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Spontaneous Vocal Mimicry and Production by Bottlenose Dolphins (*Tursiops truncatus*): Evidence for Vocal Learning

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Two female bottlenose dolphins (*Tursiops truncatus*) and their 2 male offspring were presented with an underwater keyboard to observe how the dolphins would use such a system to obtain specific objects and activities. When a dolphin pressed visual forms on the keyboard, whistles were generated underwater, and the dolphin was given a specific object or activity. Both vocal and nonvocal behaviors were recorded. Only the males used the keyboard. In the 1st year spontaneous vocal mimicry and productive use of facsimiles of the computer-generated whistles were recorded. In the 2nd year productive use increased significantly over mimicry, and apparent combinations of discreet whistle facsimiles in behaviorally appropriate contexts were observed. The patterns of vocal mimicry and production suggest a new model for analyzing dolphin vocalizations and vocal development with respect to signal structure and organization.

The bottlenose dolphin is widely known for its propensity for both behavioral (Adler & Adler, 1978; Tayler & Saayman, 1973) and vocal (Caldwell & Caldwell, 1972; Tyack, 1986) mimicry in captivity. Dolphins have been observed to spontaneously mimic species-specific whistles (Tyack, 1986) and other biological and artificial signals (Lilly, 1965; Penner, 1966; Richards, Wolz, & Herman, 1984). This behavior indicates that dolphins, like humans (Bloom, Hood, & Lightbown, 1974; Kuczaj, 1987) and many songbirds (Baylis, 1982; Kroodsma, 1982; Marler & Peters, 1982), may acquire their vocal repertoire through learning. However, the role and process of vocal mimicry in dolphin learning and communication remains unknown.

We designed an underwater keyboard system in order to investigate the functional and developmental aspects of dolphin vocal learning. The use of an interactive keyboard system was pioneered by Rumbaugh, Gill, and Von Glaserfeld (1973) for training chimpanzees artificial language skills. Although most investigators have trained dolphins to make discriminations through food reinforcement, our approach provided animals with a free choice system (Reiss, 1981), in which they used elements that they could physically produce or manipulate. This system was designed to allow the dolphins to freely interact with a self-reinforcing system without any explicit training procedures. A pilot study (Reiss, 1981) and contemporaneous research by Savage-Rumbaugh (1986; Savage-Rumbaugh & Rumbaugh, 1978) revealed that free-choice methods allow animals more freedom in exploring the contingencies of keyboard use. This approach (Savage-Rumbaugh, 1986; Savage-Rumbaugh & Rumbaugh, 1978) has revealed new information about the natural abilities and behavioral propensities of these subjects, rather than the capabilities and shaped responses found in more traditional studies (Richards et al., 1984).

Four captive bottlenose dolphins were presented with an underwater keyboard, which displayed visual forms that they could use to obtain specific items, over a period of 2 years. The dolphins' use of visual forms resulted in a systematic chain of events: a specific computer-generated whistle followed by the presentation of a specific object or activity (e.g., ball, ring, or rub). By observing and recording the dolphins' behavior in interacting with this system, we explored the possible role and process of mimicry in dolphin vocal learning.

Method

Subjects

The social group consisted of 2 female Atlantic bottlenose dolphins (*Tursiops truncatus*), Terry and Circe, and their 2 one-year-old male offspring, Pan and Delphi, born at our research facility. The research commenced 11 months after the birth of the 2 males. At that time Pan's mother, Terry, was approximately 20 years old, and Delphi's mother, Circe, approximately 9 years old. The female dolphins were research and exhibit animals and not participants in public demonstrations. The young males had no prior training other than positioning at specified locations during feeding sessions. Both young male dolphins were still nursing at the onset of this study.

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Facility

During Year 1 (1984–85), the 4 dolphins resided in a 7 ft (2.13 m) deep, 57,000 gal (215,769 L), kidney-shaped pool filled with treated bay water. In Year 2 (1987–88), they resided in two larger connected pools, each 50 ft (15.24 m) in diameter and 16 ft (4.88 m) deep. In addition, a 12 ft (3.66 m) wide × 4 ft (1.22 m) high × 4 ft (1.22 m) deep concrete insert was installed in one of the pools to facilitate the dolphins' interaction with the keyboard and experimenter. The keyboard system was installed on the pool side of this insert.

Apparatus and Procedures

Underwater keyboard. The underwater keyboard, individual key faces, and visual forms were constructed from ½-in. (1.27-cm) dark gray polyvinyl-chloride (pvc) plastic as shown in Figure 1. The keyboard was 21 in. (53.34 cm) wide × 24 in. (60.96 cm) high with a displacement distance of ½ in. (1.27 cm) between the back of each key and the face of the keyboard. The top edge of the keyboard was 8½ in. (21.59 cm) below the water surface. The 3½ × 3½ in. (8.89 × 8.89 cm) key faces were spray painted with flat black spray paint. All visual forms were cut from a 3 × 3 in. (7.62 × 7.62 cm) squares and spray painted with flat white spray paint and were designed to be distinct from each other and share few if any similar features (see Figure 2, Column A). The forms were fixed to the key pads by a pvc dowel, and a 1/16-in. (0.16-cm) stainless steel pin locked the visual form to the key, which allowed for rapid repositioning of the visual elements during sessions. The keyboard was mounted on the dolphin pool wall by pvc brackets constructed from white pvc pipe (1 in. [2.54 cm] in diameter) and was mounted to the top of the pool wall with copper thumb screws so the unit could be removed when not in use. The concrete wall of the dolphin pool extended 3½ ft (1.07 m) above ground and was approximately 12 in. (30.48 cm) thick. Plastic fiber-optic cables (HPE 898328 AWM VW-1, Hewlett Packard, Palo Alto, CA) interfaced the dolphin keyboard to an Apple II (Cupertino, CA) computer in our office that recorded all instances of key use.

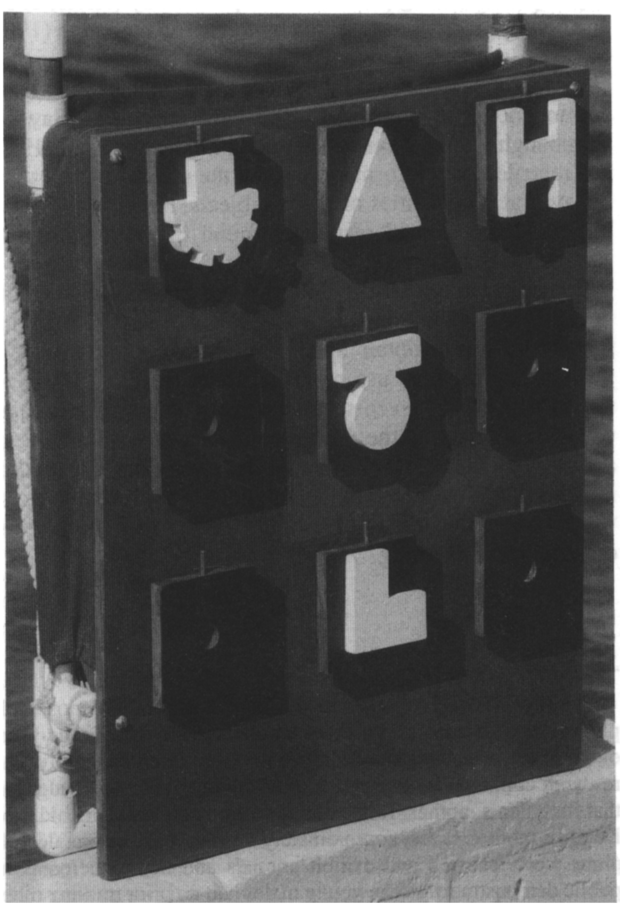

Figure 1. The underwater keyboard.

