Vocal Exchanges between Dolphins

Bottlenose dolphins "talk" to each other with whistles, clicks, and a variety of other noises.

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Abstract. Observations of the vocal exchanges of bottlenose dolphins under various conditions are presented. Experimental conditions under which isolated emissions from each animal of a pair are separately recorded and in which the distance between the rostrum and the hydrophone is controlled are described. The exchanges consist of vocal alternations (A, then B, then A, and so on), "duets"(A plus B simultaneously), and long "solos" or "monologues." The emissions exchanged are: (i) whistles alone; (ii) slow click trains alone; (iii) simultaneous whistles and clicks from either or both animals; and (iv) squawks, quacks, blats, and so on, alone or simultaneously with whistles. Any or all of these sounds may occur in a given period. The significant carriers of meaning are to be determined. (Suggestions include various functions of relative amplitudes, absolute and relative frequency, frequency modulations, phaseshift variations, and durations of whistle emissions.) Average and peak amplitudes (at the rostrum) of each class of sound cover at least a 100-decibel range (controlled by the dolphin).

In a previous article (1) it was shown that the individual bottlenose dolphin (Tursiops truncatus) emits several classes of complex and varied sounds. At least one of these classes (click-creakings) is used in finding food, ranging, and navigating; other classes of sounds may be used for communication between individuals. These latter classes are (i) click trains (not creakings), (ii) whistles, (iii) quacks, blats, and squawks, and (iv) combinations, such as click trains or quacks plus whistles. In this report the first experiments on the possibilities of communication between two dolphins are presented. The techniques and ap-

The authors are affiliated with the Communication Research Institute of St. Thomas, U.S. Virgin Islands, and Miami, Florida. Dr. Lilly is director of the institute. paratus were those described previously (1). Emphasis is placed here on the elicitation of vocal exchanges and on the formal description of these exchanges.

Special experimental conditions are set up (Table 1).

Condition 1. The animals are in solitude, confined and isolated to the extent given in Table 1. This is the "nearzero exchange" state (2, 3). The "dullness" and "evenness" of the situation is purposefully maximized. (These conditions are analogous to solitary confinement of a human being in a small box.)

Condition 2. One set of physical constraints is attenuated, and more three-dimensional movement is allowed. (These conditions are analogous to solitary confinement of a human being in a large room.)

Condition 3. Each animal is allowed to hear and reply (in water or air, or in both) to one other unseen, untouched, untasted dolphin (Fig. 1); the dolphinto-hydrophone distance is controlled, and vocal emissions from the two animals are separated in the recordings. A hydrophone is placed near the rostrum of each dolphin. The animal is so held that it cannot move its head more than a few inches from the hydrophone. The water space is so shallow (10 to 15 in.). so narrow (15 in.), and so short (slightly over one body length) that the animals cannot swim. Each one rests on the bottom most of the time unless it is disturbed by the presence or intervention of a human being.

Condition 4. The animals are no longer confined to the extent of "enforced resting," and each animal has the option of swimming. The distance between the animal and the hydro-

phone is controlled to a lesser degree than in condition 3 but is still limited to a maximum distance of a few feet. Play with floating "toys" is allowed.

Condition 5. Free bodily contact, biting, mutual play with "toys," racing, courting, mating, stealing and giving food, and so on are all allowed. The animal-to-hydrophone distance is not controlled, and there is some confusion between emissions from one animal and those from the other. After a period of study and observation, the individual emitting whistles, blats, or quacks, can be identified, but identification is less easy in the case of clicking.

Condition 6. Human beings are present and "intervene" through feeding, "rewarding," "punishing," operant-conditioning (especially in production of specific kinds of emissions), play, vocal interspecies "exchanges," transporting, direct brain stimulation, and other measures.

Condition 7. In the oceanaria, captive colonies can be observed. To date, no experiments have been undertaken to study possible exchanges between individuals in such colonies. (Such experiments have been proposed as possible controls for the experiments described here; there are many technical difficulties, such as that of identifying the vocal emissions of specific individuals.)

