Data were taken with a modified method of limits and the same stimulus values as in the avoidance procedure. The subjects were presented with a series of flashes at a given wavelength starting at a subthreshold intensity. Successive flashes were intensified unless the subject saw a given flash, at which time those trial conditions were repeated. If the subject released the lever before a flash was presented, that trial was repeated. Threshold was taken to be that intensity at which the subject indicated (by responding to the flash within 622 msec) that he saw two successive flashes.

Figure 2 compares complete spectral sensitivity functions obtained by this technique (designated S^{+R}) on three monkeys (M1, M3, M5), with the one previously obtained (M2) using cued avoidance. It is apparent that essentially the same function was obtained by both techniques. This figure also indicates that the peak found near 610 nm and the deep cleft at 580 nm are probably characteristic of the photopic spectral sensitivity of these primates. Monkey M4 was the only one of five monkeys not showing these features. It is interesting to note that M4 shows a peak at 580 to 590 nm, which is most prominent for the 2-deg field condition (Fig. 1). It may be noted in Fig. 1 that a slight shoulder shows up at 610 nm for M4 which corresponds to the large peak found there with all the other animals. Data on humans obtained with 1000-troland adaptation shows peaks at 580 to 590 nm and at 600 to 610 nm. These rarely appear as distinctly as those of monkeys 1, 2, 3, and 5; rather, in human data, they frequently appear as shoulders or slight humps. In Fig. 3, data obtained for a human subject with a similar-sized, white-light surround and 2-deg test field show the similarities in these features between M2 and M4 and humans. The two human curves were obtained on the same observer at two different luminances of the adapting field—1000 and 10,000 trolands. The M2 data, as well as the data for the other three animals of Fig. 2, agree favorably with the human function for the higher adapting luminance.

The M4 data (Fig. 3) agree in surprising detail with the human adapted to the lower luminance. A possible explanation for the difference between M4 and other monkeys is that M4 has much greater light absorption in the preretinal pigment, making the 3000-troland surround effectively dimmer.

Spectral sensitivity data on a single rhesus monkey obtained by Grether (*4*), in an early experiment on absolute thresholds, show the deep cleft near 580 nm and the secondary peak at 610 to 620 nm. Recent data on the rhesus monkey reported by De Valois (*5*) do not show these features. It is believed, however, that measurements in the latter study were made at too few wavelengths to permit conclusions on the presence or absence of the features reported here. Several studies have shown the dip at 580 nm in humans (*3*).

In addition to demonstrating the usefulness of the two procedures described, these data, although incomplete, show a similarity between monkey and man which may eventually support the conclusion that rhesus monkeys and man have identical mechanisms of spectral sensitivity. While both procedures yield satisfactory data and require about the same investment in time and apparatus, the positive reinforcement paradigm has the additional advantage of keeping the subjects more cooperative.

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2. Trolands were used in order to compare data with those obtained on human subjects. The surround was calibrated with a MacBeth illuminometer 3 inches from the ground glass positioned in front of the final lens and artificial pupil. The average luminance of several readings was 48 mlam. With the formula $T = 10 \cdot B \cdot r^2$, where T = trolands, B = the brightness in millilamberts (48 for our surround), and r = the radius of the limiting pupil (in this case, animal's pupil taken to be 2.5 mm), the surround was calculated to be 3000 trolands. The relative radiant energy of the 2-deg test spot was measured at the pupil of the eye with a platinum-black, compensated thermocouple. The attenuation of the continuous-density filter, used to vary luminance of the test spot, was measured with the thermocouple over two log units at 35 wave bands in the region from 380 to 720 nm.
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Communication between Dolphins in Separate Tanks by Way of an Electronic Acoustic Link

Abstract. *Two isolated dolphins* (Tursiops truncatus) *were provided with an electronic acoustic link during alternate periods of approximately 2 minutes. The dolphins repeatedly communicated in a tight sequence when the acoustic link was connected. Their responses varied as the experiment progressed. Some information regarding possible meaning of the whistles was obtained.*

