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Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: mimicry of signature whistles?

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Summary. The whistle vocalizations of two bottlenosed dolphins, *Tursiops truncatus*, were recorded at the Sealand Aquarium in Brewster, Massachusetts. The identification of which dolphin within the group produced a vocalization was made possible by a telemetry device attached to the dolphin's head with a suction cup. 77% of the identified whistles (219 our of 284) fell into two primary categories, type 1 and type 2 (Table 1). The remaining 23% of whistles fell into five secondary categories. Of the primary whistles produced by one dolphin, 78% were of type 1 (22% type 2), while 69% of primary whistles from the other dolphin were of type 2 (31% type 1). The result that each of the dolphins favored a different primary whistle supports the findings of Caldwell and Caldwell (1965), that each dolphin produces an individually distinctive whistle. But in the present study, both dolphins produced both primary whistle types. This may represent mimicry of signature whistles.

Introduction

Ever since captive dolphins were first studied, they have been reported to produce a large repertoire of complex vocalizations (Popper 1980). Aside from pulsed sounds used for echolocation, the most intensively studied dolphin sounds are frequency modulated narrow band sounds called whistles or squeals (Herman and Tavolga 1980; Watkins and Wartzok 1985). Most authors have categorized dolphin whistles using variation in the dominant frequency as a function of time, called a whistle's contour (Dreher 1961). Early work on the function of dolphin whistles attempted to associate particular whistle contours with specific behavioral contexts such as fright or disturbance (Dreher 1966; Dreher and Evans 1964; Lilly 1963). These authors studied whistles recorded from groups of dolphins; they were only able to associate vocalizations with the behavior of the whole group because of their inability to identify which individual dolphin produced a sound.

Caldwell and Caldwell (1965) presented a different approach to studying how dolphin whistles function. In this study sounds were recorded from five bottlenosed dolphins all caught from one wild group. In order to determine which animal produced a whistle, the Caldwells recorded dolphins that were isolated from conspecifics, often stranded out of the water for veterinary attention. In this and subsequent papers (Caldwell and Caldwell 1968, 1971, 1979; Caldwell et al. 1970, 1973), the Caldwells presented evidence that over 90% of the whistles from any one dolphin of the over 100 individuals from four species tested conformed to one contour which was easily distinguished from that of any other dolphin within the same group. The Caldwells called these individually distinctive whistles "signature whistles" and proposed that the function of signature whistles was to broadcast the individual identity of the whistler to other members of its community.

The most serious problem with the Caldwells' data in support of the signature whistle hypothesis is that they were only able to report on whistle repertoires of isolated dolphins, often stranded out of the water. In this unusual context, whistling may be abnormal. Isolated dolphins also cannot interact normally. In order to study whistle repertoires in more normal circumstances, one must be able to identify which dolphin produces a whistle within an interacting group. This paper reports a new technique to determine which dolphin produces a sound, and compares the whistle repertoires of two captive bottlenosed dolphins, *Tursiops truncatus*.

Methods

Identification of which dolphin within a group produced a sound was made possible by a telemetry device I call a "vocalight," which is attached to a dolphin's head with a suction cup. The design and construction of the vocalight is described in Tyack (1985). The vocalight lights up a variable number of light emitting diodes (LEDs) depending upon the loudness of sounds received at a contact hydrophone within the suction cup. The louder the sound, the more LEDs light up. To identify which dolphin produced a sound, two vocalights matched for sensitivity were used, one with red LEDs for one dolphin, the other with green LEDs for the other dolphin. Dolphin sounds were broadcast in air to four observers around the pool who called out the response of any vocalight under observation when a dolphin whistle was heard. The dolphin with the vocalight that lit up most during a whistle was presumed to have produced the whistle.

Two captive *Tursiops* at Sealand, an aquarium in Brewster MA on Cape Cod, were trained to wear the vocalight in a few days for the study presented here. These two dolphins, named Spray and Scotty, were caught in Tampa Bay, Florida in 1977 and were moved directly to Sealand. When caught, the dolphins were 2 m long and were judged to be five to six years of age (current age = 12 to 13 years). Spray is a female (current length = 249 cm) and Scotty is a male (current length = 244 cm). After a few days of training, the dolphins showed no obvious differences in behavior whether wearing the vocalight or not. They also showed no obvious response when the LEDs lit up. We noticed no response of one dolphin to a device worn by the other.