Condition 8. At sea, the difficulties of experimenting with wild animals and studying their exchanges are increased by the difficulties of finding and staying near the animals for a significantly long period of time. To determine the effects of capture and of captivity on the vocalizations, control experiments should eventually be carried out at sea, with the dolphins in their most free state.

Results

From the standpoint of measurement of physical acoustical quantities, conditions 1 and 3 give the best results; condition 3 gives the best physical recordings of exchanges. From the standpoint of the health and vigor of the animals in captivity, conditions 5 and 6 are best and give the greatest variety of vocalizations. We have a few data for condition 7 but none for condition 8. Most of the results given here are for conditions 3 and 4.

In conditions of solitude the animals' vocal behavior is different from their

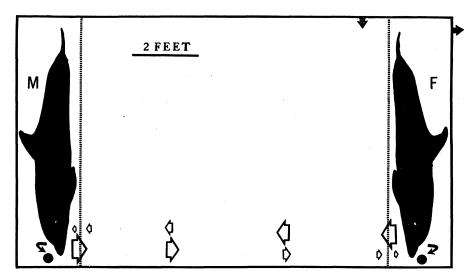


Fig. 1. Configuration for recording vocal exchanges between a pair of isolated and confined dolphins. The animals are resting on the bottom and are shown in lateral elevation, the male (M) from his left side, the female (F) from her right. (Dotted line) Foam-covered barrier preventing the dolphin from entering the rest of the pool; (black rectangle) inner walls of the salt-water pool; (open arrows, decreasing in size) acoustic-energy transfer from the source-dolphin to the sink-dolphin; (curved solid arrows) energy received by the hydrophone from the dolphin nearest it (attenuated signals are received from the far dolphin); (straight solid arrows) water inflow and outflow. Spoor may possibly be transferred from M to F; however, the flow of water is greatly impeded by the barriers, so that any exchanges of spoor that may occur probably have little value as signals. Other configurations eliminate spoor-trace clues completely, since no water can move from one dolphin to the other.

Table 1. The most frequent forms of vocalization and vocal exchanges (one and two dolphins). This classification applies best to newly captured animals. After several weeks unpredictable, complex vocalizations appear that are inconsistent with the classification given here.

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	Condition	Vocal emission (initial or response)	
	Condition	Dolphin A	Dolphin B
1.	One in solitude, confined*, isolated†, (nearzero exchange)	Whistles and clicks	No response
2.	One in solitude, free- swimming‡ (objects-and- background-exchange only)	Whistles, clicks, creakings §	No response
3.	Pair, confined, isolated, limited to acoustic ex- change path, intraspecies only	Whistles; clicks and/or whistles; clicks	Whistles; clicks and/or whistles; clicks
4.	Free-swimming pair, iso- lated, limited to intra- species acoustic exchange	Whistles; clicks and/or whistles; clicks; creakings §	Whistles; clicks and/or whistles; clicks (see 3)
5.	Free-swimming pair, free body contact, free acous- tic and mating exchanges of all kinds, interspecies isolation	Whistles; clicks and/or whistles; clicks; creakings \$; quacks, squawks, blats, etc., with or without whistles.	Whistles; clicks and/or whistles; clicks (see 3); whistles; clicks or quacks, etc., with or without whistles
6.	Condition 1, 2, 3, 4, or 5 plus presence or intervention of human being	Same exchanges as in 5 with increase in quacks, etc.; airborne sounds sud- denly increase in frequency of occurrence and in amplitude	Same exchanges as in 5 with increase in quacks, etc.; airborne sounds suddenly increase in frequency of occurrence and in amplitude
7.	Confined in oceanaria in colony	Not yet examined experi- mentally	Not yet examined experi- mentally
8.	Free-swimming, unisolated, unconfined in the sea in colony	Not yet examined experi- mentally	Not yet examined experi- mentally

^{*} Confined in a box 7½ ft by 15 in. in water 10 to 15 in. deep. † Separated by a barrier to prevent bodily contact with another dolphin or with human beings. ‡ Swimming in one of three pools with, respectively, (i) rough rock sides, 70 by 20 ft, with water up to 12 ft deep; (ii) vinyl sides and bottom 10 by 8 ft, water 22 in. deep; (iii) Fiberglas, smooth sides and bottom 9 by 7½ ft, water up to 30 in. deep. § Creakings do not occur as responses to another dolphin's vocalizations but do occur during feeding, navigation in murky water for novel objects, and so on—that is, as "sonar" for recognition and ranging. || No other species of animals entered or were near the pool, especially no human beings.