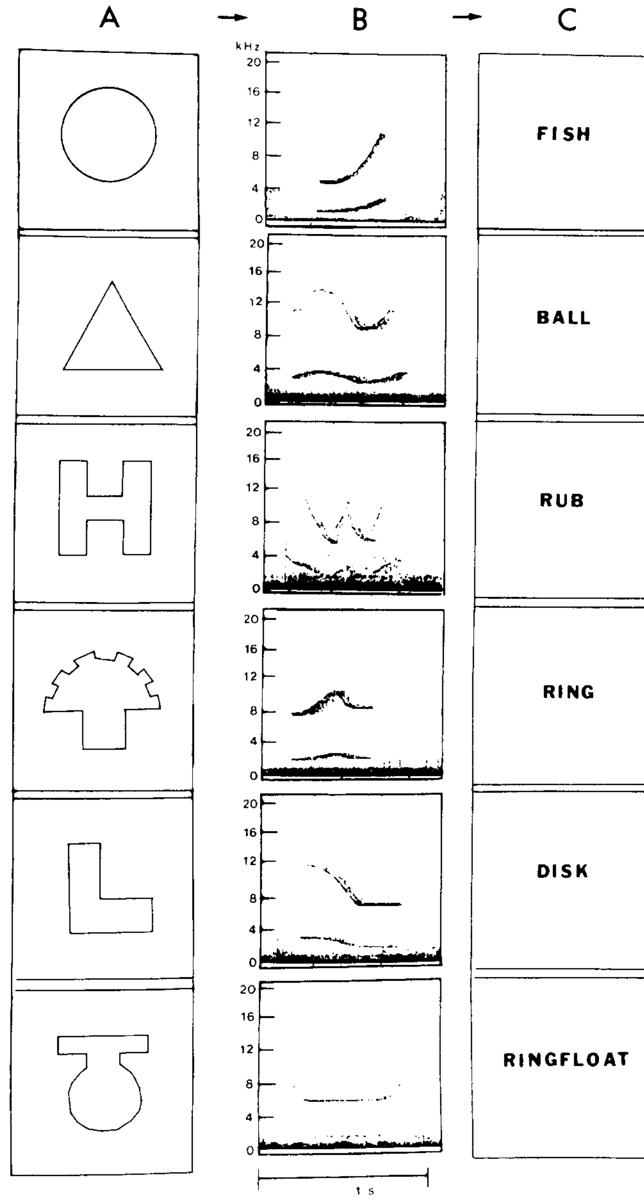

Figure 2. The stimulus elements provided by the keyboard system. (A dolphin's use of the three-dimensional, white visual forms, Column A, resulted in computer-generated whistles, Column B, and then specific objects or an activity, Column C, were given to the dolphin.)

Keyboard procedures. The keyboard system provided the dolphins with a systematic chain of events, as shown in Figure 2: The use of a visual form (Column A) was followed by a specific computer whistle generated underwater (Column B) and an object or activity offered to the dolphin (Column C). During experimental sessions an experimenter operated the computer in the laboratory, and two others collected behavioral data from an observation deck adjacent to the pool. A fourth experimenter (the *agent*) stood behind the pool wall where the keyboard was mounted and gave the dolphins the appropriate objects or activities on the basis of their key use. The agent wore a Beyer (Heilbronn, Germany) Model DT 209 headset and microphone that permitted communication with the person at the computer and the monitoring of all sounds in the dolphin pool, including the computer-generated whistles played underwater. The person at the computer informed the agent where to reposition the visual forms at the end of each minute according to the preprogrammed files. The keyboard was locked and inoperable while the visual forms were repositioned. When a dolphin pressed a key, a Votrax (Sunnyvale, CA) Model 100 Type N'Talk speech synthesizer interfaced with the computer informed the agent which key was used and which object or activity ought to be given to the dolphin.

Computer-generated whistles. The whistles were frequency modulated narrow-band signals that we designed and generated with a Computer Mountain Music System (Mountain View, CA) board in the computer. Two oscillators produced different frequency-modulated, saw-toothed waveforms at a sampling rate of 32 kHz. The saw-toothed waveform and use of two oscillators produced whistles with harmonics that approximated the quality or timbre of biologically produced whistles. The computer whistles ranged from 2 to 16 kHz and had a duration of 0.4–0.8 s as presented in Figure 2, Column B. There was a 0.3-s delay between the emission of two successive computer-generated whistles even if the time between two successive key presses was less. The whistles were played underwater in the dolphin pool through a Hansen (Redwood City, CA) underwater transducer (with output to 20 kHz) when the dolphins pressed specific keys. The underwater speaker was located 6 ft (1.83 m) to the left of the keyboard (from the dolphins' orientation) and positioned 3 ft (0.91 m) below the water surface.

The signals were designed to be similar to dolphins' natural whistles, yet different in their frequency modulation from whistles extant in our dolphins' repertoire as determined by our baseline recordings (see *Baseline observations*). It was necessary to use whistles that were distinct from the dolphins' own signals for several reasons. First, although this system was not explicitly designed to elicit vocal mimicry, we wanted to provide signals that could be readily perceived and easily reproduced if the dolphins chose to do so. The computer whistles therefore approximated the frequency range and duration of the dolphins' own whistles, under the assumption that this factor might facilitate the dolphins' processing, remembering, or producing these signals. Second, if the dolphins were to mimic the computer signals, we required the model sounds to be distinct from the dolphins' own repertoire in order to establish vocal mimicry, which has been operationally defined by Thorpe (1963) and Richards et al. (1984) as the copying of an otherwise improbable act or utterance, rather than the mere elicitation of their own whistles by playing similar whistles (Andrew, 1962).

Acoustic recording and analysis. Vocalizations were recorded on one track of audio or video, and a simultaneous narrative describing concurrent behaviors (e.g., key hits, play behavior, and tactile, postural, and spatial states) was recorded on a second track. Recordings were made on an Ampex (Redwood City, CA) ATR 700 tape recorder (tape speed at 19 cm/s, flat frequency responses to 22 kHz) with a Finley-Hill (Sausalito, CA) EM 8 hydrophone. The dual-channel tape recording method permitted both the hydrophone (acoustic) and behavioral information to be simultaneously recorded. In Year 1, the narrator monitored both channels during recording. In Year 2, the narrator discontinued monitoring the hydrophone channel while recording in order to avoid bias in reporting the dolphins' activity. Dolphin vocalizations were analyzed and sonograms produced with a Multigon (Mount Vernon, NY) Uniscan II Model 4600 Fourier fast-transform sonogram spectral display and a Kay (Pinebrook, NJ) Model 7029A Sona-Graph.

Determination of whistle facsimiles. Dolphin whistles that resembled the computer-generated whistles were considered facsimiles if their spectral parameters matched the computer signals with respect to both relative frequency and time parameters. Whistles were also played back on the tape recorder at full speed (19 cm/s) and half speed to determine precise audio matching. Categories of whistles included species-specific vocalizations, ambiguous facsimiles (those which matched only one of the specifications), and unambiguous facsimiles (those which matched both specifications). In order to avoid analyzer bias during matching, two levels of analysis were conducted. First, facsimiles were scored on a 5-point scale from *poor* (1) to *excellent* (5) on the basis of the spectral parameters of the signal. Second, the contexts of all facsimiles were determined from playback of the narratives that described the behaviors around or during the facsimile production.The number of facsimiles reported in this study include only those considered unambiguous and those which were scored good, very good, or excellent.

Defining mimicry and production. A facsimile was categorized as *mimicry* if the whistle facsimiles immediately followed the computer-generated whistle (the model sound), that is, if it occurred within 0.5 s of the computer-generated whistle and there were no intermediate signals before the facsimile. Whistle facsimiles that began after the onset of but overlapped the computer-generated whistles were also classified as mimicry.

A facsimile was referred to as *production* if the whistle did not immediately follow the computer-generated whistle. Productions included facsimiles that preceded key hits by the dolphins or that occurred in such contexts as toy play, dolphin–dolphin interactions, or solitary swimming during keyboard sessions.

Session procedures. Experimental sessions lasted for 30 min and were conducted at variable intervals. Generally one session was run per day. On occasion, two sessions were run. The dolphins were fed three times per day, and experimental sessions occurred 1–1½ hr after feeding times. The dolphins were not deprived of objects or human interaction outside of keyboard sessions.

In the first 39 sessions of Year 1, the elements presented were ball, tactile interaction (*rubs*), and fish (silver or river smelt). In 10 intermittent sessions the fish key was not presented in order to encourage the dolphins to use the other symbols more frequently. From Session 40, the fish key was discontinued and replaced with the ring key, a third visual form and whistle; when this key was pressed, rings were offered to the dolphins. A total of 56 free-choice sessions were conducted during Year 1. The results presented are from the 23 sessions that were audiorecorded.