A Sony TC-D5M stereo tape recorder was used to record observers' comments on one channel using a microphone and dolphin sounds on the other using AN/SSQ-41A sonobuoy hydrophones. This system had a frequency response from 30–15,000 Hz (±5 dB when recorded at −13 dB VU) with Maxell UDXLII tape. Whistle sounds were analyzed with a Kay Elemetrics Corp. Sonagraph Model 7029A Spectrum Analyzer with a narrow band (90 Hz) filter. The frequency range of all analyses was 160–16,000 Hz.

Results

Whistle sample

The whistle sample described in this paper was recorded from the two Sealand *Tursiops* on 28 February 1984. Altogether 1083 whistles were recorded in five sessions from 0930 to 1600. During 77.6 min of these recordings, the vocalights were removed from the dolphins for control observations: 586 whistles were recorded during this period, yielding a rate of 7.6 whistles/min. The dolphins were wearing vocalights for the remaining 110.1 min: 497 whistles were recorded during this period, a rate of 4.5 whistles/min. Observers used the vocalights to identify which dolphin produced 252 of these 497 whistles. 32 whistles were audible in air and observers could locate the source to identify which dolphin produced them.

A random sample of 50 whistles from the 497 recorded when both dolphins were wearing the vocalights was compared with a random sample of 50 whistles from the 586 recorded when they were not wearing the devices. The whistles were combined into three categories described in the next section: type 1, type 2, and all secondary whistles. A Chi-square analysis (Siegel 1956) of these data comparing the kinds of whistles produced under these two conditions indicates no significant differences (Chi-square = 0.68, $df = 2$, $P > 0.7$). Thus while the dolphins produced whistles at rates that differed when they were wearing vocalights compared to not wearing them, they produced similar proportions of each kind of whistle in both conditions.

Categorization of whistles

The spectrograms of whistles were categorized by visual inspection of the contours. Sound spectrograms of the most commonly product whistle, primary contour type 1, are presented in Fig. 1. The spectrograms on the upper row show variation of 82% in duration with little variation in contour. Both dolphins also produced just the first section of this whistle contour with no terminal increase in frequency. Two examples of this truncated type 1 whistle, termed 1A, are shown in the bottom row of Fig. 1. The two sections of the type 1 whistle, termed 1A and 1B, are marked on the upper left spectrogram of Fig. 1, a complete type 1 whistle, termed 1AB. The 1B section of the type 1 contour was only produced as part of 1AB whistles.

Spectrograms of the second most commonly produced whistle contour, primary contour type 2, are presented in Fig. 2. The whistle shown in the spectrogram on the middle left has only 70% the duration of that on the upper left while the contours are otherwise quite similar. Three different sections of whistle type 2 (2A, 2B, and 2C) are labelled on the upper left spectrogram of Fig. 2. All three of these sections were produced separately; the most frequent was 2C, shown on the middle of the bottom row of Fig. 2. On two occasions, sections A and B of whistle 2 occurred together in sequence (termed 2AB, bottom left of Fig. 2) and on two occasions sections B and C occurred together (termed 2BC, bottom right of Fig. 2). The complete type 2 whistle was termed 2ABC.

Secondary whistles were much less common than primary whistles and were not as stereotyped. Any whistle with a monotonic rise in frequency different in structure from 1B or 2C was classed as a RISE whistle (upper right of Fig. 3). Whistles with little frequency modulation were classed as FLAT whistles (second half of the spectrogram on