vocal behavior when they are in pairs. When they are maintained under condition 1 for a few hours a day (the condition of near-zero exchange), there are usually no creakings. The slow click trains gradually decrease and finally cease. Whistles become less and less frequent over a period of days to weeks when there is a continued lack of "response" from the environment and from other animals, including man. To keep the dolphins healthy, exposure to condition 1 must be limited to short periods.

In condition 2 creakings occur as needed for food finding, exploring new objects, and navigating in muddy water or at night. Whistles and slow click trains gradually cease in a few days or weeks; they are elicited immediately by (i) presentation of the spoor of other dolphins in the water; (ii) visual or acoustic stimuli from another dolphin; (iii) human stimuli of various sorts; or (iv) presentation of toys or novel objects. In other words, a change to conditions 3, 4, 5, 6, or 7 increases the rate of occurrence of vocalizations.

Under conditions 3, 4, or 5, where the dolphins are in pairs, spontaneous vocalizations (Table 1) occur fairly frequently, in bursts lasting from a few seconds to many minutes. In a typical 24-hour day there is a total of at least 4 hours of vocalization, and on many days there is more than this. Under condition 5 (with freedom to swim, to make body contacts, and to mate), a male and a female emit various sounds steadily for periods up to 20 or more minutes, concurrently with play, courtship, and mating behavior.

Under conditions 3 and 4, where members of a pair are in acoustic and vocal contact, definite vocal "exchanges" are demonstrable (Fig. 2). These exchanges are briefer and rarer than the vocalizations that occur under condition 5 (body contact). A "monologue" or a "solo" by one or the other animal may precede, follow, or be unrelated to, an exchange, in the same few minutes; most monologues, however, occur in a close time relation to an exchange. These monologues differ from those of the same animal in solitude (see Table 1, conditions 1 and 2): they are more frequent and more varied in amplitude and frequency.

As shown in Table 1, when the dolphins are in pairs (conditions 3, 4, and 5), the two animals produce alternating emissions (Fig. 2). Rare interruptions of one by the other, or "overlaps," do

occur. A special phenomenon, called a "duet" (Fig. 2: F4 and M10; F5 and M11), also occurs: the two animals whistle simultaneously, sometimes matching frequencies and time-patterns so exactly that the relatively low-frequency difference between their simultaneous whistles can be heard.

Alternations without interruptions, overlaps, or duets are the most frequent exchanges. Such alternations consist of whistles or slow click trains, or both (Table 1 and Figs. 2 and 3).

If two dolphins are transferred from condition 3 (confined and isolated with only an acoustic path between them) to condition 4 (free to swim but with no body contact), they make creaking sounds. The creaking can be related to detection, ranging, and recognition of novel objects, to finding food, to pursuit games with a toy, or to navigation in the dark or murkiness to avoid rough walls or other obstacles (1, 3).

If a dolphin is allowed to touch the body of another dolphin (Table 1, condition 5), it makes another set of sounds -squawks, quacks, blats, barks, and so on-both under water and in the air. [Graphic results of analyses of some such individual sounds are shown in the previous paper (1).] If a human intervenes with one of a pair of dolphins limited to acoustic exchange (thus changing condition 3 to condition 6), the dolphin barks, squawks, and quacks, apparently at the human, and it may whistle simultaneously every so often, apparently in exchange with the other dolphin. When two dolphins are swimming freely together (condition 5), they exchange such complex mixtures of sounds, but deciding which dolphin emits which sounds is extremely difficult.

After several weeks in captivity in shallow water (18 to 30 inches), a dolphin begins to emit each and every class of sounds in air, including clicks and whistles in addition to quacks.