In Year 2, after a 2-year hiatus, keyboard sessions recommenced, and the same procedures were followed as reported in Year 1, excluding any presentation of the fish key. A total of 38 sessions were conducted in Year 2.

Baseline observations. Baseline observations commenced at our facility in 1982 with the female dolphins, 11 months before the calves' births. With the births of the 2 males, we began a 1-year program of systematic observation and recording of the ontogeny of their evolving vocal repertoire and behavior (McCowan & Reiss, 1993; Reiss, 1988). These observations provided baseline data on the dolphins' vocal and nonvocal repertoires before the onset of the keyboard research. We found the average temporal and frequency parameters of the dolphins' whistles to be consistent with those reported in the literature (Caldwell & Caldwell, 1968; Dreher, 1966; Evans, 1967). Whistles were generally between 0.3 and 1.5 s in duration, and the frequency range extended from 2 to 40 kHz. A sequence of whistles was operationally defined by an intersignal duration of at least 1.6 s and ranged from approximately 2 to 10 s. Baseline observations of vocalizations were made before the studies in both Year 1 and Year 2 to determine if there were changes in the overall vocal activity as a consequence of keyboard sessions.

Results

Although all 4 dolphins had the same opportunity for interaction, only the 2 young males used the keyboard consistently. During the first session of Year 1, 1 of the adult females used the keyboard twice. Neither of the adult females were exposed to the keyboard in Year 2. We report only on changes observed in the dolphins' vocal behavior. Analysis of audio- and videotapes recorded in experimental sessions during Year 1 demonstrated spontaneous vocal mimicry and apparent productive use of facsimiles of computer-generated whistles by the dolphins.

Onset of Vocal Mimicry

Vocal mimicry of the computer-generated ball and rub whistles was first recorded during the 10th keyboard session in which only the ball and rub keys were presented. The ball whistle was mimicked after 19 exposures to the computer model.

Analysis revealed an interesting process of vocal mimicry. In 3 successive trials the end of the ball whistle was first mimicked (Figure 3, Panel A), then the beginning of the ball whistle was mimicked (Figure 3, Panel B), and finally a dolphin mimicked the harmonic structure of the whistle (Figure 3, Panel C). In each of the sonograms in Figure 3, the model sound appears to the left and the dolphin's emission follows it. In the initial instances of mimicry (Figure 3, Panels A and B), the dolphin matched the temporal parameters of the model sound. Both the absolute frequency as well as the frequency modulation of the model was matched in the dolphin's first mimicry of the end of the model sound (Figure 3, Panel A). In Figure 3, Panel B, the dolphin mimicked the relative rather than the absolute frequency modulation of the model sound. In Figure 3, Panel C, the frequency modulation of the dolphin's signal appeared to be less accurate than in the earlier trials when only the fundamental was mimicked. In this latter case, however, the dolphin's mimicry of the harmonic structure of the model sounded like the computer-generated ball whistle. Figure 3, Panel D presents the first complete mimic of the ball whistle, in which the frequency modulation closely matches the preceding model sound.

Similar patterns were also observed with the initial mimicry of the rub whistle. The rub whistle was mimicked after nine instances of exposure. In a single sequence that followed the model sound (Figure 4), the first signal reproduced the end component (a rise in frequency), the second resembled the entire whistle compressed in time, and the third reproduced the initial component of the model (a fall in frequency). The model sound and the three instances of mimicry occurred within 1.6 s. The model sound was 0.7 s in duration, and the three mimicked elements occurred within a 0.7-s period (Figure 4).

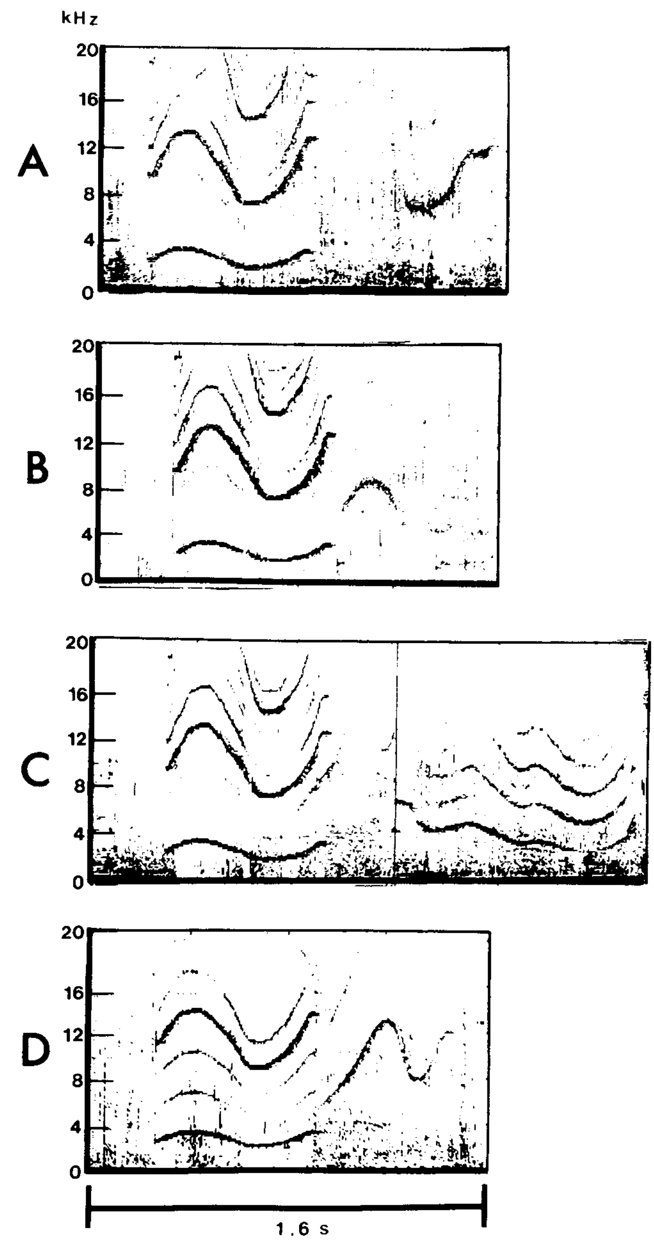

Figure 3. Spectrograms of the initial spontaneous mimicry of the computer-generated ball whistle after 19 exposures to the model sound. (In each case the computer model appears at the far left of the spectrogram and the example of dolphin mimicry is on the right. Panel A: The first instance of mimicry in which the end of the computer model was mimicked. Panel B: The second instance of mimicry in which the initial component of the model was mimicked. Panel C: The third occurrence of mimicry in which the harmonic structure was approximated and the frequency modulation was less accurate yet this whistle sounded like the computer model. Panel D: From the same session an early mimic of the model sound that shows compression of the temporal parameter.)

When the new visual form and whistle presented with the rings were first introduced (30th session), spontaneous vocal

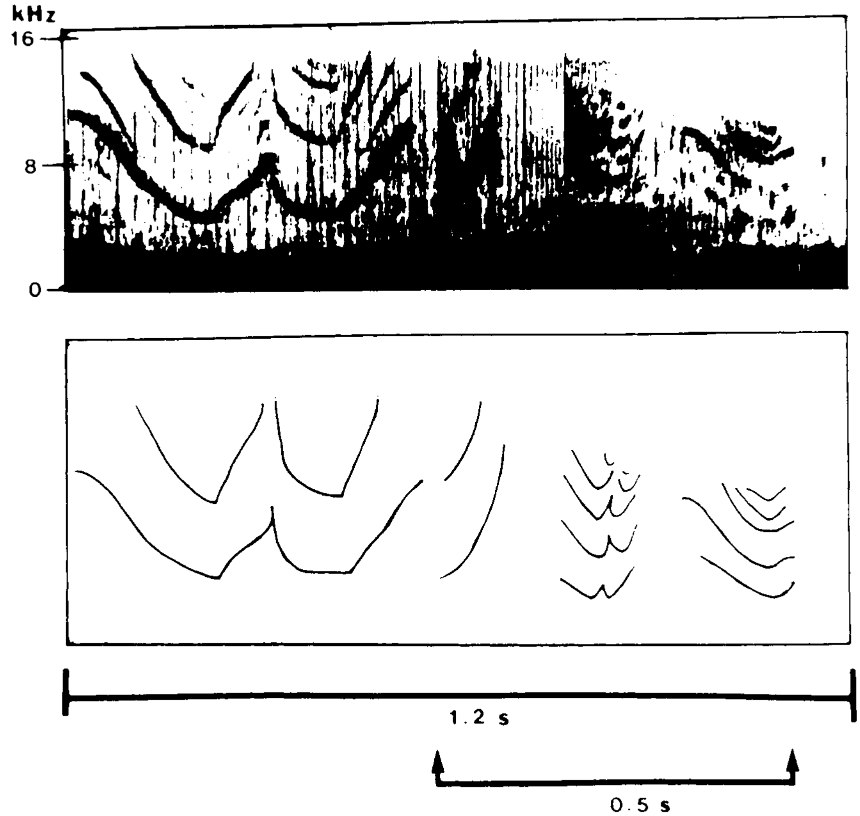

Figure 4. Spectrogram (top panel) of the initial spontaneous mimicry of the computer-generated rub whistle, and a tracing (bottom panel) of the same spectrogram for illustration of mimicked components.

