DISCRIMINATIVE ECHOLOCATION IN A PORPOISE^{1,2}

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Operant conditioning techniques were used to establish a discriminative echolocation performance in a porpoise. Pairs of spheres of disparate diameters were presented in an underwater display, and the positions of the spheres were switched according to a scrambled sequence while the blindfolded porpoise responded on a pair of submerged response levers. Responses which identified the momentary state of the display were food-reinforced, while those which did not (errors) produced time out. Errors were then studied in relation to decreased disparity between the spheres. As disparity was decreased, errors which terminated runs of correct responses occurred more frequently and were followed by longer strings of consecutive errors. Increased errors and disruption of a stable pattern of collateral behavior were associated. Since some sources of error other than decreased disparity were present, the porpoise's final performance did not fully reflect the acuity of its echolocation channel.

Certain of the cetacea are capable of inspecting the underwater environment by analyzing reflected sound which originates in pulse trains emitted by the animal (Kellogg, 1958; Norris, Prescott, Asa-Dorian, and Perkins, 1961; Schevill and Lawrence, 1953, 1956). Cetacean echolocation systems are presently not well understood, and are being studied from various viewpoints (Evans, Sutherland, and Beil, 1964; Norris, 1964; Turner, 1962, 1964).

The present experiment sought to apply operant conditioning techniques to determine the acuity of the echolocation channel, and, through acoustical analysis of tape-recorded experimental sessions, to begin to elucidate the mechanisms underlying the animal's discriminative echolocation performance. The acoustical analysis will be presented elsewhere. The present paper emphasizes the behavioral

aspect of discriminative echolocation in a single subject.

METHOD

Subject

An Atlantic bottlenose porpoise (*Tursiops truncatus*, Montagu), was selected from a small captive school at Pt. Mugu and transported by truck to the research facility at Los Angeles. The animal, Alice, was a mature female, 7 ft long, weighing an estimated 300 lb at the start of the experiment.

Apparatus

Alice was maintained in an outdoor installation on the UCLA campus. Two 13,500 gallon tanks, each 24 ft in diameter and 4 ft high, were set up within a fenced compound. One tank was filled with industrial water to which water softener salt was added until the specific gravity of the solution reached that of sea water. Low levels of a quaternary ammonium compound were added as an algicide. The water was recirculated through a diatomaceous vacuum filter system for periods of 2 to 3 weeks. At the end of that time, the tank was drained, and Alice was moved to clean water in the alternate tank. Group manpower was used to move the animal: it was stranded in low water, rolled onto a stretcher, and lifted across the space separating the tanks.

¹These studies were aided by Contract NONR (G)-0007-64 between the Office of Naval Research, Department of the Navy, and the University of California. Additional support was provided by NASA Grant Nsg 237-62 and Brain Research Institute, University of California. Reprints may be obtained from Ronald N. Turner, Dept. of Zoology and Brain Research Institute, University of California, Los Angeles, Calif. 90024.

²The porpoise was obtained on loan from NOTS/NMC Cetacean Research Facility, U. S. Naval Missile Center, Pt. Mugu, California.

During experimental sessions, the porpoise was blindfolded with 3 in. diameter by $\frac{1}{2}$ in. suction cups formed by pouring RTV silicone rubber over a special glass mold. Half-inch cubes of styrofoam were sealed into the domes for floatation. In application, the flanges were lightly lubricated with petrolatum, and the suction cups were pressed over the eyes, completely blocking vision.

The stimulus display and response apparatus are shown in Fig. 1, and their placement in relation to the tank and to the porpoise are illustrated in plan view in Fig. 2.

The effective display consisted of a pair of steel ball bearings of disparate diameters. Uniform stems were fixed to the spheres and inserted into the tubular support as shown.

Figure 1 shows the display in one of two possible states. In this state, the standard $2\frac{1}{2}$ -in. sphere is on the right side of the display, and the variable sphere is on the left. The diameters of the variable spheres are listed across the top of Table 2.