Dolphins emit a variety of sounds underwater that include whistles, click trains, and miscellaneous signals. The complexity and extent of dolphin communication are not known. The click trains are used for echolocation (*1, 2*); the whistles correlate with evident communication and variations in behavior and emotional state (*1, 3–5*). Miscellaneous signals appear during feeding, sexual activity, and playing (*3*). Dreher (*6*) reported considerable vocal response by a group of six dolphins (*Tursiops truncatus*) to each of six different recorded dolphin whistles. Lilly (*7*) reported that *Tursiops* can match numbers and durations of human vocal bursts. Lilly and Miller (*8*) physically restrained each of two dolphins at opposite ends of a tank of water using visual barriers that still permitted them to hear each other and to reply. The animals emitted numerous sounds in sequenced exchanges with but few superpositions. Each dolphin

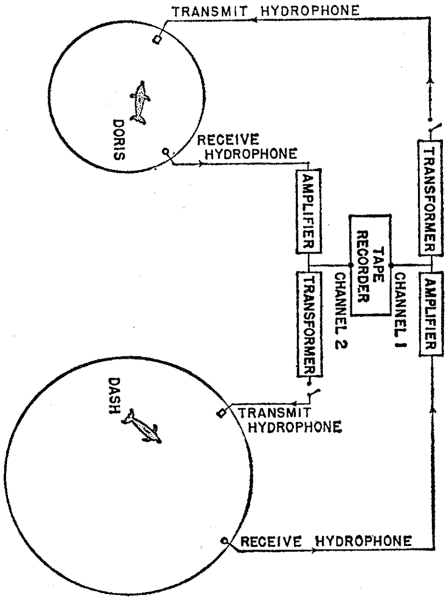


Fig. 1 Diagram of intertank communication test.

emitted whistles and click trains both individually and simultaneously. Which signals were the significant carriers of information was not determined.

Two Atlantic bottlenose dolphins (*Tursiops truncatus*) were placed in separate tanks that were coupled acoustically by hydrophones. The acoustic link was intermittently connected and disconnected by the experimenters. The dolphins were free to swim and were out of contact with each other except for the acoustic link.

The experiment was conducted on 11 November 1963 at the Marine Biology Facility (*9*) at Point Mugu, California. Figure 1 shows the general arrangement of tanks, animals, and electronic equipment. The sounds in each tank were continuously recorded on separate tracks of a stereo magnetic tape recorder. The acoustic link was connected and disconnected at approximately 2-minute intervals during the study. A dash-dot signal at 2.7 kcy was transmitted into each tank at the beginning of each acoustic link period, and a dot-dash signal at 2.7 kcy was transmitted when the link was disconnected. The experimenters and their equipment (*10*) were located in a trailer out of sight of the dolphins.

A 5-year-old female dolphin named Doris that had been captured off Florida and weighed 114 kg was isolated in a steel-walled plastic-lined tank 9.1 m in diameter. The tank rested on sand and was filled to a depth of 1.1 m. A 5-year-old male dolphin named Dash that had been captured off Mississippi and weighed 173 kg was isolated in another tank. This tank was of concrete and was 15.2 m in diameter; it had a separate water supply and was recessed in the sand 9.1 m from the other tank. The two dolphins had been held in one tank prior to these experiments. Each had participated in a prior intertank communication test with one other dolphin on the day of this experiment. Several earlier intertank communication tests had been conducted on various combinations of other animals, tanks, and equipment in order to perfect the experimental procedure. In general, the results were qualitatively similar.

The experiment lasted 32 minutes and consisted of 16 periods. The tanks were acoustically coupled only during even-numbered periods. The acoustic link was disconnected or cut off during odd-numbered periods.

The tape recording was processed by a Miller cathode-ray oscillograph to provide the graph shown in Fig. 2 of amplitude versus time for each track. The dolphin sounds are labeled by type; types A, B, C, D, E, and F are whistles, an *o* is a click train, an *x* is a single "cracking" sound resembling a distant rifle shot, similar to that reported by Caldwell *et al.* (*11*), and each *z* is a grunt-like or squawking sound. Some of the recorded vocalizations were not of sufficient amplitude to appear on the trace in Fig. 2 and were labeled on the basis of auditory review. The primary use of the amplitude traces in Fig. 2 is to show time relationships. The whistles were categorized into types A, B, C, D, E, and F on the basis of their frequency-versus-time characteristics as processed by an Alden comb-filter analyzer.