mimicry occurred after the dolphins' second exposure to the model sound (Figure 5). Figure 5, Panel A shows the 0.5-s model sound. The first instance of mimicry is shown in Figure 5, Panel B, in which the frequency modulation of the signal was approximated but the temporal aspects were compressed to 0.28 s. The next instances of mimicry occurred after the third and fourth exposure to the model (Figure 5, Panels C and D). In these cases the frequency modulation and temporal parameters were more closely matched. After the dolphins' fifth exposure to the model sound, we recorded instances of mimicry in which the frequency modulation resembled the model but the signal was expanded in both the time and frequency domain as shown in Figure 5, Panels E and F. Figure 5, Panel G shows a spectrogram of an early ring production (produced immediately before a dolphin pressed the ring key) that showed slight expansion in frequency and duration in comparison with the model. Figure 5, Panel H represents two ring facsimile productions in which the frequency range and durations were more expanded in comparison with the model sound.

Patterns of Vocal Mimicry and Production

Facsimiles of the computer whistles were frequently similar in duration, relative frequency, and frequency modulation to that of the model sound (Figure 6, Panels A and B). Facsimiles were often produced with different fundamental frequencies and occasionally with expanded or compressed parameters with respect to frequency and time as shown in Figure 6, Panels C and D. In addition, the dolphins occasionally emitted whistles that, although they did not match the spectral parameters of the computer models, sounded exactly (at full and half speed) like the model sounds (Figure 6, Panel E).

In both Year 1 and Year 2, facsimile activity was only a small proportion of total vocal activity[1] (Figure 7, Panels A and B; facsimile activity ÷ total vocal activity; in Year 1, 304 ÷ 2,474 = .123; in Year 2, 229 ÷ 6,136 = .037). In Year 1 (Figure 7, Panel A), the amount of vocal mimicry in relation to production followed a consistent relation across keyboard sessions (simple regression [values were natural log transformed to normalize data for simple regression], $r^2 = .539$, F test, $p = .0118$). Across all sessions vocal mimicry ($n = 165$) was about 19% higher than production ($n = 139$). In addition, the overall amount of both vocal mimicry and production of ball facsimiles was higher than ring facsimiles;

[1] Vocal activity was measured by the number of species-specific whistle sequences. Sequences were defined as whistle bouts separated by at least 1.6 s. For example, a whistle sequence could contain one or several whistles. Therefore, vocal activity measured by sequences is an underestimate of total species-specific whistles.

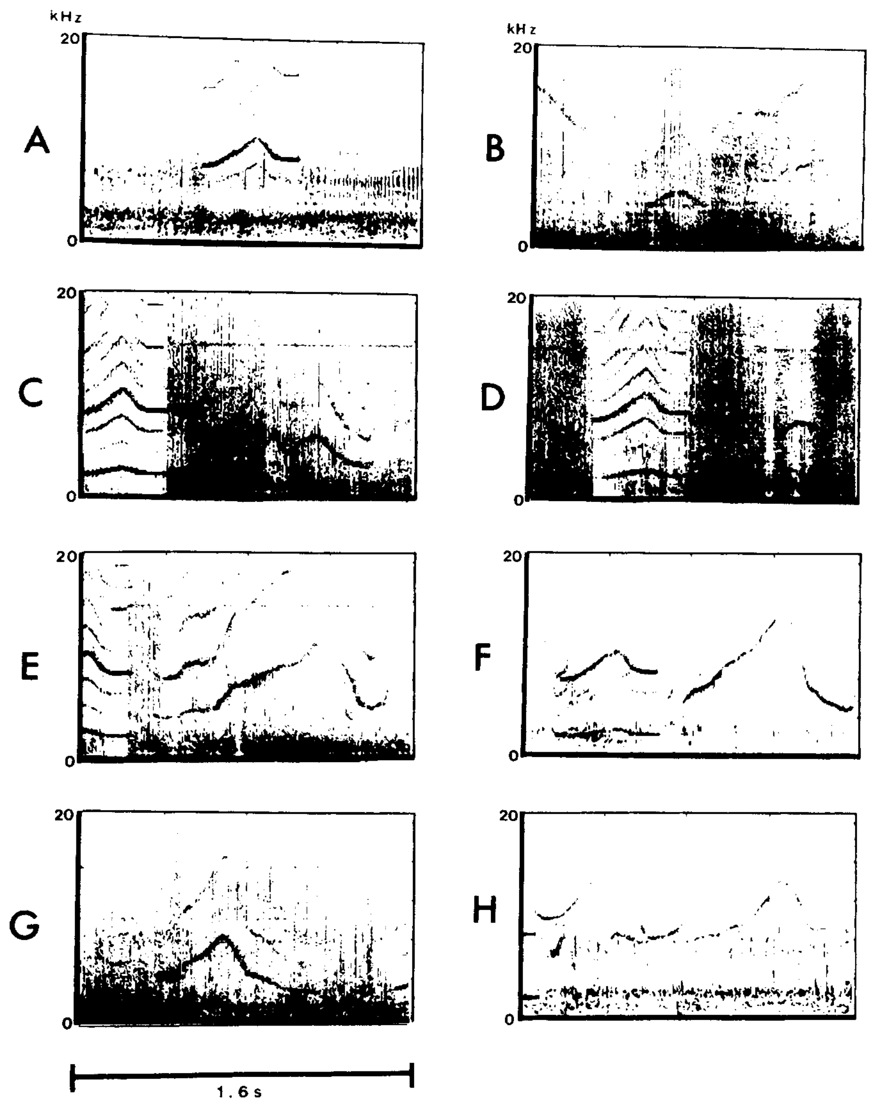

Figure 5. Spectrograms of initial spontaneous mimicry of the computer-generated ring whistle. (Panel A: The model sound. Panel B: The first instance of mimicry in which the frequency modulation was approximated after the second exposure to the model sound. In Panels C, D, E, and F, the model sound appears to the left of the spectrogram and the example of mimicry is on the right. Panel C: The second instance of mimicry in which the duration of the model was matched and the frequency modulation was approximated. Panel D: The fourth instance of mimicry. Panel E: The fifth instance of mimicry in which the temporal and frequency parameters were expanded but the general frequency modulation was approximated. Panel F: This spectrogram shows the same type of expansion of the frequency and temporal parameters as in Panel E. Panel G: After the eighth exposure to the model sound, this production was recorded before a dolphin used the ring key. Panel H: This spectrogram shows two early ring facsimile productions in which the frequency range and durations were expanded, as compared with the model.)

ball was most often reproduced (n = 104 for mimicry and n = 90 for production), and ring was the second highest (n = 45 for mimicry and n = 34 for production). The ring visual form and correlated whistle were introduced after the 30th session, but the ring key (303 total hits per year) was used less than the ball key (363 total hits per year). In contrast, ring was more frequently emitted than rub (231 total hits per year; n = 16 for mimicry and n = 15 for production).