In Fig. 1, the tubular support is attached to a vertical rod which projects through the center of a circular sealed styrofoam pontoon. The $3\frac{1}{2}$ -in. disc above the pontoon served as a marked dial by which the ball bearings were rotated manually into either of two display positions.

The response apparatus consisted of a pair of Plexiglas levers mounted on vinyl-coated

pontoons. The pontoons were rigidly connected by a 2 ft Plexiglas bridge, and the system was moored to tankside supports. A response was counted when the blindfolded animal swam up to the levers and pressed one or the other with its rostrum (or "nose") in such a way as to bring the lever into positive contact with an excursion limiter. Correct responses were immediately reinforced by a short, loud signal from a police whistle (auditory feedback), followed by food-reinforcement delivered manually into the reinforcement zone indicated in Fig. 2.

Underwater sound emissions from the animal were monitored. Echolocation signals were picked up by hydrophone, amplified, and monitored through a speaker system. In tape-recorded sessions, the signals were picked up by hydrophone (Atlantic Research Corp. LC-10), pre-amplified (Ballantine Labs Model 220B decade amplifier), and deposited on tape running at 7.5 in. per sec through a Uher 4000S recorder.

Fig. 1. Stimulus display and response apparatus, to scale. In display position, the centers of the spheres were 1 ft beneath the surface. The levers projected 6 in. beneath the surface. Surface bobbing caused very little fluctuation in these values.

Fig. 2. Schematic of the tank and animal, to scale. The broken outline shows the animal at the blindfolding station. The approximate boundaries of the porpoise's stable approach path are shown by broken lines. The broken lines forward of the porpoise show the paths it took from that position to the levers. The forward mooring line constituted an off-limits line which the animal never crossed. The mooring lines were 2 ft apart. Thus, minimum distance from the stimulus display was 2 ft, and most decisions were probably taken at a distance of 4 ft or more from the display. Alignment of the spheres underwater is shown on the circular pontoon.

Procedure

At the start of each session, the porpoise was summoned to tankside. The experimenter placed his hand in the water, palm up, and the animal swam to station and placed its rostrum ("chin") in his hand. The blindfolds were then pressed firmly in place over the eyes. As soon as the animal was blindfolded, it was released from the station, and the stimulus display was placed in the water in the state (R or L) specified by a list.

A list consisted of 24 sequential elements scrambled in a specified way.

List No. 1

L RR LLL R LL RR L RRR L R L R L R LL R

In this list, RRR appears once; RR twice; and R, five times. The elements L of the series are grouped in the same way and distributed among the Rs. Five such lists were constructed. The lists specified a non-random alternation of the standard sphere from left to right, and were designed to allow the assessment of elementary sequential dependencies as sources of control over behavior.

Placing the stimulus display in the water signaled the animal to begin responding. The splash-in was audible, and the stimulus display apparatus constituted a gross echolocation target. Upon receiving this signal, the animal swam to the response levers and pressed one or the other. The response was counted as correct, and was food-reinforced, if it was emitted on the lever which corresponded in position, R or L, to the position of the standard sphere. The response was counted as an error, and produced time out (TO) if it was emitted on the lever which did not correspond to the position of the standard sphere.

The contingencies for blocks of 24 consecutive responses are schematized in Fig. 3.

If the right lever was pressed when the standard sphere was on the right side of the display, the porpoise received immediate auditory feedback, and a fish was thrown into the SR zone at the far side of the tank. As the subject swam away to locate and collect the fish, the experimenter quickly dialed the next display state listed. The spheres were rotated by manual dialing while the animal was swimming away from the display whether or not the next state was the same as the last. There was thus no predictable relation between the

Fig. 3. Contingency diagram of the conditioning procedure for blocks of 24 consecutive responses. Each element of the list specified whether the standard sphere would appear on the right or on the left side of the display, and specified the response that would be food-reinforced. The display was advanced to the next state specified by the list only after a reinforced response. After an error, the display was stopped at the last state specified, and remained there until the correct response was emitted. The diagram is not continued for the case where an L appears in the list, since the subsequent events are parallel to those shown for R.

fact of dialing and the state of the display. Further, dialing involved scrambled numbers of complete rotations of the display before it was brought to rest to minimize the probability that the characteristic 180° of rotation necessary to change its state would exert any control over behavior.