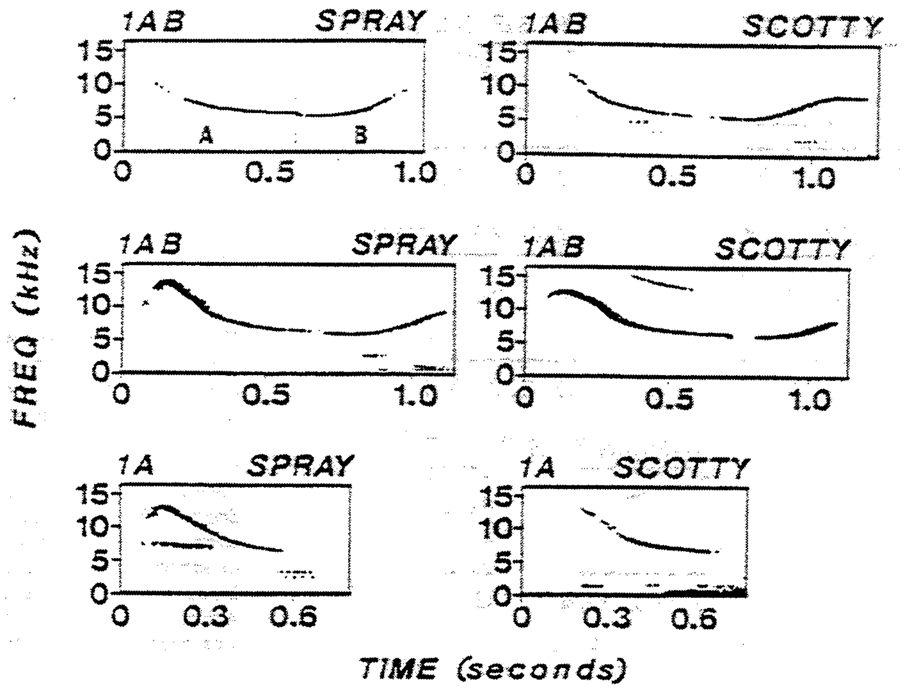

Fig. 1. Spectrograms of Type 1 whistles. The whistles on the left were all produced by Spray: those on the right were produced by Scotty. Type 1 whistles were formed of two segments, 1A and 1B. These are separated by a vertical line in the spectrogram on the upper left of the figure. The top two rows show complete type 1 whistles, while the bottom row shows whistles that included only the 1A segment

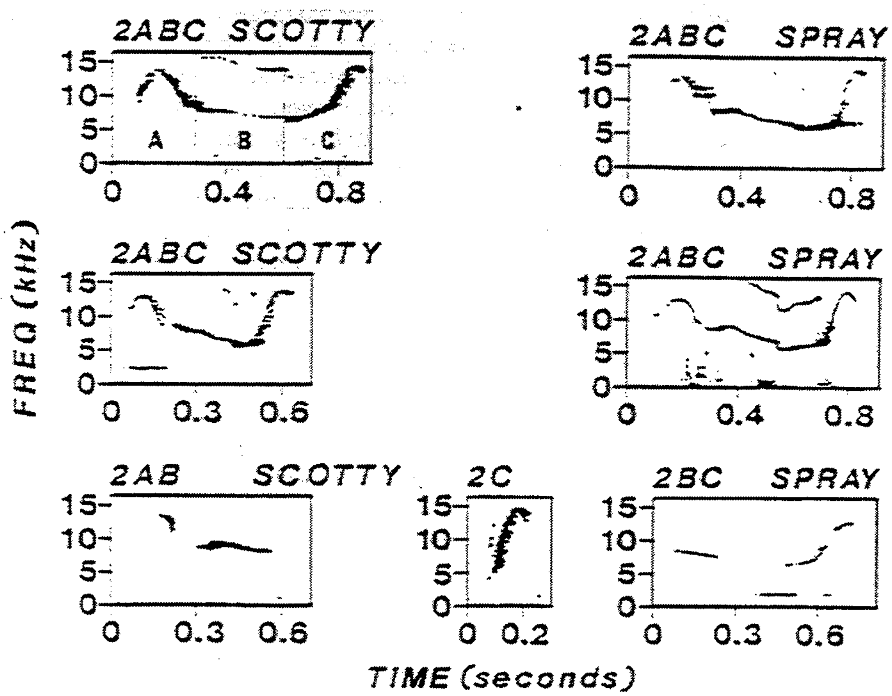

Fig. 2. Spectrograms of Type 2 whistles. The whistles on the left were all produced by Scotty: those on the right were produced by Spray. Type 2 whistles were formed of three segments, 2A, 2B and 2C. These are separated by vertical lines in the spectrogram on the upper left of the figure. The top two rows show complete type 2 whistles, while the bottom row shows whistles that included only one or two of these segments

the upper left of Fig. 3). DOWN whistles had a monotonic decrease in frequency (middle right of Fig. 3). SINE whistles were frequency modulated in a sine wave pattern (middle left of Fig. 3).