In Year 2, the occurrence of vocal mimicry in relation to production showed no consistent relation across sessions, unlike Year 1 (Figure 7, Panel B; simple regression, r^2 = .047, F test, p = .8777). Vocal productions (n = 210) were observed to be approximately 1,005% higher than vocal mimics (n = 19). In comparison with Year 1, there was a significant increase in the ratio of productions to vocal mimics (chi-square test, p = .0001), and productions were 13.2

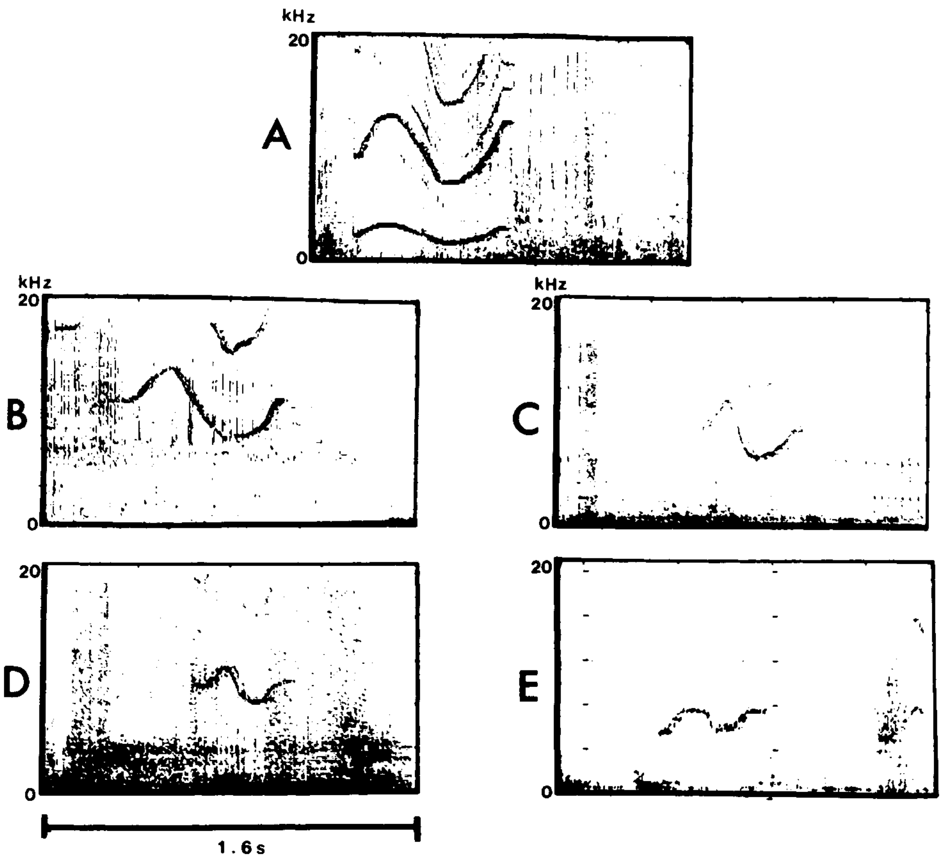

Figure 6. Spectrograms of the computer-generated ball whistle and dolphin productions of ball facsimiles. (Panel A: The model sound. Panel B: Spectrogram of ball facsimile production in which frequency modulation and duration closely approximated the model. Panels C and D: Spectrograms in which the duration and frequency range was compressed but the relative frequency modulation of the model was approximated. Panel E: Spectrogram of the ball facsimile produced by a dolphin at the beginning of Year 2 after a single exposure to the model sounds during the 2-year hiatus. The relative frequency modulation of the signal was closely matched).

times more likely to be produced in Year 2 than Year 1 (odds ratio of 13.2, range of 10.1–17.1, at 95% confidence interval). However, although the ratio of productions to mimics was significantly higher in Year 2 than in Year 1, the overall number of facsimiles was higher in Year 1 (facsimile activity in Year 1, n = 304, and in Year 2, n = 229).

The relative number of mimics and productions of ball, rub, and ring followed the same general pattern as reported in Year 1 (291 total hits per year for ball, 280 hits for ring, and 245 hits for rub). Ball facsimiles were most frequent (n = 11 for mimicry and n = 92 for production), ring facsimiles were less frequent (n = 8 for mimicry and n = 64 for production), and rub facsimiles were rare (n = 0 for mimicry and n = 5 for production).

In addition, facsimiles in Year 2 showed greater structural fidelity to the computer sounds than in Year 1 (in Year 1, 18 excellent or very good vs. 39 good facsimiles, and in Year 2, 85 vs. 76; chi-square test, p = .0004). The dolphins' production of facsimiles and mimicry matched relative time and frequency parameters more closely, yet they still emitted facsimiles that were expanded or compressed with respect to time and frequency parameters. For example, a comparison of Year 2 ring facsimiles (Figure 8) with those of Year 1 (Figure 4) showed less expansion and compression of the time and frequency parameters.

Anecdotal Evidence for Short-Term and Long-Term Auditory Memory

During early sessions in Years 1 and 2, the dolphins occasionally produced facsimiles before appropriate keyboard hits (n = 5). During the first session of the Year 1 study (July 13, 1984), Pan produced two ball facsimiles before he produced ball key hits. In the Year 2 study, Pan produced two preceding productions of ring (January 25 and February 1, 1988). Although the sampling of this behavior is quite low, it is important to note that the dolphins never produced inappropriate facsimiles before key hits (i.e., ring production before ball key hit).

On September 28, 1987, after the 2-year hiatus between studies, we recorded and analyzed a nonambiguous produc-

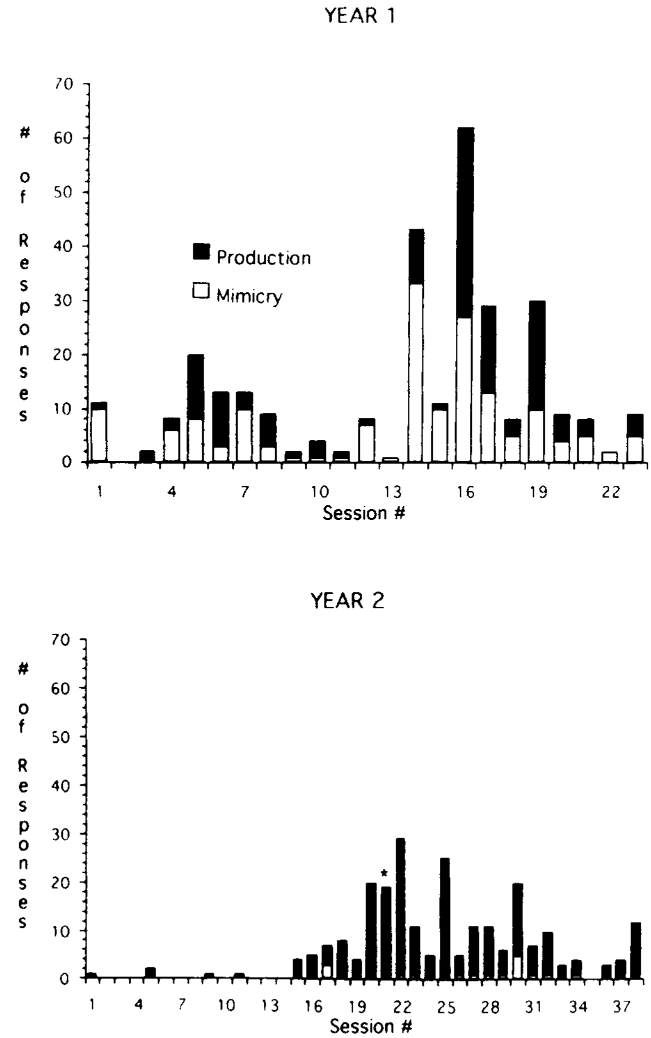

Figure 7. Vocal mimicry and facsimile production during Years 1 and 2. (* = a session in which the underwater speaker was accidentally not activated during the session and no model sounds were presented.)

tion of a ball facsimile as the blank keyboard was positioned on the wall at the session's onset. This production of ball, shown in Figure 6, Panel E, closely matched the relative frequency modulation of the computer-generated ball whistle, although the temporal parameter was compressed. The dolphins had heard the computer-generated ball whistle only once during this 2-year hiatus, 2 months before this excellent production. Neither of the young males used the keyboard again until 13 sessions later on October 14, 1987, when active keyboard use resumed.