Having collected the fish, the animal then homed on the apparatus to make another response.

If it pressed the left lever when the standard sphere was on the right side of the display, the display was immediately removed from the water, initiating a 5-min TO. The rate of lever-pressing when the display was absent was effectively zero. To terminate TO, the display was again placed in the water, with the larger sphere in the last displayed position.

Parallel contingencies prevailed when the standard sphere was on the left side of the display. Under this procedure, responses emitted on the lever which corresponded to the state of the display (correct responses) produced food-reinforcement, while those which did not (errors) produced TO.

Coinciding with the 24th response outcome, the display was removed from the water and the spheres were changed. The order of presentation of different stimulus pairs during the experiment is shown in Table 1.

Because of a normal slow mucus secretion from the animal's eyes, pressure inside the suction cups tended to increase gradually. Accordingly, the animal was summoned to the

Table 1

Number and Order of Conditions of Stimulus Disparity per Experimental Session. The entries correspond to the diameters of the variable sphere listed across Table 2. A corresponds to maximum (1.5 in.) and K to minimum (zero) disparity. Phase C, Session 14, is excluded from the data.

Session	Phase			Session	Phase				Session	Phase					
	1	2	3		1	2	3	4		1	2	3	4	5	6
1	A	K	A	15	B	C	D	C	28	D	E	F			
2	B	C	A	16	C	D	E	F	29	F	G	H	I		
3	C	F	B	17	D	E	F	G	30	G	H	I			
4	F	H	C	18	E	F	G	H	31	G	H	I	I		
5	H	B	F	19	F	G	H	I	32	G	H	I	I		
6	H	K	A	20	E	E	G	G	33	H	I	J	J		
7	F	B	H	21	F	F	G	G	34	H	I	J	I		
8	B	C	B	22	G	H	I	I	35	H	I	J	I		
9	B	B	B	23	G	H	I	I	36	H	I	J	J		
10	B	C	B	24	G	H	I		37	G	H	I	J		
11	C	F	C	25	H	I	I	I	38	G	H	H	I	G	I
12	C	F	C	26	H	I	I	I	39	G	K	G	H		
13	F	F	H	27	I	I	I	J	40	H	I	K			
14	H	H	(C)												

side of the tank during each period of TO, and the blindfolds, still in place, were pressed firmly, to ensure that they would not come off during a long run of reinforced responses. The reinforcement for this behavior was termination of time out from lever-pressing.

The subject was non-portable, except by group manpower, as noted above. Further, it showed a chronic sinistral spinal curvature, and the course this condition might take, given the additional stresses of daily hoistings, was unpredictable, from a veterinary standpoint. Accordingly, the control of food deprivation on the basis of body-weight was deemed ill-advised for this subject.

Adjustment of the daily food ration was therefore based on the animal's readiness to respond in the preceding session. Because of the value of the porpoise, the overriding criterion in adjusting the daily ration was to allow the largest ration possible, consistent with obtaining steady behavior. Over the course of the experiment, the porpoise's average ration was 9 lb of fish, with adjustments fluctuating around this value. The subject was held to an average ration equal to about 60% of the amount an animal of this size will consume on daily free feeding. It was capable of consuming as much as 26 lb of fish in less than 1 hr, and did so immediately after the final experimental session.

The animal was maintained on a mixed diet of frozen white bait, silver smelt, and mackerel, thawed just before each session, and supplemented with a multi-vitamin formula to compensate for loss of food value due to freezing. The smaller fish were used for reinforcement (maximum weight of smelt was 0.1 lb), and mackerel were used to round out the ration.