In Fig. 2 are shown some results obtained in studies made under condition 3—the best condition for controlling and distinguishing the underwater vocal emissions of the dolphins. The upper trace is that of the female dolphin F of Fig. 1; the lower trace, that of the male M of Fig. 1. This particular exchange opens with the male's slow click train, followed by four whistles (Fig. 2, M1, 2, 3, and 4). During whistle M1, the male stops clicking shortly after the female begins to click, and the female maintains the train during whistles M1,

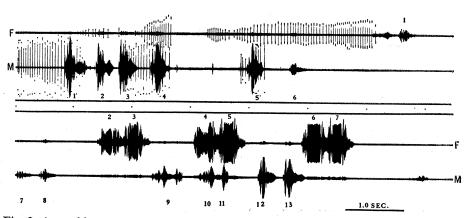


Fig. 2. A graphic record of a vocal exchange between two dolphins. (Top trace in each pair) Emissions of the female (F); (bottom trace in each pair) emissions of the male (M). The upper pair of traces shows a click-and-whistle exchange; the lower pair, a continuation of the same record without the clicks. (Dots between pairs of traces) Seconds of elapsed time; elapsed time for the whole record, 15 seconds. For reproduction, the peaks of the clicks of the female were marked with black dashes; the tips of those of the male, with black dots. Whistles are numbered in sequence for each animal. Other disturbances in the base line are, in most cases, water noises (see text).

2, 3, and 4. During M3, the male starts clicking and continues to click and to whistle (M4) throughout the rest of the female's click train. He keeps his click train carefully out of step with hers, and stops his when she stops hers. The female starts clicking again before his whistle M5; the male joins in with a few clicks, whistles once (M5), and stops clicking. The female continues her clicks for a total interval of 3 seconds. The male whistles once again, faintly (M6). The female moves her head

(water noises appear at the end of the train) and whistles faintly (F1). He answers with two faint whistles (M7 and 8). She suddenly whistles loudly twice (F2 and 3); he replies with a long single whistle of medium intensity (M9). She responds with whistles of high intensity (F4 and 5), and he joins her (M10 and 11) in a precise "duet," matching her time pattern, and goes on to "reply" more loudly with two whistles (M12 and 13). She answers loudly (F6 and 7), and both become silent.

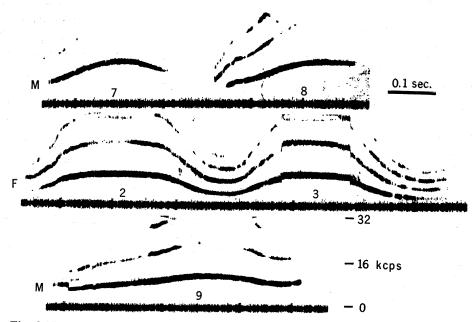


Fig. 3. Sonograms of a portion of an exchange between two dolphins. (M) Emissions of the male; (F), of the female. Emissions are numbered to correspond to the numbering of the amplitude trace in Fig. 2. The fundamental (f) and the first two overtones (2f and 3f) may be seen on these sonograms. Additional sonograms with twice this frequency scale show that energy in the 3rd, 4th, and 5th overtones decreases rapidly as compared to that of the fundamental and the first two overtones. There was some enhancement of the higher frequencies in recording the sonograms (6).

Individual Differences

Inspection of these amplitude-time graphs shows some differences between the whistles of these two animals. The male tends to become silent briefly between his pairs of whistles (M1 through 8 and 12 and 13). The female tends to "fill in" between what correspond to his pairs of whistles with sound. He builds his average intensity to a fast peak and drops it to a lower level in the last half of the record. A male may have one or more fast notches and fast peaks in his record. A female also does this (other records); she may often start at a lower level, rise suddenly to a higher one, and drop back to the lower one (Fig. 2, F6 and 7). She also may have one or more deep fast notches and peaks in the amplitude record.

In analyzing these sounds for their frequency, these amplitude variations can be correlated with the frequencies emitted. Figure 3 shows sonograms of frequency versus time for emissions M7 and 8 (top traces), F2 and 3 (middle traces), and M9 (bottom traces). In general all of the time pattern of the fundamental (frequency f) is shown; the second harmonic (2f) and third harmonic (3f) sometimes do not show because of their low intensity. At other times all the harmonics up to the sixth (6f) have sufficient intensity to be recorded. (Almost all of the frequencies are integral multiples of the fundamental.)