Combination Whistles: Emergence and Patterns of Use

In Year 2, the dolphins began to emit *combination whistles*. These were two or more discrete whistles that were apparently combined to form one continuous whistle. Spectrographic analysis of the combination whistles indicated one continuous emission produced by a single dolphin. We found ball–ring combination whistles (a ball facsimile continuing into a ring facsimile; $n = 4$) and, more frequently, ring–ball combination whistles (a ring facsimile continuing into a ball facsimile; $n = 28$). The dolphins could not have heard the

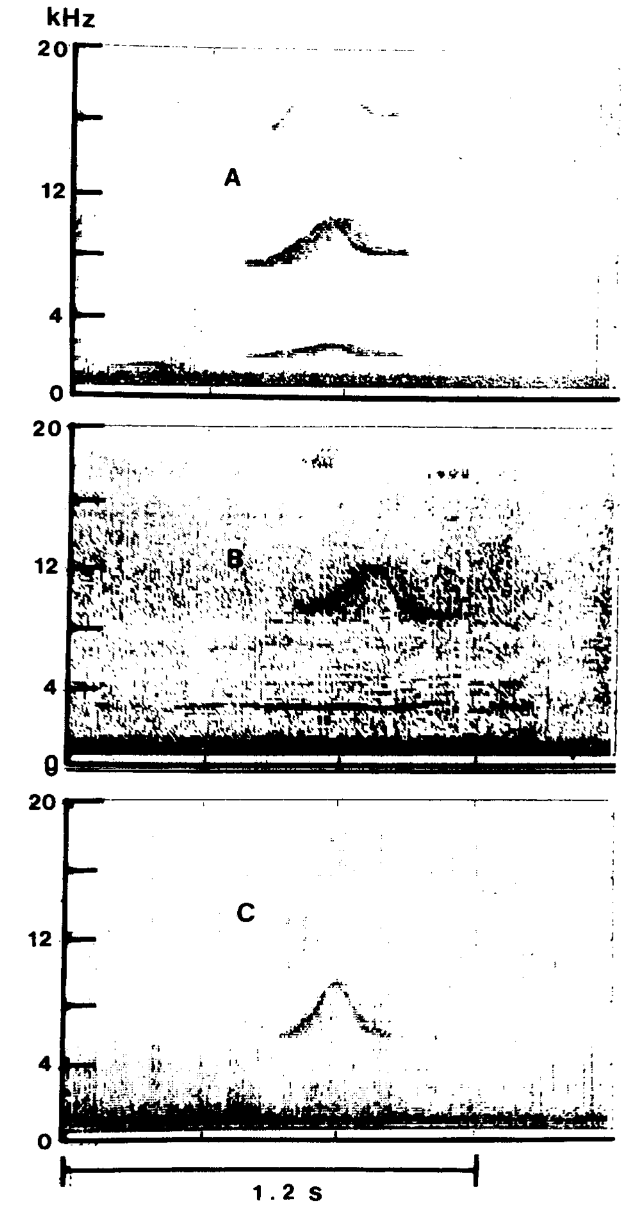

Figure 8. Spectrograms of facsimile productions of the ring whistle during Year 2. (Panel A: The model sound. Panels B and C: Spectrograms of facsimiles that showed close fidelity to the model sound in terms of the frequency modulation. In both cases the relative-frequency modulation was matched, but the actual frequency was transposed either higher or lower than that of the model. In Panel B, the dolphin mimicked both oscillators or the harmonic structure of the model. Both whistles shown in Panels B and C were produced while the dolphins were interacting with rings or interacting with a ring and ball at the same time during keyboard sessions.)

two computer whistles in rapid succession. There was always a minimum delay (of 0.3 s) between successive computer generations. These combination whistles appeared to be novel signals produced by the dolphins.

The components of a ring facsimile and ball facsimile can be clearly seen in the combination whistle shown in Figure 9. Ring–ball productions were first recorded during the 20th session in Year 2, when five ring–ball facsimiles were produced. The ring–ball combinations (n = 23) continued to persist through the remaining sessions of Year 2 (Figure 10).

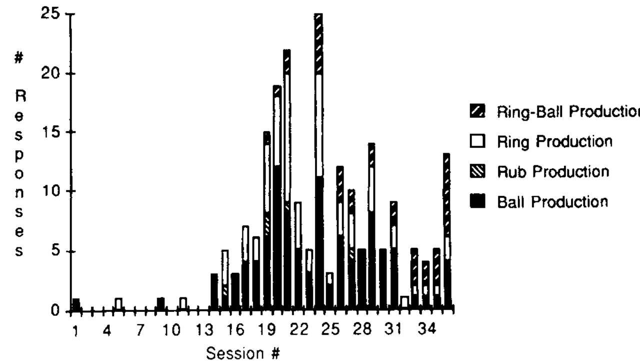

Figure 10. Facsimile productions of the ball, ring, rub, and novel ring–ball whistles in Year 2.

Behavioral Concordance: Facsimile Productions and Combination Whistles

Analysis of the behavioral narratives recorded during sessions in Year 2 enabled us to determine the contexts in which the dolphins produced whistle facsimiles. Data on behavioral concordance of facsimile production and combination whistles were gathered only from the Year 2 study. All productions from Year 2 were included in these analysis. Table 1 presents the summation of the appropriate, inappropriate, and other contexts in which facsimile productions occurred. *Appropriate* contexts were narrowly defined by those contexts in which a dolphin had physical contact with the appropriate object. In order to be conservative in our analysis, we did not consider approaching or orienting to an object as appropriate. *Inappropriate* contexts were defined as situations in which the dolphin physically interacted with an inappropriate object or activity. *Other* contexts were defined by either ambiguous or general behavior (i.e., swimming, resting, or orienting to or approaching an object) in which productions were emitted.

Analysis revealed that the dolphins were using the whistle facsimiles in behaviorally appropriate contexts. In a total of 92 ball productions, 74 (80%) were emitted in the context of ball play; of 64 ring productions, 47 (73%) were emitted during ring play; and in 5 rub productions, all (100%) were produced during contexts of physical contact between the dolphin and experimenter. For the 28 ring–ball productions, 23 (82%) were emitted during simultaneous ring and ball play.

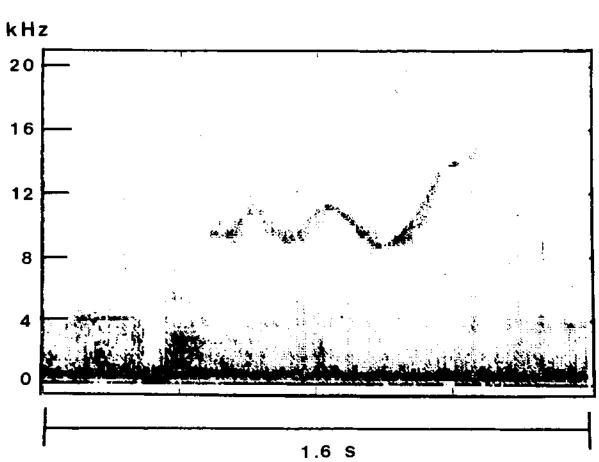

Figure 9. Spectrogram of an apparent combination whistle, in which the initial element resembles the computer-generated ring whistle and the end of the whistle resembles the computer-generated ball whistle.

Discussion

Dolphins show a high degree of plasticity in their behavior, as evidenced by reports of spontaneous vocal and behavioral mimicry (Caldwell & Caldwell, 1965; Sayleigh, Tyack, Wells, & Scott, 1990; Tayler & Saayman, 1973; Tyack, 1986; see Richards, 1986, for a review) and observational learning (Adler & Adler, 1978). However, little is known about the role of mimicry in vocal learning. Our study was designed to answer the question, What do dolphins learn and how do they learn it given the freedom to interact with a self-reinforcing system? Instead of our examining to what extent we could train and control dolphin behavior, we designed the keyboard system to encourage the animals to explore the contingencies of keyboard use and computer-generated signals within a social environment.