During initial training, the porpoise was taught to station at tankside, to accept blindfolds, to press levers, to distinguish the standard sphere from those of less than 1 in. in diameter and to vocalize. During this period, the experimenters frequently swam with the animal and attempted, through training and direct manipulation, to correct the spinal curvature which kept the animal swimming in a counterclockwise direction. It was taught to swim clockwise, but would do so only if explicitly required, and then only by rolling onto the left side and bending the body forward. This is not a normal posture for a porpoise, and this maneuver indicated that the curvature was rigid. Further attempts to correct it were abandoned.

The final procedure was in effect for 40 experimental sessions. After the seventh session, an inflammation of the left external ear opening was noted, and the porpoise was placed under veterinary care for 10 days. Response to treatment was satisfactory, and the animal was

put back to work. After seven more sessions, there was an unaccountable loss of behavior (Phase C, Session 14). The animal was allowed free food for a number of days, and then the daily food ration was again sharply reduced. After a final block of 26 sessions, the experiment was terminated. The term of loan was up, and the porpoise was returned to Pt. Mugu.

RESULTS

Collateral Behavior

During long runs of reinforced responses, behavior between responses was extremely stable. Since more than one-half (.55) of the

runs in the final block of 26 experimental sessions contained 4% error or less, and roughly one-third (.32) were error-free, a substantial portion of the total behavior is described by the typical interresponse sequence below. The sequence may be read with reference to Fig. 2 and 4.

Figure 4 shows the time course of changes in the amplitude of recorded signals, against a background of fluctuating ambient noise. A detailed analysis of acoustical behavior will be presented elsewhere. Figure 4 was prepared to display the gross features of the animal's signal output in relation to the experimental procedure, and to illustrate the stability of this output.

Fig. 4. Sample record of acoustical events associated with the porpoise's discrimination performance, for three consecutive reinforced responses. (a) Echolocation pulse trains emitted as the porpoise homed on the levers while scanning the display before a response. R_1 , R_2 , R_3 : Consecutive reinforced responses, with vertical arrows showing amplitude changes in the record due to the conditioned reinforcement (an auditory stimulus) that accompanied each response. The slanted arrows show the moment at which the porpoise contacted the food reinforcement following R_1 and R_2 . (b) Short trains of high amplitude pulses emitted as the animal rolled away from the levers after responding. (c) Pulse trains emitted as it scanned the tank and homed on the food fish. (d) Low amplitude pulses, often close to the momentary level of ambient noise in the record, emitted on the return path from the S^R zone. In this record, the animal was comparing a 1.75-in. sphere with the standard 2.50-in. sphere. The standard was on the animal's left before R_1 , on its right before R_2 , and on its left again before R_3 . The overlapping panels of the record were produced by processing a section of a tape-recorded session through a Visicorder (Minneapolis Honeywell Model 1508). The overlapping parts of the record indicate roughly the variation to be expected in two runs of a single section of tape through the Visicorder.

Pulse trains emitted are made up of a series of discrete "clicks" or "pops", each of which covers a broad frequency spectrum. Due to limitations of the recording apparatus, the record shows changes in sound energy only for the portions of each pulse below 20 kc. Then in any time interval where no pulse, or a low amplitude pulse, was recorded, a high amplitude pulse with all, or nearly all, of its sound energy concentrated above 20 kc may have been emitted. The figure illustrates stable patterning of output below 20 kc.

Substantial rises in errors were generally associated with a disruption of this stable colateral performance.

Auditory feedback accompanied the emission of food-reinforced responses. Upon receiving this signal (arrows at R_1 , R_2 , R_3 , Fig. 4), the animal breathed and submerged, rolling counterclockwise away from the levers and emitting a short train of high amplitude signals (Fig. 4b). With one or two beats of its flukes, the subject glided toward the S^R zone. As it moved through the water toward the S^R zone, pulse emission (Fig. 4c) was accompanied by "scanning" (Kellogg, 1960) which decreased

in extent of excursion as the animal veered sharply from the glide path to home directly on the food-fish. Sound emissions stopped at the moment of contact with the fish (slanted arrows, Fig. 4). As the animal continued the counterclockwise path from the S^R zone to the levers, low amplitude sound emissions were typically resumed (Fig. 4d). The animal surfaced at about the mid-point of the path, rested, and breathed once or twice before submerging again. As it submerged, sound emissions (Fig. 4a) and scanning occurred as it moved an additional body-length toward the display, bringing it into the position shown in Fig. 2. From this orientation, the subject either continued to home on the lever dead ahead, or snapped its head to the left and veered sharply to home on the farther lever.