Inspection of the traces of the male show that, in general, the recorded harmonics are enhanced during his amplitude peaks—that is, when the amplitude is high the harmonic content is high (M8, M9). The traces of the female show in general that her high amplitudes correspond to her highest frequencies of the fundamental. The harmonic content of the female's emissions tends to be more constant than that of the male during a given emission. The frequencies covered by his fundamental are from 6 to 15 kcy/sec; her fundamental varies from 3.5 to 11 kcy/sec. Some of her low-frequency and her low-amplitude emissions correspond to his short silences between pairs of whistles (Figs. 2 and 3, F2 to F3).

The separation of the emissions of whistles into countable integral units is based on measurements of occurrences and durations and on graphical records of isolated single whistles, on repetitions of similar (but not necessarily identical)

patterns of frequency variation in pairs and triplets, and on the qualities of their total effect as heard (slowed down) by experienced observers. When the female whistles, she emphasizes the relatively flat, high-frequency portion and deemphasizes the low-frequency "slump," somewhat the way some people fill in between words with a low-intensity "aaaah." (Listening to records obviously does not give us the same acoustical experience that the dolphins have; the dolphins have a much wider hearing range than we do and they may have special resonators in the hearing side as well as on the transmitting side which may make the hearing experience of sounds an entirely different kind of experience for them than for us.)

Usually, but not always, the duration of the whistles is of the order of 0.2 to 0.4 second (see Fig. 2). Under special conditions yet to be thoroughly determined, extremely short (0.1 second) or extremely long (2 to 3 seconds) whistles, or both, occur. Most whistle transmissions are in the middle range.

Trains of clicks cover the full range of duration of the whistles and sometimes continue as long as 15 seconds without pause. The most frequently observed durations for click trains are close to those of the longer whistles (0.5 to 1 second).

The amplitudes of the middle-frequency components (less than 40 kcy/sec) of each click are varied by the dolphin in systematic ways. Sonograms and detailed high-speed oscillograph recordings show each click to be a complex train of sine waves whose components vary in frequency and in amplitude with time within the train. From click to click there is more controlled variation in the middle and low range of frequencies (1 to 20 kcy/sec) than in the high range (20 kcy/sec to apparatus limits at 64 kcy/sec). The clicks are not "white noise" in the range below 20 kcy/sec. The lower-frequency portion of the train lasts up to 5 msec and can have mean frequencies as low and as high as the whistle frequencies, with variations ranging from ½ to 2 times the mean value. The high-frequency portion of the train (above 20 kcy/sec) is very brief (0.1 msec) and may, with certain kinds of frequency analyzers, appear to be white noise (4).

If one listens to slowed tape recordings (slowed to 1/16 of normal speed) the complex tonal variations can be perceived within each click, from one click to the next, and from animal to

animal. The clicks of "creakings" (Table 1) are higher pitched, shorter, and "harder-sounding" than those of exchanges (4). The "sonar" click is usually one of high frequency; the exchange click, one of lower frequency.

Conclusion

In this report (5) we have presented something of what dolphins transmit in their exchanges—signals plus noise. A few tentative, simple "meanings" have been found ("distress," "attention," "irritation," and so on); however, most of the exchanges are not yet understood.

Note added in proof: Since this report was submitted we found that dolphins can emit ultrasonic clicks independently of sonic clicks and vice versa.

References and Notes

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 6. The sonograms were made with a Kay Electric Company Sonograph
- Company Sonograph.
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Cutaneous Molt Induced by Calciphylaxis in the Rat

Abstract. A molt, conducive to the loss and subsequent replacement of all cutaneous layers, can be induced by topical "calciphylaxis" in the rat. This is accomplished by sensitization with dihydrotachysterol followed by challenge with egg white or ferric dextran.

Calciphylaxis is a condition of induced systemic hypersensitivity in which, during a "critical period" after sensitization by a systemic calcifying factor (for example, vitamin-D compounds, parathyroid hormone, sodium sulfathiazole), treatment with certain challengers (for example, metallic salts,