Although numerous whistles were analyzed, only a few contours that represent typical whistles from Doris

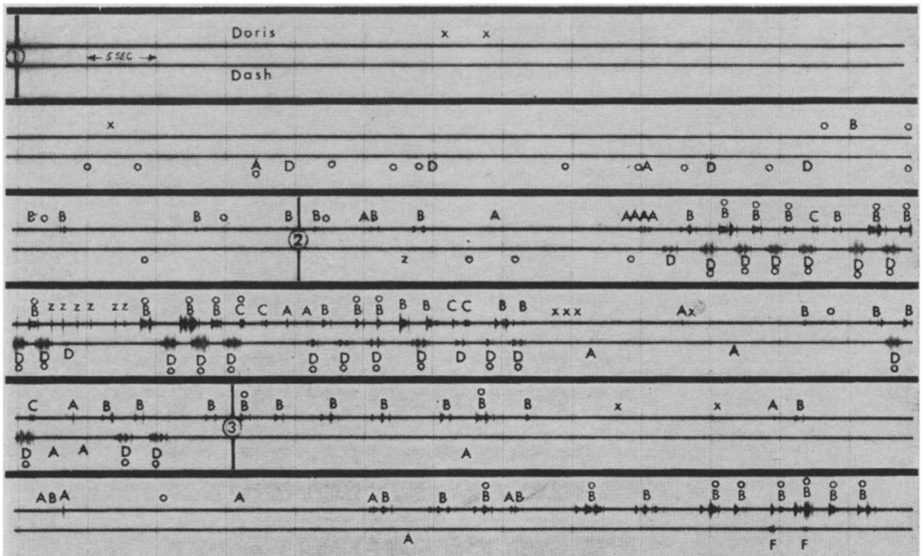


Fig. 2. (Above and right) A graphic record of the acoustic responses between Doris and Dash. Circled numbers = periods; A, B, C, D, E, and F = whistles, *o* = click trains, *x* = cracks, *z* = other sounds.

and Dash are shown in Fig. 3; these contours were traced from the Alden record for clarity. The dotted sections of the whistles were not of sufficient intensity to be analyzed by the Alden, but were drawn in on the basis of auditory review at reduced tape speed. Harmonics that appeared on the Alden record were not reproduced in Fig. 3; the harmonics were relatively weak, appeared only when the signal was unusually strong, and may have been introduced by the equipment.

Figure 2 shows that numerous exchanges of sounds occurred during the acoustic-link periods (even-numbered periods). Acoustic exchanges are not uncommon in the animal world (*12*). It is perhaps significant that sounds were exchanged by the dolphins even though they were out of visual and physical contact with each other and in an artificial situation. Neither animal vocalized for more than a few seconds at a time, and there was no obvious evidence of long one-sided vocalizations.

The whistles varied in frequency from 4 kcy to about 18 or 20 kcy and varied in amplitude from close to background noise level to recorder saturation. On the basis of their frequency variation the different whistle types were clearly recognizable during auditory review at reduced tape speed. Although the whistles could have been categorized differently, the selected categories were believed to be the most significant groupings from the viewpoints of machine analysis and auditory review.