Any whistle that did not match any of the six categories or that could not be sorted into just one category was entered into a seventh VARIANT category. Some of the VARIANT whistles were too short to assign them unambiguously to one of the other six categories. Some of these may have been contours similar to 1A or 2A but were not well enough defined for certainty, e.g. middle

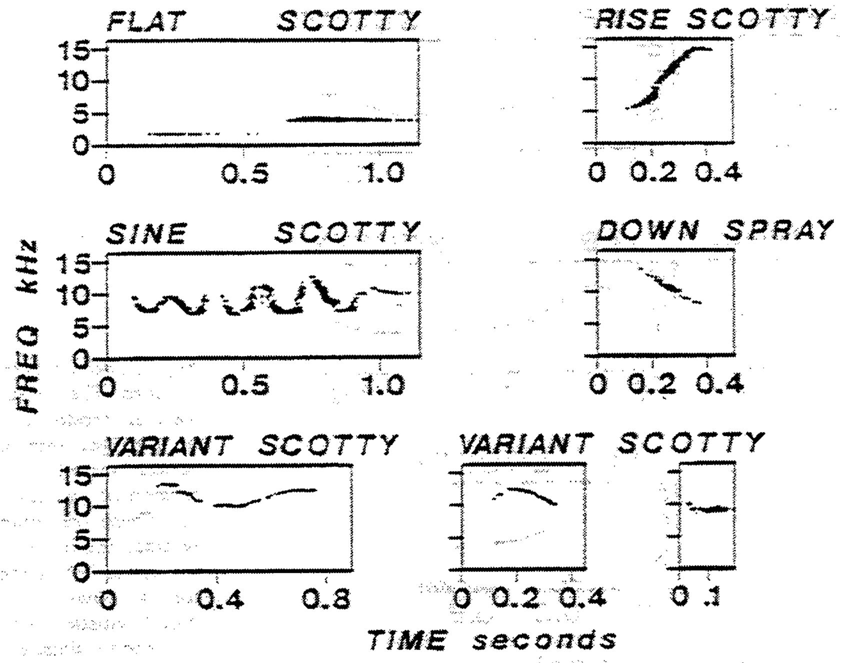

Fig. 3. Spectrograms of secondary whistle contours. The first half of the spectrogram on the upper left shows a 1.5 kHz signal from the trainer's whistle, while the second half shows a FLAT whistle of approximately 3 kHz produced by Scotty. The rest of the spectrograms all show examples of secondary whistles produced by Scotty, except for the DOWN whistle on the middle right, which was produced by Spray

of the bottom row of Fig. 3. The rest of the whistles of this category were highly variable, e.g., left of the bottom row of Fig. 3.

Whistle production by individual dolphins

Table 1 lists how many whistles of each contour category were identified with one of the dolphins. These dolphins were seldom seen to emit bubbles during whistle production, but 11% of the whistles were audible in air. Observers could hear and locate these whistles directly and thus identify the source. These whistles are listed in the first and sixth rows of the table. The second and seventh rows list those whistles when both vocalights were under observation and one device lit up more than the other. The third and eighth rows list whistles when one vocalight did not light up at all but the other vocalight was not under observation. Since one of the two vocalights always lit up when we could see both devices and heard a whistle, these observations are probably reliable indicators that the dolphin with the device not under observation produced the whistle. The fourth and ninth rows of this table indicate cases when one device was seen to light up most of the LEDs, but when the other device was not under observation. Since most of the LEDs lit up on both devices in 16 of the 110 cases where both devices were under observation, data from these rows alone might lead to an error rate of approximately 15%. But most of the LEDs lit up on both devices only when the dolphins produced loud whistles and were separated by approximately 1 m. Any cases where observers noted a particularly loud whistle when the dolphins were very close to one another were not included in these analyses, so the error rate is probably much less than 15%.