Deviations from this stable pattern of behavior, emitted between lever-pressing responses, are described below.

Sources of Error

The overall error level associated with discriminative echolocation performance is presented in Table 2 and in Fig. 5. The data fall

Table 2

Mean and Range of Relative Error under each Condition of Stimulus Disparity, by Blocks of Experimental Sessions

Sessions	Variable	A	B	C	D	E	F	G	H	I	J	K	Total Responses
	Sphere Diameter (inches)	1	1¼	1½	1⅞	1⅞	1¾	1¾	2	2½	2¾	2¾	
1-7	Mean	.09	.03	.14			.21		.19			.71	
	Range *min	0	0	.13			.13		.13			.54	
	*max	.25	.13	.17			.29		.29			.88	
	Responses	96	96	72			96		96			48	504
8-14	Mean		.07	.02			.05		.26				
	Range min		0	0			0		.21				
	max		.17	.04			.13		.33				
	Responses		168	144			96		72				480
15-27	Mean		0	.04	.04	.06	.06	.03	.05	.11	.54		
	Range min			.04	0	0	0	0	0	0			
	max			.04	.08	.08	.17	.08	.21	.25			
	Responses		24	72	72	120	144	240	168	360	24		1224
28-40	Mean				0	0	0	.02	.07	.14	.34	.71	
	Range min						0	0	0	0	.13	.58	
	max						0	.08	.29	.41	.63	.83	
	Responses				24	24	48	216	312	384	168	48	1224
	Total Responses	96	288	288	96	144	384	456	648	744	192	96	3432

*min and max of relative error for blocks of 24 successive responses

naturally into three main blocks of sessions, as described under *Procedure*, and are presented accordingly. In addition, the final block of 26 sessions has been divided into two blocks of 13 sessions for purposes of analysis.

Relative error (errors per responses) was found for each phase of each session. The minima and maxima of these values are presented in Table 2 as the range of relative error under each condition of stimulus disparity.

Mean relative error (errors per responses, at each degree of stimulus disparity) was found for blocks of sessions. The numbers of responses on which the means are based are given in Table 2, and the means are plotted in Fig. 5.

In Fig. 5, the means for the first seven sessions show that relative error tends to increase with decreases in stimulus disparity. The means for the second block of seven sessions show that, given sufficient stimulus disparity, the overall error level drops with continued exposure to the conditioning procedure. Both relationships are borne out and

Fig. 5. The relationship between errors and stimulus disparity for the first 14 sessions (top) and for the last 26 sessions (bottom). The points plotted give errors per responses, by degree of stimulus disparity. Disparity was zero when the diameter of the variable sphere equalled that of the standard, at 2.50 in.

clarified by the means plotted for the first and final blocks of 13 sessions.

The principal source of error in the final performance was decreased stimulus disparity. Performance appears to have been still improving when the experiment ended.

The data of the final block of 26 sessions analyzed for the type of error generated by decreasing stimulus disparity, under the following classification of errors.

An *initial error* terminated a run of one or more correct responses. Equivalently, it is the first error in a run of one or more errors. An initial error could occur in just two ways. Either the porpoise failed to switch to the other lever when the display was switched, or it switched to the other lever when the display had not been switched. Both types of initial error necessarily occurred at some point in the switching series illustrated by List No. 1. All five lists had the same properties as List No. 1 in terms of the relative frequency of opportunity to emit initial errors by failing to switch or by switching.