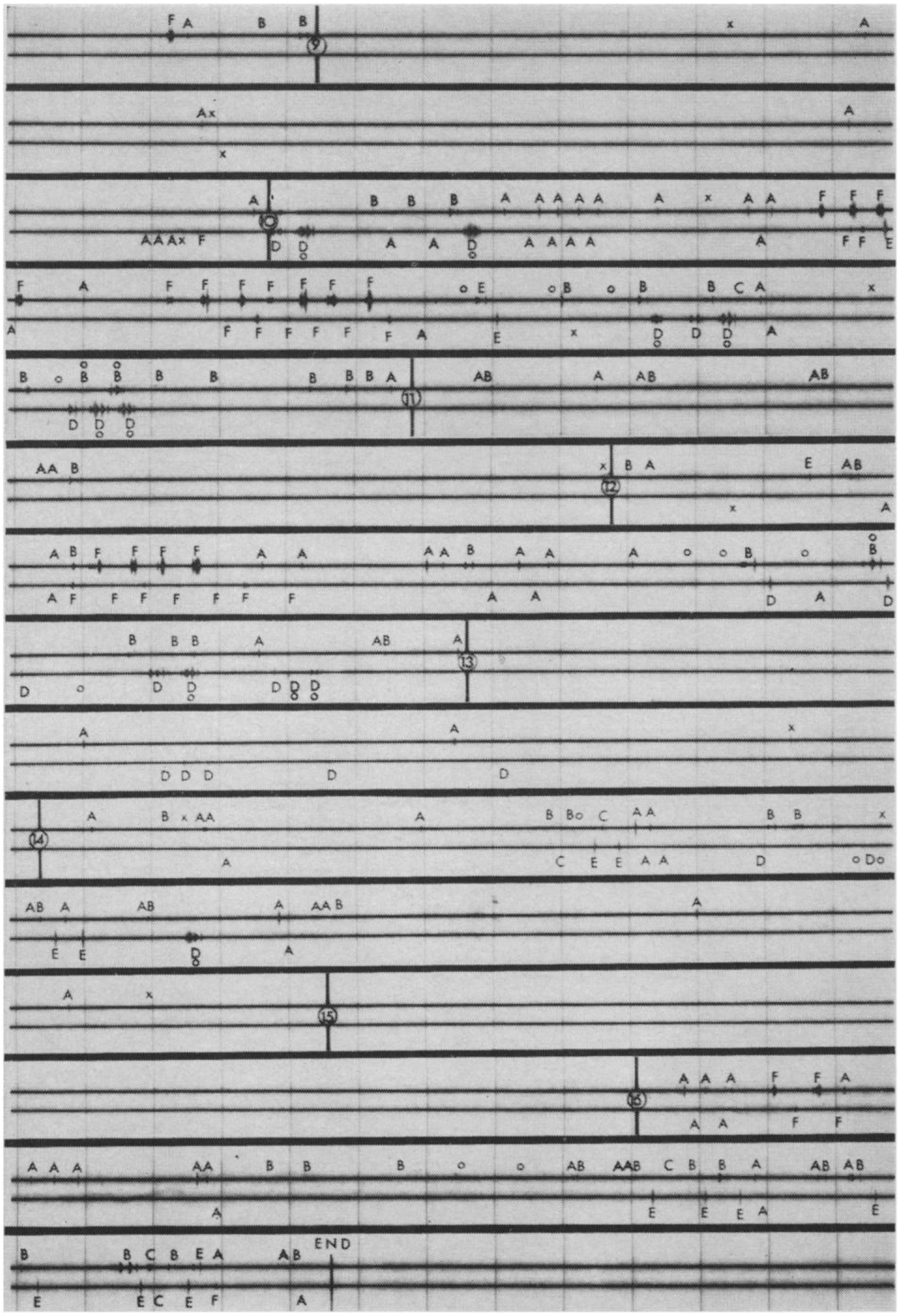
Figure 2 shows no evidence of acoustic exchanges based solely on click trains or any single type of sound other than whistles. The use of click trains in communication, however, should not be ruled out entirely since clicks and whistles were often emitted simultaneously. Moreover some evidence exists that at least one species of cetacean, the sperm whale, utilizes clicks for communication since they have never been heard to whistle (*13*).

During periods 2 and 4, Dash emitted the most click trains and was seen to jump several times. No jumping was seen or heard either before or at any time during the experiment. Since click trains are used for echolocation, it is conceivable that Dash was attempting to locate Doris. Doris emitted fewer click trains, but 61 percent of these were also emitted during periods 2 to 4.

Figure 4 is a bar graph derived from Fig. 2 showing the number of whistle groups and click trains emitted by Doris and Dash during each period. A single whistle or a group of whistles emitted within 1 second of each other is counted as one whistle group. A simultaneous whistle group and click train are counted as one of each. A total of 394 whistle groups (235 from Doris and 159 from Dash) was emitted during the acoustic-link (even-numbered) periods, and only 68 were emitted during cut-off periods. Few click trains were emitted after period 4, suggesting that they were no longer useful. The increased incidence of whistles during the acoustic-link periods continued throughout the experiment, suggesting that whistles are the primary means of communication. The average whistle-group duration was about one second.

No C-type or E-type whistles were emitted during the cut-off periods, and only 4 percent were F-type. The predominant whistles emitted during the cut-off periods were types B (43 percent), A (41 percent), and D (12 percent). No sequenced exchanges of sound occurred during these periods.