Process of Vocal Mimicry

Our results were inconsistent with the results reported in past studies (Richards et al., 1984; Sigurdson, 1989). First, the rapidity with which the model sounds were mimicked by the dolphins in our study greatly contrasts with the results reported by Richards et al. (1984) and later by Sigurdson (1989), in which over 1,000 trials were required to train initial mimicry. This high number of trials required to train vocal mimicry in other studies may reflect problems with methodology rather than the animals' own abilities. Second, in contrast to those studies, our dolphins needed far fewer exposures to model sounds before initial mimicry when they were given the freedom to choose the parameters to mimic than when the parameters they ought to mimic were predetermined. Richards et al. (1984) and Sigurdson (1989) determined the parameters of the model sound to be mimicked, selectively reinforcing approximations of the duration, the base frequency, and the modulation parameters of the model. Third, our dolphins mimicked new model sounds without losing the fidelity of the production of previously acquired

Table 1
Behavioral Concordance Between the Facsimile Productions by the Dolphins and the Behavioral Context in Which They Occurred

	Behavioral concordance		
Context	Appropriate	Inappropriate	Other
Ball	74	2	16
Ring	47	2	15
Rub	5	0	0
Ring–ball	23	0	5

facsimiles. Finally, the spontaneous and continued use of facsimiles in behaviorally appropriate contexts is unique to our study. The disparity between our results and these earlier studies may be due to age- or sex-related factors. In both Richards et al. (1984) and Sigurdson (1989) studies, the subjects were older females (from 5 to 7 years old).. In our study the subjects were two juvenile males. However, there is still little known about the significance of these differences in the production of species-specific vocalizations to warrant generalization of these differences to the species level (but see Sayleigh et al., 1990). Our results more likely suggest that exposing dolphins to a social and interactive environment may encourage them to learn new signals (Pepperberg & Neapolitan, 1988) and to use them in functional contexts similar to the process of repertoire acquisition during early development (McCowan & Reiss, 1993).

Mimicry As a Process for Vocal Learning

The importance of mimicry in vocal learning has been well demonstrated in human language (Bloom et al., 1974; Kuczaj, 1987; Valentine, 1930) and avian song (Baptista & Petrinovich, 1986; Kroodsma & Pickert, 1984; Marler & Peters, 1982). Our results have provided evidence for the use of vocal mimicry in acquiring novel signals into the dolphins' repertoires. The process of mimicry and productive use of whistle facsimiles provided information with respect to how dolphins may perceive, associate, and store information. The fact that they quickly and spontaneously mimicked the frequency modulation, the duration, and often the harmonic structure of the model sounds suggests that these are salient acoustic features, which may play an important role in the dolphins' discrimination and use of whistles in communication. In the initial instances of mimicry, the tendency by the dolphins to mimic the last element and then the first element of the the model sounds suggests that the processing of new sound stimuli may involve order effects and selective attention as shown by recency and primacy effects in recall experiments with humans (Robinson & Brown, 1926).

The role of imitation in human language acquisition has been the subject of much debate (Bloom et al., 1974; Kuczaj, 1987; Valentine, 1930). Children often imitate lexical items before they spontaneously use the items in their repertoire, which suggests that imitation is a developmental step in language acquisition (Bloom, 1970; Kuczaj, 1982; Slobin, 1968). Other studies have demonstrated that deferred imitation (reproduction of a novel sound some time after hearing it rather than immediately) can also introduce lexical items into children's repertoires (Kuczaj, 1987).

The results from our study and the data from studies of avian song and human language suggest that mimicry may be a more widespread strategy for vocal learning than previously suspected. This, in turn, suggests that these divergent communication systems may share underlying mechanisms in vocal learning.

Learned Associations and Referential Communication

The contexts in which facsimiles were produced suggest the dolphins developed associations between the visual forms, the whistle facsimiles, and the objects and activity. Their behavior suggests the eliciting stimulus for facsimile production was often their interaction with the corresponding objects and that their behavior involved both vocal learning and learned associations constrained by context. This does not presuppose that the dolphins were labeling these objects. In fact, the semiotic level or functional use of such signals by other animals or prelexical children is unclear (Synder, Bates, & Bretherton, 1982). However, this perspective does not exclude the possibility of referential associations by dolphins or other species. Field studies with free-ranging vervet monkeys have reported that the young vervets learn referential associations between specific calls and specific predators in their environment (Seyfarth, Cheney, & Marler, 1980). The use of labels has also been reported in several other species, such as European jays (Goodwin, 1956), toque macaques (Dittus, 1984), and ground squirrels (Owings & Lager, 1980). The results of studies in which artificial codes have been taught to other species have also provided evidence for the capacity for referential labeling (Fouts, 1973; Gardner & Gardner, 1969; Pepperberg, 1981; Premack, 1971; Savage-Rumbaugh, 1986).

Any speculation about referential communication needs to question the level of association in effect. The animals in this study were originally presented with temporally related stimuli through their use of the keyboard. Functionally, they learned to use the keyboard to obtain both acoustic and nonacoustic events (objects and activities that followed). Much of their initial behavior, especially in early sessions when new sounds were first introduced, suggested the sounds themselves were reinforcers. In those sessions the dolphins frequently mimicked the computer-generated whistle and rejected the given object. They also produced the facsimiles before they pressed the corresponding visual forms during the early stages of the experiment. This suggests that the dolphins were learning associations between the visual and acoustic elements that may have contributed to the process of acquisition. In addition, the difference in the patterns of vocal mimicry and production in Year 1 and Year 2 (more production in Year 2) suggests that the dolphins were attending less to the keyboard itself and more to the interactions with the objects and corresponding sounds in Year 2. The behavioral concordance data further supports that associations were developed between the acoustic elements and the objects and activity. However, there is insufficient evidence to support any claim that associations were developed between the visual element and the object or activity.

There are different levels of associations possible in learning. In this study there were temporal associations in which the mimicry of sounds was not necessarily tied to meaning: The visual form preceded the computer-generated whistle, which preceded the object or activity offered. There were also functional or pragmatic associations in which there were associations between sound patterns and environmental contingencies: The use of a key resulted in receiving a computer-whistle, which resulted in receiving an object or activity. Finally, there were semantic or referential associations in which one element was used to refer to another element: The visual form represented a computer-generated whistle, which represented an object or activity. Although the dolphins' vocal behavior may suggest that referential associations were formed, we cannot conclusively show that a functional relationship existed among the facsimiles, objects, or visual forms. We can only take a descriptive approach to the dolphins' behavior at this time.

There are also different but compatible interpretations for the results of this study. One level suggests that principles of operant conditioning were used in a more flexible context in which the dolphins chose to initiate and explore contingencies of keyboard use (Skinner, 1957). Another level suggests that there may be optimal strategies for processing, encoding, and storing information in morphologically divergent species.

Implications for the Analysis of Dolphin Communication Signals

Although there is a growing literature on dolphin behavior and communication (reviewed in Herman & Tavolga, 1980, and Schusterman, Thomas, & Wood, 1986), little is understood about the repertoires, function, and organization of dolphins' vocal and nonvocal signals or the scope of their abilities. We lack information on the acoustic parameters dolphins attend to and use in their communication. The structure and organization of their vocalizations and how they function with their nonvocal signaling and behavior is unknown. The results of this study may provide a framework for the investigation into the nature of the dolphin's vocal repertoire. The tendency of dolphins to match, compress, and expand the temporal and frequency modulation parameters of their signals suggests that these factors ought to be considered when researchers develop acoustic analysis and pattern recognition programs for investigating dolphin vocalizations. Whether these parametric differences are significant to the dolphin or serve to convey information is not known and needs to be determined. The persistence of the production of complex whistles we termed *combination whistles* prompted us to review sonograms of our baseline recordings. In many cases complex whistles appeared to be composed of smaller combined elements that also occurred individually in their repertoire. This observation suggests that in analyzing dolphin vocalizations researchers must consider this level of organization.

Relinquishing a degree of experimental control to the dolphins has perhaps illuminated otherwise overlooked features of their own communication systems and cognitive abilities. The procedure used in this study allowed us to investigate the dolphins' abilities and propensities as contrasted with their capacity for learning tasks that we determine. There is a significant difference between training patterns of behavior and the spontaneous development and use of patterns of behavior. The latter reveals much more about the animal's perceptions and information-processing strategies.

References

Adler, H. E., & Adler, L. L. (1978). What can dolphins (*Tursiops truncatus*) learn by observation? *Cetology, 30,* 1–10.

