outcome, in cases in which the animal selected the first sound in the sequence of two.

Other techniques for stimulus control that differed from Beach and Herman (1972) included the use of an externally paced intertrial interval and the requirement for a stationing response within the listening area. Though the use of the call tone stimulus to control intertrial interval duration could not be shown to improve discrimination performance, testing for its effects preceded the introduction of the playback condition. The importance of the intertrial interval to DLS performance in highly trained monkeys has recently been demonstrated (Deets, Harlow, and Bloomquist, 1970) so that control of this variable seems desirable. The relatively short intervals used in this study (7 to 10 sec) served to reduce the frequency of unwanted behaviors between trials, *e.g.*, rapid swimming, leaping, *etc.*, thereby possibly assisting in the retention of the discrimination through the

reduction of interference from these activities. By holding the animal in the listening area until onset of the flashing light stimulus, the animal heard the two sequential discriminanda under favorable listening conditions. Without the stationing response, a paddle press might have been made before presentation of the second sound of a pair, possibly increasing the error probability if the two sounds were similar on some important acoustic dimension.

Food deprivation was not used. The animal received a daily intake of food normal for its weight, without any substantial evidence of adverse motivational effects. The most sustained period of testing took place during the 144 problems of Experiment 3A. The error rate during afternoon sessions (4.9%) was significantly greater than the rate during morning sessions (1.8%), but most of this error increase was accounted for by a mid-day "slump" occurring between 1 and 2 pm. Hence, there was no consistent or monotonic increase in error rate as the food intake accumulated over the day. Failure of the animal to respond on time to the limited-hold call tone was rare, as were inappropriate stationing responses. These observations, in conjunction with the high level of DLS skill shown, suggest that deprivation conditions may not be an important variable in simple discrimination learning or in DLS tasks for the bottlenose dolphin. A similar conclusion on the effects of the deprivation variable for various species of monkeys in discrimination learning and DLS tasks was reported in the study by Miles (1965).

Though firm conclusions are premature, the present evidence, taken together with results of DLS testing of primates (Harlow, 1949; Riopelle, 1960; Rumbaugh and McCormack, 1967; Warren, 1965), suggests the parallel evolution of a capacity for a high degree of learning efficiency in advanced species of non-human primates and in one species of Odontocete (toothed) whale, the bottlenose dolphin, *Tursiops truncatus*. This is not an unreasonable expectation in view of the impressive brain development of *T. truncatus* (Flanigan, 1972; Jansen and Jansen, 1969). It is possible that other species of Odontocetes, with comparable levels of brain development, might exhibit comparable levels of learning efficiency under DLS testing. In any event, testing for

additional complex learning skills in the bottlenose dolphin would be of interest.

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Received 1 May 1972.

(Final Acceptance 3 January 1973.)