A *successive error* was preceded by an error. Equivalently, it is any error after the initial error in a run of two or more errors. A successive error could occur in just one way: the porpoise failed to switch to the other lever after an error.

Errors which occurred at the outset of a phase are excluded from the treatment of initial and successive errors. There were just nine of these during the experiment.

Finally, any of these errors were necessarily emitted on either the right or left lever.

Figure 6 displays the contributions of initial and successive errors to the overall level of error, and also shows the proportion of initial errors due to the animal's failure to switch when the display was switched.

Decreased stimulus disparity tended to increase the frequency of both initial and successive errors. When disparity was $\frac{3}{8}$ in. or more of sphere diameter, most errors were initial errors terminating runs of correct responses, and successive errors were emitted in relatively short and infrequent strings. When disparity was reduced below $\frac{3}{8}$ in. of sphere diameter, errors were sharply compounded due to the emission of longer strings of successive errors which followed initial errors more frequently. This increased frequency of longer strings of successive errors was neither a neces-

Fig. 6. The relationship between errors and stimulus disparity, by type of error, for the last 26 sessions. In both graphs, the upper curve shows the proportion of initial errors which were due to the porpoise's failing to switch when the display had been switched. The lower curves show initial and successive errors relative to responses, by degree of disparity.

sary nor a predicted outcome, since, under the procedure used, the probability of reinforcement was 1.0 if the animal switched to the other lever after an error. Throughout, most initial errors were due to the animal's failure to switch when the display had been switched.

The data from the final block of 26 sessions were examined for the point in the list at which the animal made an initial error by failing to switch. List No. 1 shows that errors of this type could occur only after groups of 1, 2, or 3 elements of a kind. The relative frequencies with which such opportunities for error appeared in the lists are compared with observed errors in Table 3. Initial errors due to failure to switch occurred in almost exactly the same proportion as opportunities.

The same relationship was found for switching when the display had not been switched. Errors of this sort could occur only after the

Table 3

Initial Errors due to Failure to Switch, and Opportunities for this error. (The proportionality of observed errors to opportunities in 26 sessions is displayed by multiplying the opportunities in a single run through the list by a suitably chosen factor).

<i>Failure to switch after</i>	<i>L or R</i>	<i>LL or RR</i>	<i>LLL or RRR</i>
Frequency in the list	10	4	2
Frequency in the list $\times 6$	60	24	12
Observed Frequency	61	23	13

first of two or three elements of a kind, or after the second of three elements of a kind. The relative frequencies with which such opportunities for error appear in the lists are compared with observed errors in Table 4.

Table 4

Initial Errors due to Switching, and Opportunities for this Error

<i>Switching after the first element of</i>	<i>LL or LLL, RR or RRR</i>	<i>Switching after the second element of</i>	<i>LLL or RRR</i>
Frequency in the list	6		2
Frequency in the list $\times 4$	24		8
Observed Frequency	25		9

Initial errors due to switching occurred in very nearly the same proportion as opportunities.

Finally, errors on the right lever were compared with those on the left lever.

In sessions 15-27, errors that terminated runs of correct responses were evenly split (.51 on the right), but about three-quarters of successive errors (.74) were emitted on the right-hand lever. Having made an initial error on the right, the animal tended to follow with a string of responses on the same lever. The proportion of errors emitted on the right therefore reached .59, for this block of sessions.

In the final 13 sessions, .49 of initial errors were emitted on the right, as were .45 of suc-

cessive errors. The proportion of errors emitted on the right was .47.

When analyzed by type, most of the error generated by decreased stimulus disparity proves to be due first to the animal's failure to switch when the display was switched and then to its following this error with strings of successive errors. Both types of initial error were committed in direct proportion to opportunities; hence, they were committed at random with respect to the lists, and elementary sequential dependencies (for example, the probability of reinforcement is 1.0 if the animal switches after three successive reinforced responses) exerted no control over the behavior. Since the animal failed to respond to simple dependencies, higher order dependencies were not examined.