Andrew, R. J. (1962). Evolution of intelligence and vocal mimicking. *Science, 137,* 585–589.

Baptista, L. F., & Petrinovich, L. (1986). Song development in the white-crowned sparrow: Social factors and sex differences. *Animal Behaviour, 34,* 1359–1371.

Baylis, J. R. (1982). Avian vocal mimicry: Its function and evolution. In D. E. Kroodsma, E. H. Miller, & H. Ouellet (Eds.), *Acoustic communication in birds: Vol. 2. Song learning and its consequences* (pp. 51–83). San Diego: Academic Press.

Bloom, L. (1970). *Language development: Form and function in emerging grammars.* Cambridge, MA: MIT Press.

Bloom, L., Hood, L., & Lightbown, P. (1974). Imitation in language development: If, when, and why. *Cognitive Psychology, 6,* 380–420.

Caldwell, M. C., & Caldwell, D. K. (1965). Individualized whistle contours in bottlenosed dolphins (*Tursiops truncatus*). *Nature, 207,* 434–435.

Caldwell, M. C., & Caldwell, D. K. (1968). Vocalization of naive captive dolphins in small groups. *Science, 159,* 1121–1123.

Caldwell, M. C., & Caldwell, D. K. (1972). Vocal mimicry in the whistle mode by an Atlantic bottlenosed dolphin. *Cetology, 9,* 1–8.

Dittus, W. P. J. (1984). Toque macaque food calls: Semantic communication concerning food distribution in the environment. *Animal Behaviour, 32,* 470–477.

Dreher, J. J. (1966). Cetacean communication: Small-group experiment. In K. S. Norris (Ed.), *Whales, dolphins, and porpoises* (pp. 529–543). Berkeley: University of California Press.

Evans, W. E. (1967). Vocalization among marine mammals. In W. N. Tavolga (Ed.), *Marine bio-acoustics* (Vol. 2, pp. 159–186). Oxford, United Kingdom: Pergamon Press.

Fouts, R. S. (1973). Acquisition and testing of gestural signs in four young chimpanzees. *Science, 180,* 978–980.

Gardner, R. A., & Gardner, B. T. (1969). Teaching sign language to a chimpanzee. *Science, 165,* 664–672.

Goodwin, D. (1956). Further observations on the behaviour of the jay *Garrulus glandarius. Ibis, 98,* 186–219.

Herman, L. M., & Tavolga, W. N. (1980). The communication systems of cetaceans. In L. M. Herman (Ed.), *Cetacean behavior: Mechanisms and functions* (pp. 149–209). New York: Wiley.

Kroodsma, D. E. (1982). Learning and the ontogeny of sound signals in birds. In D. E. Kroodsma, E. H. Miller, & H. Ouellet (Eds.), *Acoustic communication in birds: Vol. 2. Song learning and its consequences* (pp. 1–23). San Diego: Academic Press.

Kroodsma, D. E., & Pickert, R. (1984). Sensitive phases for song learning: Effects of social interaction and individual variation. *Animal Behaviour, 32,* 389–394.

Kuczaj, S. A., II. (1982). Language play and language acquisition. In H. W. Reese (Ed.), *Advances in child development and be-*

havior (Vol. 17, pp. 197–232). San Diego: Academic Press.

Kuczaj, S. A., II. (1987). Deferred imitation and the acquisition of novel lexical items. *First Language, 7,* 177–182.

Lilly, J. C. (1965). Vocal mimicry in *Tursiops*: Ability to match numbers and durations of human vocal bursts. *Science, 147,* 300–301.

Marler, P., & Peters, S. (1982). Subsong and plastic song: Their role in the vocal learning process. In D. E. Kroodsma, E. H. Miller, & H. Ouellet (Eds.), *Acoustic communication in birds: Vol. 2. Song learning and its consequences* (pp. 25–50). San Diego: Academic Press.

McCowan, B., & Reiss, D. (1993). *Quantitative analysis of whistle development in captive bottlenose dolphins (*Tursiops truncatus*): Postpartum through the first 3 months.* Unpublished manuscript.

Owings, D. H., & Lager, D. W. (1980). Chatter vocalizations of California ground squirrels: Predator- and social-role specificity. *Zeitschrift für Tierpsychologie, 54,* 163–184.

Penner, R. H. (1966). *Conditioned whistle replication in* Tursiops truncatus *(Montague)* (Contract No. N123–[60530]55399A). China Lake, CA: U.S. Naval Ordinance Test Station.

Pepperberg, I. M. (1981). Functional vocalizations by an African grey parrot (*Psittacus erithacus*). *Zeitschrift für Tierpsychologie, 55,* 139–160.

Pepperberg, I. M., & Neapolitan, D. M. (1988). Second language acquisition: A framework for studying the importance of input and interaction in exceptional song acquisition. *Ethology, 77,* 150–168.

Premack, D. (1971). Language in chimpanzee? *Science, 172,* 808–822.

Reiss, D. (1981). Pragmatics of human–dolphin communication. *Dissertation Abstracts International, 44,* 356B. (University Microfilms No. 83–11642)

Reiss, D. (1988). Observations on the development of echolocation in young bottlenose dolphins. In P. E. Nachtigall & P. W. B. Moore (Eds.), *Animal sonar: Processes and performance* (pp. 121–127). New York: Plenum Press.

Richards, D. G. (1986). Dolphin vocal mimicry and vocal object labeling. In R. J. Schusterman, J. A. Thomas, & F. G. Wood (Eds.), *Dolphin cognition and behavior: A comparative approach* (pp. 273–288). Hillsdale, NJ: Erlbaum.

Richards, D. G., Wolz, J. P., & Herman, L. M. (1984). Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenosed dolphin, *Tursiops truncatus. Journal of Comparative Psychology, 98,* 10–28.

Robinson, E. S., & Brown, M. A. (1926). Effect of serial position upon memorization. *American Journal of Psychology, 37,* 538–552.

Rumbaugh, D. M., Gill, T. V., & Von Glaserfeld, E. C. (1973). Reading and sentence completion by a chimpanzee (*Pan*). *Science, 182,* 731–733.

Savage-Rumbaugh, E. S. (1986). *Ape language: From conditioned response to symbol.* New York: Columbia University Press.

Savage-Rumbaugh, E. S., & Rumbaugh, D. M. (1978). Symbolization, language, and chimpanzees: A theoretical reevaluation based on initial language acquisition processes in four young *Pan troglodytes. Brain and Language, 6,* 265–300.

Sayleigh, L. S., Tyack, P. L., Wells, R. S., & Scott, M. D. (1990). Signature whistles of free-ranging bottlenose dolphins *Tursiops truncatus*: Stability and mother-offspring comparisons. *Behavioral Ecology and Sociobiology, 26,* 247–60.

Schusterman, R. J., Thomas, J. A., & Wood, F. G. (Eds.). (1986). *Dolphin cognition and behavior: A comparative approach.* Hillsdale, NJ: Erlbaum.

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Animal Behaviour, 28,* 1070–1094.

Sigurdson, J. (1989, April). *Frequency-modulated whistles as a medium for communication with the bottlenose dolphin (*Tursiops truncatus*).* Paper presented at the Animal Language Workshop, Honolulu.

Skinner, B. F. (1957). *Verbal behavior.* New York: Appleton-Century-Crofts.

Slobin, D. I. (1968). Imitation and grammatical development in children. In N. S. Endler, L. R. Boulter, & H. Osser (Eds.), *Contemporary issues in developmental psychology* (pp. 437–443). New York: Holt, Rinehart & Winston.

Synder, L. S., Bates, E., & Bretherton, I. (1982). Content and context in early lexical development. *Journal of Child Language, 8,* 565–582.

Tayler, C. K., & Saayman, G. S. (1973). Imitative behaviour by Indian Ocean bottlenose dolphins (*Tursiops aduncus*) in captivity. *Behaviour, 44,* 286–298.

Thorpe, W. H. (1963). *Learning and instinct in animals* (2nd ed.). Cambridge, MA: Harvard University Press.

Tyack, P. (1986). Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: Mimicry of signature whistles? *Behavioral Ecology and Sociobiology, 18,* 251–257.

Valentine, C. W. (1930). The psychology of imitation with special reference to early childhood. *British Journal of Psychology, 21,* 105–132.

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