The predominant whistles during the acoustic-link periods were types A (36



percent), B (25 percent), D (15 percent), and F (14 percent); 5 percent were type C and 5 percent were type E. Listed in order of the number recorded, Dash emitted whistle types D, A, F, E, and C, and Doris emitted whistle types B, A, F, E, and C. Defining an exchange of sounds as being a tight sequence of at least three alternate whistles from each dolphin, it is noteworthy that 25 exchanges occurred during the acoustic-link periods. Nine of the exchanges consisted predominantly of B-type whistles from Doris and D-type whistles from Dash (primarily periods 2 and 4). Five exchanges were predominantly F-type whistles (periods 8, 10, 12), three exchanges were A-type whistles (periods 4, 8 10), and the remaining seven exchanges were mixtures of several different whistle types (periods 8, 10, 14, 16). The exchanges varied in time, beginning with B and D whistles, followed by either F or A whistles, and ending with mixed whistle types.

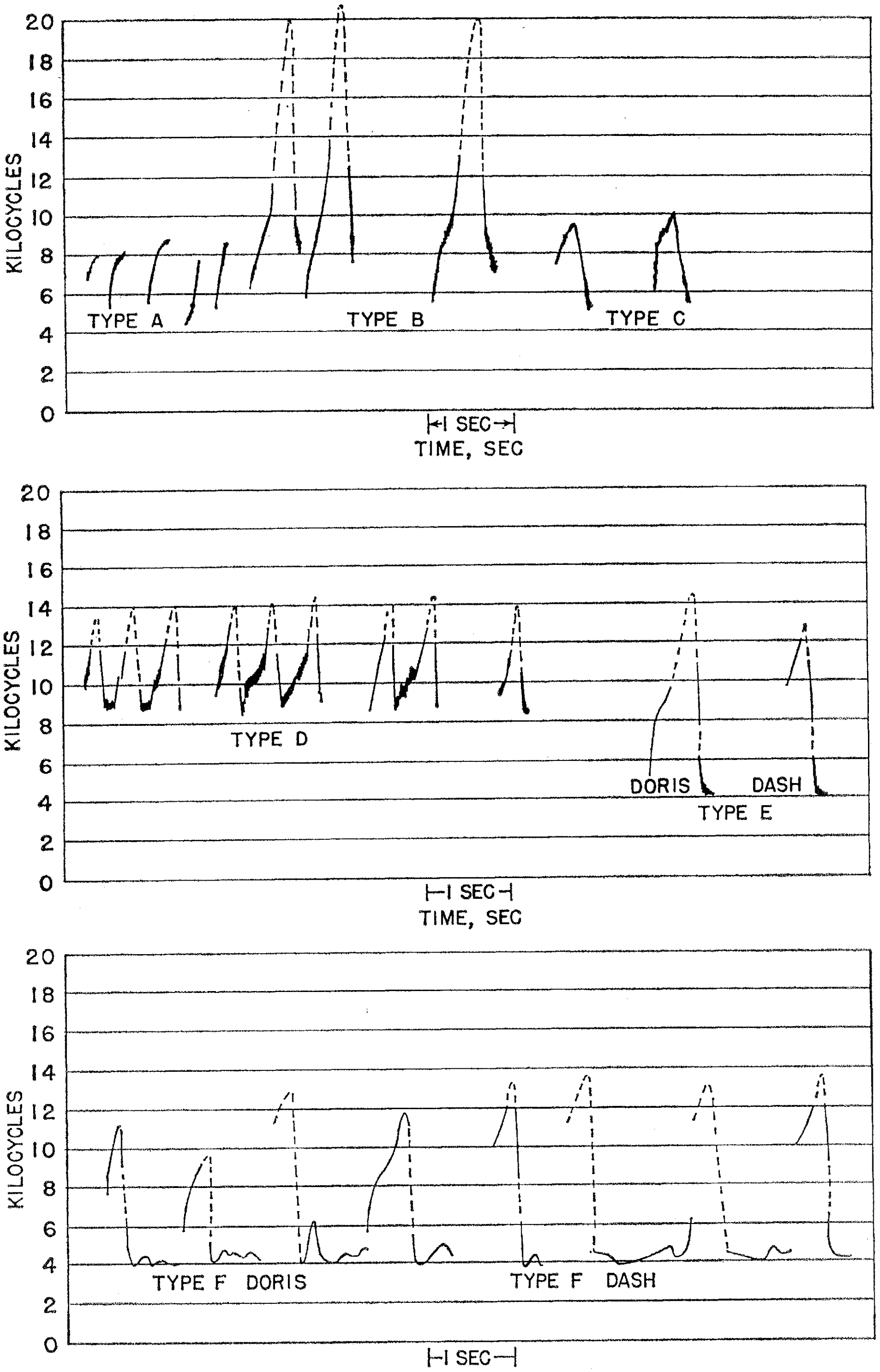


Fig. 3. Examples of dolphin whistles.