After an initial tendency to emit a disproportionate number of consecutive errors on the right lever had faded, errors were fairly evenly distributed between the right and left levers.

Most substantial rises in errors were associated with a disruption of the extremely stable collateral behavior observed between responses when errors were infrequent. There were two very typical deviations, which came to predict error.

In Fig. 2, the approximate boundaries of the porpoise's typical approach path are indicated. Whenever the animal exceeded the boundary centrifugally, homing on the display along a path which lay between the outer boundary and the tank wall, the experimenters were generally correct in predicting an error and in predicting that the impending error would be committed on the porpoise's right lever. Exceeding the boundary centripetally, the animal was as likely as not to swing to the right when a response on that lever was called for.

Normally the animal surfaced about one body-length behind the position shown in Fig. 2, breathed, submerged, and began the echolocation run on the display. Whenever the animal glided too close to the levers before submerging, the experimenters were generally correct in predicting an error. Errors due to too great a proximity to the levers at the start of the discriminative echolocation run seemed to be correlated with shorter-than-normal sound emissions (event a, Fig. 4).

Some factors associated in a prior way with these deviations from the stable pattern of collateral behavior were identifiable.

The main factor was decreased stimulus disparity, which led to strings of errors. The stable pattern of behavior typically emitted between responses decayed rapidly as errors accumulated, and deviations from the stable pattern were most frequent and pronounced when equal 2.50-in. spheres were displayed. Here, long strings of successive errors were more frequently interspersed among short runs of reinforced responses.

In delivering food-fish to the animal, the fish were pressed to collapse the swim bladder and reduce gas content. An occasional fish floated on the surface despite this precaution. The porpoise had difficulty locating fish which lay near the interface, and was apt to home eccentrically on the display after protracted searching maneuvers had disrupted normal orientation to the boundaries of the tank.

Finally, instability in the collateral behavior appeared to be tied to the animal's readiness to respond at the outset of a session. The more or less intuitive way in which food intake was restricted was an undoubted source of error in performance, with losses of motivation leading to elevated error levels, and, very probably, to the temporary loss of behavior toward the end of the 14th session.

DISCUSSION

The present experiment has replicated the findings of others (Kellogg, 1958; Norris, *et al.*, 1961) with respect to the existence of echolocation systems in *Tursiops truncatus*. The evidence is overwhelming that the events in a, b, c, and d, Fig. 4, represent active echolocation signals, and that disruption of this channel would incapacitate the blind-folded animal. Since the visual channel was ruled out, information obtained through the echolocation channel was the basis of discrimination performance.

Further, the experiment demonstrated that operant conditioning procedures can be applied to explore the quality of such systems. When the experiment was terminated, behavior was clearly under stimulus control provided by the display, for all values of disparity equal to or exceeding $\frac{3}{8}$ in. for diameter in the spherical targets. Regarded as an estimate of the acuity of the system under the stated conditions, this is a probable underestimate. The curve in Fig. 5, which represents the final

performance, would probably have been translated to the right if exposure to the procedure had continued.

It would be interesting to know which properties of the display were controlling behavior. From Fig. 1, it is apparent that responses which were reinforced on the basis of parity between the lever pressed and the position of the standard sphere could have been emitted after the animal had made any of a number of measurements. Some of these are more plausible than others. For example, comparison of the diameters of the spheres, of the distances from the standard sphere to each of the levers, or of the rates of curvature of the spheres away from the vertical rod, singly, or in any combination, would correctly identify the state of the display. We are left with the loose interpretation that the distinctiveness of the "sonic signatures" coordinated with the two states of the display became more and more blurred as the size of the variable sphere approached that of the standard, and that increased errors were the consequence of this blurring. The present experiment does not describe the signatures which enabled the animal to perform as it did. Further experiments in this area are currently underway. In these, coded vocal responding is being substituted for the lever pressing response to eliminate unnecessary hardware from the tank. This

in turn is expected to clarify the acoustical picture and to simplify the steps necessary to isolate the exact controlling stimuli.

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Received July 21, 1965