Both Spray and Scotty, the two dolphins at Sealand, produced both type 1 and type 2 whistles. While the type 1 whistles from both animals had very similar contours, there tended to be a difference between the type 2 whistles of the two dolphins. Inspection of Spray's type 2 whistles on the upper and middle right of Fig. 2 shows that the signal is not pure tone for a short section of 2C. Instead, a series of sidebands are visible on the spectrogram. Scotty's type 2 whistles on the upper and middle left of Fig. 2 do not have sidebands, although the whistle structure is blurred slightly due to reverberation in the pool. A systematic investigation of all whistles made by Spray and containing the 2C segment show that sidebands are present in 16 whistles, absent in five, and indeterminate in four. Only three of Scotty's whistles including 2C have sidebands, 58 show no such structure, and three are indeterminate. Thus the 2C whistles of Spray and Scotty tend to have predictable differences in acoustic structure.

Of the 131 whistles from Spray (row 5 of Table 1), 88 were type 1 (67%), 25 were type 2 (19%), and 18 were secondary types (14%). Of the 153 whistles from Scotty (row 10 of Table 1), 33 were type 1 (21%), 73 were type 2 (48%), and 47 were

Table 1. Tally of the number of whistles of each category produced by two captive bottlenosed dolphins, Spray and Scotty. This table includes all whistles recorded on 28 February 1984 where it was possible to identify which dolphin produced the whistle. Under the column titled "Identification Data", "In-Air" indicates that the whistle could be heard in air and its source located aurally by observers, "Y" indicates that the LED telemetry device was seen to light up nearly completely, "N" indicates that none or only a few of the LED segments were seen to light up, and "DK" (don't know) indicates that observers could not determine the response

	Row No.	Identification data		Primary whistle types										Secondary whistle types					Total
		Spray	Scotty	1AB	1A	Type 1 Subtotal	2ABC	2A	2B	2C	2AB	2BC	Type 2 Subtotal	Rise	Flat	Sine	Down	Variant	
Whistles from Spray	1	In-Air		0	0	0	11	0	0	0	0	0	11	1	0	0	0	0	12
	2	Y	N	33	1	34	3	0	0	0	0	0	3	0	0	0	0	1	38
	3	DK	N	8	0	8	0	0	0	0	0	0	0	0	0	0	0	1	9
	4	Y	DK	38	8	46	9	0	0	1	0	1	11	7	1	0	1	6	72
Subtotal	5			79	9	88	23	0	0	1	0	1	25	8	1	0	1	8	131
Whistles from Scotty	6	In-Air		1	2	3	12	0	0	2	0	0	14	0	0	0	0	3	20
	7	N	Y	13	2	15	11	2	0	4	1	1	19	0	5	2	1	7	49
	8	N	DK	2	0	2	3	0	1	2	0	0	6	0	0	0	0	0	8
	9	DK	Y	8	5	13	12	4	0	17	1	0	34	9	9	2	2	7	76
Subtotal	10			24	9	33	38	6	1	25	2	1	73	9	14	4	3	17	153
Grand total	11			103	18	121	61	6	1	26	2	2	98	17	15	4	4	25	284

secondary types (31%). Spray produced 73% of the type 1 whistles while Scotty produced 74% of the type 2 whistles.

Scotty produced more of the secondary whistles than did Spray. He was the only one identified as producing SINE whistles, and he produced many more FLAT whistles than Spray. Two of the FLAT whistles were produced immediately after the trainer blew his training whistle, which was also constant frequency. As can be seen on the upper left of Fig. 3, while the trainer's whistle and Scotty's FLAT whistle differ in frequency, their contours were otherwise very similar.

The dolphins in this study may have used different whistles in different behavioral contexts. As an example, compare whistles audible in air with those not audible in air. On seven occasions, Spray produced a total of 12 whistles audible in air. Of these, 11 were complete type 2 whistles, and the other was a RISE whistle. This is very different from Spray's production of whistles not audible in air, where 74% were type 1. Scotty's whistles heard in air were more like those he produced when the sounds were not audible in air.

Discussion

Do dolphins mimic each other's signature whistles?