All of the B-type whistles were emitted by Doris, and all of the D-type whistles were emitted by Dash. Since the B and D whistles are similar in pitch variation, quantity emitted, and order of appearance, it is likely that these whistle types should have been grouped together. If the B and D whistles belong to the same group, then their differences as shown in Fig. 3 represent individual variation and could therefore serve for individual identification.

A detailed analysis of Fig. 2 suggests that the animals may have learned to quickly detect whether the acoustic link was connected or not. From period 7 on, the average elapsed time between the dot-dash signal (beginning of a cut-off period) and the first whistle from each animal was 64+ seconds, while the average elapsed time between the dash-dot signal (beginning of an acoustic-link period) and the first whistles was only 6 seconds. No such pattern existed before period 7. If learning occurred, it may have resulted from hearing either the transmitted dot and dash signals or the change in background noise when the acoustic link was connected or disconnected.

On 23 March 1964, about 4 months after the original experiment, Doris' sound track was transmitted into a tank where Dash was isolated. The playback level was set low to reduce the possibility of Dash's hearing his old responses. Dash immediately responded to most of Doris' whistles, using a D-type whistle. He intermittently emitted a few additional D-type whistles and an occasional click train, and then suddenly stopped responding after 113 seconds of period 8. He did not emit another sound during the remaining portion of the playback (through period 16).

On the following day Doris' sound track was once more transmitted into Dash's tank as a repeat experiment. This time Dash again responded to most of Doris' whistles with a D-type whistle and suddenly stopped responding 95 seconds into period 8, approximately as before. He began responding again, 56 seconds into period 14, and continued responding to the end of the playback.

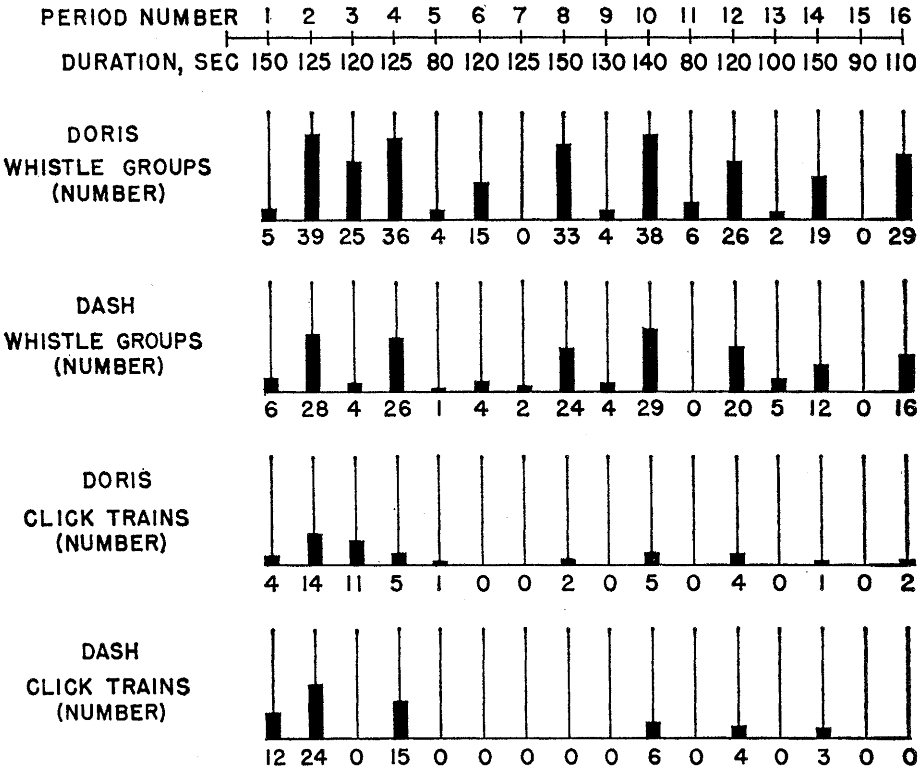


Fig. 4. Quantity of whistle groups and click trains emitted by each dolphin during each period. Whistle groups are defined as either single whistles closely spaced whistle combinations, or closely spaced repetitions of the same whistle. The acoustic link was connected only during the even-numbered periods.

About a half hour later, the experiment was repeated a third time. Dash again responded to Doris' whistles and then suddenly stopped responding 128 seconds into period 8. He started responding again 41 seconds into period 14.

The only apparent correlation found between the three playback experiments was that Dash stopped responding after hearing several F-type whistles, which were first heard on Doris' sound track in period 8. In the first playback, Dash heard nine F whistles before stopping, in the second he heard seven, and in the third he heard thirteen. Dash began responding again during period 14 which was the first acoustic-link period since period 8 when no F whistles were emitted.

This experiment was too limited to provide conclusive determination of whistle meaning. A few conjectures, however, are presented that may aid in future communication experiments. The facts that the B and D whistles appeared during both acoustic and cut-off periods, that they appeared in numerous exchanges during the early acoustic periods, and that Dash persistently answered most of Doris' B-type whistles with his D-type whistle during the one-way playback experiment suggest that they might be used as a call signal to localize and identify other dolphins. The variations between the B- and D-type whistles suggest that similar whistles from other dolphins should be analyzed to determine whether relationships exist between specific sound patterns and sex, age, or emotional state. The B- and D-type whistles appear to be suited for long-range transmission since they are loud, repetitive, and frequency-modulated in a siren-like manner. The normal time lag between the B and D whistles in an exchange was 0.20 ± 0.10 seconds. Occasionally, the signals overlapped. If the time delay between a given whistle and the response whistle was used to measure distance, as in a transponder, the animals could localize each other within 152.4 m; if so they would be accurate to within approximately 10 percent at a distance of 1.5 km. Repeated exchanges reduce the amount of error. If the animals were sufficiently close, echolocation could be used for determining distance.

The A-type whistle appears simple and stereotyped from the viewpoint of frequency versus time. It was emitted intermittently during both acoustic-link and nonlink periods, but was seldom emitted by Dash during the one-way playback experiment. A possible question for future experiments is whether the A-type whistle is a simplified signal to maintain acoustic contact between dolphins.

The C-, E-, and F-type whistles were emitted primarily during exchanges in the acoustic-link periods, and were not emitted by Dash during the one-way playback experiment. They appear to be associated with communication after acoustic contact is well established. Of the three whistle types, only the F whistle was used as the sole whistle type in acoustic exchanges between Doris and Dash as seen in Fig. 2. Another feature of the F-type whistle is that it appears to be the least stereotyped of all the recorded whistles from the viewpoint of frequency variation; if the variation is significant, there may be considerable flexibility in information content of the whistle. The presence of the F-type whistles during the playback experiment, moreover, appeared to correlate with the termination of Dash's responses; the correlation suggests that these whistles are meaningful only in an active two-way exchange and not meaningful in a one-way playback.

In comparing the whistles with those recorded by Dreher and Evans (*4,* chart I, p. 375), the A-type whistles are somewhat like contours 1 and 2 in (*4*), the B- and D-type whistles are like contours 3, 5, and 7, the C whistle is like contour 3, and the F whistle is like contour 32. These comparisons are qualitative since the Dreher and Evans contours are not quantitative plots of frequency versus time. No distress signals, such as those described by Lilly (see *14*), were recorded.

The considerable complexity of vocal interaction between the two dolphins in this experiment suggests that further experimentation is needed of the type reported here. The experiments by Dreher and Evans (*4*) indicate that many more types or variations of whistles may appear in such future experiments.