The two dolphins studied for this paper each produced stereotyped whistle contours similar to those described by the Caldwells. But the whistle repertoires of these dolphins do not fit a narrow definition of the Caldwells' (1965, 1968) signature whistle hypothesis: that >90% of the whistles from a dolphin conform to one individually distinctive contour. While the two dolphins favored different contour types, only 67% of Spray's whistles were of type 1 and only 48% of Scotty's whistles were of type 2. Even more important, both dolphins produced both of the distinctive primary contour types. The second most common whistle of both dolphins was the other animal's favored whistle.

Two interpretations of this overlap in Scotty and Spray's whistle repertoires are possible: either the animals simply shared a repertoire of stereotyped sounds and the signature whistle hypothesis did not hold for them, or each dolphin was mimicking the other one's signature whistle. Most of the data on *Tursiops* indicates that they do not share a fixed repertoire of stereotyped whistles. Reviews of whistles from over 100 *Tursiops* (Graycar 1976; Caldwell and Caldwell 1979) have indicated that isolated adult dolphins tended to produce stereotyped individually distinctive calls. Caldwell and Caldwell (1979) studied the ontogeny of whistling in captive *Tursiops*. Of the 14 calves studied, 12 developed stereotyped whistles by the first year of age. Apparently each calf developed only one stereotyped contour type. Stereotyped whistles in *Tursiops* thus do not appear to be drawn from a fixed repertoire of stereotyped whistles shared by conspecifics. The second case, that for mimicry, is based on the exceptional abilities of dolphins for vocal mimicry. *Tursiops* has been shown to mimic man-made sounds spontaneously (Lilly 1965; Caldwell and Caldwell 1973; Herman 1980). *Tursiops* also has been trained to mimic man-made whistle-like sounds upon command (Penner 1966, cited in Evans 1967; Richards et al. 1984).

Gish (1979) found apparent mimicry of signature whistles in vocal interchanges between dolphins in separate pools connected by acoustic links of hydrophones and underwater sound projectors. The rates for this apparent mimicry were approximately 1%. Burdin et al. (1975), also using an electroacoustic link, reported that each of two *Tursiops* produced the other animal's signature whistle at rates of 0.5% and 2.5%. The high rates of apparent whistle mimicry reported in this paper contrast with the two papers just cited and with the Caldwell's report that over 90% of the whistles of any dolphin conform to its individually distinctive contour. This difference may stem from the different contexts in which the data were recorded. For example, when animals are isolated or under stress, they may be less likely to mimic the whistle of a group member.

Given the evidence that individual *Tursiops* do not share a large number of distinctive stereotyped whistles, if one animal produced a stereotyped whistle more typically produced by a different individual, this would seem to represent whistle mimicry. However, proof that the overlap in primary whistles represents vocal mimicry of individually distinctive stereotyped whistles will require study of the vocal repertoires of dolphins before and after they come into acoustic contact.

Possible social functions of Tursiops whistles

Caldwell and Caldwell (1965) suggested that the function of the signature whistle was to broadcast the identity of the whistler to other members of its group. For this to occur, each member of a social group would have to learn to associate each signature whistle with the individual that produced it. Is the signature whistle hypothesis compatible with the apparent mimicry of whistles reported in this paper? Mimicry of signature whistles need not interfere with the association of these whistles with their hypothesized referent, for example, if the mimicked whistles occur significantly less often than those produced by the "appropriate" animal, or if the mimicked whistles have a similar contour but include some acoustic features that are different from those produced by the "appropriate" animal. Both of these conditions appeared to hold in the present study for type 2 whistles. Each dolphin tended to produce a different one of the two primary whistles. Spray's type 2 whistles tended to include a section with sidebands, a feature that was very rare in Scotty's type 2 whistles.

If the signature whistle hypothesis is correct, how might mimicked signature whistles function? Recent experiments where dolphins have been trained to mimic man-made whistle-like sounds may be relevant. Richards et al. (1984) demonstrated that *Tursiops* can learn to produce an arbitrary whistle when shown an object; in these experiments the dolphins were able to label the objects vocally. Dolphins in more natural settings might, for example, mimic signature whistles to label other individuals within their social group.

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