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9. Operated jointly at the time by the U.S. Naval Ordnance Test Station and the U.S. Missile Center. Since January 1965, the facility has been operated by the U.S. Naval Missile Center.
10. The frequency response of the acoustic link was assumed to be flat within 2 db out to at least 16 kcy as specified by the manufacturers of the various equipment components. The fidelity of the recorded signals, however, was somewhat lower since the signals from the receiving hydrophones were not fully compensated for frequency roll-off before recording. The receiving hydrophones were Chesapeake ceramic-type, model SB-1546 with a frequency response of ±3 db to 5 kcy with a roll-off of 10 db per octave above 5 kcy. The transmit hydrophones were Massa barium titanate TR-14A with a linear frequency increase of 6 db per octave from 1 to 30 kcy. Nortronics model PL 100 amplifiers were used with a frequency response of ±2 db from 0.02 to 16 kilocycles at the neutral setting of the tone equalization adjustment. (The tone equalization adjustment was set to amplify the higher frequencies in order to compensate for the 4 db per octave difference between the transmitting and receiving hydrophones.) The amplifiers were set sufficiently low to eliminate feedback squeal and still permit the animals to hear each other. The impedance-matching transformers were Triad model H. S. ND-181 and were distortion-free for frequencies up to 20 kcy. The signals were recorded on a UHER model 8000 stereo magnetic tape recorder with a frequency response at 190.5 mm/sec of ±3 db from 0.05 to 20 kcy with wow or flutter less than ±0.15 percent. The generator for dash-dot and dot-dash signals, designed and constructed by Dr. C. Scott Johnson of the U.S. Naval Ordnance Test Station, drove two University model MM2F underwater speakers.
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15 November 1965

Genotype and Prenatal and Premating Stress Interact To Affect Adult Behavior in Rats

Abstract. *Open-field ambulation scores of rats were affected by stress received by their mothers prior to mating, whereas avoidance-conditioning scores were affected only by gestational stress. The direction of effects on ambulation depended upon offspring genotype, while those depending on conditioning were unidirectional. Both effects were mediated prenatally by the mother.*

Offspring behavior can be affected by the prenatal experiences of the mother. Differences in the effects on their offspring of prenatal treatments of female rodents dependent on the mothers' strain and on the sex of the offspring focus attention on the importance of genetic variables in determining such differences (*1–3*) and suggest that differential susceptibility of either the mother or the fetus may account for them. But some experiments on prenatal stress fail to exclude the effects of premating experiences, and others fail to exclude the possibly direct effects of stress procedures on the fetus. Consequently no experiment yet reported has conclusively implicated gestational stress mediated by the mother during pregnancy as the cause of the effects on offspring behavior.

To unravel the roles of the two organisms involved—the mother and the fetus—requires procedures enabling any effects detected to be attributed conclusively to the prenatal period. There is evidence that the experiences of mothers prior to the birth of their litters can affect the subsequent behavior of their offspring (*4*) and, in order to avoid confounding prenatal and postnatal maternal influences (*3*) in such studies, offspring must be reared not by their natural mothers, but by foster-mothers.

In my experiment females of the 23rd generation of selection of the Maudsley reactive (MR) and nonreactive (MNR) strains, bred for high and low emotional defecation, respectively (*5*), were subjected to one of three prenatal treatments:

1) Premating avoidance training plus gestational stress: training (14 days) to avoid shock (0.3 ma) on presentation of a conditioned stimulus (illumination change) in a shuttle box; they were mated and given 18 days of further trials in the shuttle box with no shock presented, and the avoidance response was physically blocked on 16 of the 24 daily trials.

2) Premating avoidance training only: 14 days of shuttle box training, mating, no further disturbance.

3) Controls: no disturbance other than mating.

Females were mated in all the four possible combinations of the two strains (a 2 by 2 diallel cross) to enable the contributions of maternal and fetal genotypes, and their interaction with prenatal stress, to be evaluated separately. All litters born to these females were fostered shortly after birth (from 2 to 34 hours, mean 8.3) to untreated females of the MNR strain in order to equate postnatal environmental variables for all offspring. The offspring were weaned at 21 days, tagged by punching metal identification clips in their ears at 50 days, and otherwise left undisturbed until tested at approximately 100 days of age.

At this stage 96 offspring (two males and two females randomly drawn from each of 24 litters), equally divided among the four offspring genotypes of the diallel table (the two pure-bred strains and their reciprocal F_1's) and the three imposed prenatal treatments, were tested in the standardized open-field test of emotionality (four daily 2-minute trials) (*5*) and on an avoidance-conditioning task (one 50-trial session; unconditioned stimulus, shock of 0.25 ma; conditioned stimulus, a buzzer), half the offspring being tested in the order stated and half in the reverse.

Two of the several possible statistical analyses of diallel crosses (*6*) were applied to these data (Table 1). Main effects and interactions based on comparisons between litters in the factorial analysis were tested against errors between litters; if between-litter error was not significantly different from within-litter error, the two were pooled to provide an overall error variance.

The significant interactions between the paternal-strain factor and prenatal-treatment factor and that between genotype factor and prenatal-treatment factor in analyses of open-field ambulation