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Importance of Contextual Saliency on Vocal Imitation by Bottlenose Dolphins

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A previous experimental study (Reiss & McCowan, 1993) on dolphin vocal learning documented the process and pattern of vocal imitation in bottlenose dolphins (*Tursiops truncatus*). This previous study demonstrated that dolphins spontaneously imitate novel signals when paired with salient environmental events. The acquisition process of the dolphins' imitations paralleled both the avian and human vocal development literature. Yet this past study did not directly test whether specific contingencies were necessary for vocal imitation by dolphins. The purpose of this study was to investigate the effects of contextual saliency on vocal imitation and acquisition in bottlenose dolphins. Over a six-month study period, we experimentally exposed two infant male bottlenose dolphins and their mothers to six novel computer-generated whistles that were either unpaired or paired with specific contextual events (preferred toy objects). The results demonstrate that acoustic exposure alone was sufficient for spontaneous vocal imitation to occur but that context affects the timing, extent and quality of vocal imitation by bottlenose dolphins.

Although some evidence exists for vocal learning in nonhuman primates (see Egnor & Hauser, 2004), bottlenose dolphins (*Tursiops truncatus*) and other species, cetaceans are the only mammals other than humans that clearly demonstrate this ability (Caldwell et al., 1990; Deecke et al., 2000; McCowan & Reiss, 1995a; Reiss & McCowan, 1993; Richards et al., 1984; Tyack, 1983, 1986). Dolphins have demonstrated analogous stages in the acquisition of their respective vocal repertoires (McCowan & Reiss, 1995a; McCowan et al., 1999; Reiss & McCowan 1993) to those previously reported for humans and songbirds (see Hauser & Marler, 1992). These similarities include the importance of imitation, auditory input and feedback, and social and environmental influences, as well as

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stages of developmental overproduction, vocal play or babbling, and attrition (see Elowson et al., 1998; Kroodsma, 1982; Locke, 1993; McCowan & Reiss, 1995a; Pepperberg & Neapolitan, 1988; Snowdon & Hausberger, 1997). Dolphins exhibit a proclivity for vocal imitation of both conspecific whistles and nonspecies-specific sounds (Caldwell et al., 1990; Caldwell & Caldwell, 1972; Reiss & McCowan, 1993; Richards et al., 1984; Sigurdson, 1989; Tyack, 1986;). Like birds, dolphins may have a predisposition to imitate a variety of sounds that flourishes in contexts paired with social and other environmental contingencies. Few researchers would dispute that social and environmental factors influence vocal development in dolphins, but it remains unclear what the critical factors are and how they may work in combination.

There have been several efforts to examine the process of imitation and vocal learning in the dolphin. Several researchers have investigated vocal imitation through experimental studies with captive dolphins (Caldwell & Caldwell, 1972; Reiss & McCowan, 1993; Richards et al., 1984; Sigurson, 1989). In two studies, operant conditioning procedures were employed to train dolphins to vocally mimic computer-generated signals (Richards et al., 1984; Sigurson, 1989). In these studies, the experimenters used extrinsic food rewards to initially shape the specific acoustic parameters for the subjects to mimic, such as duration and frequency modulation.

In another study, the process of vocal mimicry was investigated by exposing young dolphins to an underwater keyboard that allowed the dolphins to control their exposure to acoustic stimuli, which were synthesized computer whistles that were paired with specific toy objects or an activity (Reiss & McCowan, 1993). Spontaneous vocal imitation of computer-generated whistles by the young male dolphins was reported. The methods used in this study provided the opportunity to observe the process of vocal imitation without explicitly training the dolphins to imitate. The young dolphins spontaneously produced imitations both immediately following model sounds and during appropriate object play. A high level of behavioral concordance was found between whistle production and context. Furthermore, throughout the two-year study period, the dolphins' renditions of the model sounds were frequently compressed or expanded with respect to frequency and time while conserving the overall whistle contour. Therefore, this study provided evidence that (1) young dolphins spontaneously acquired whistles through imitation and (2) the context of acoustic exposure was important for the imitation, acquisition and use of computer-generated whistles by young dolphins. However, this first study did not specifically test whether particular contextual information was *necessary* for imitation and acquisition. Thus the degree to which the dolphin's vocal system is open and the factors that influence the process of acquisition remained unknown. The effects of context on the acquisition of whistles or whistle repertoires, for example, have not been directly studied in bottlenose dolphins. Does the pairing of whistles with specific contextual events affect the process of vocal imitation and acquisition in dolphins? Do dolphins improve the quality of imitations across time as a result of exposure to contextually salient model sounds?

The purpose of this study was to investigate the effects of context on vocal imitation and acquisition in the bottlenose dolphin. We experimentally exposed two infant male and two adult female bottlenose dolphins to six computer-generated whistles that were either unpaired or paired with specific contextual events (preferred toy objects) to determine the importance of contextual salience on the process of vocal learning in bottlenose dolphins.

Method

Subjects

Subjects were two captive-born infant (less than one year of age) male bottlenose dolphins and their mothers (over 10 years of age) at Six Flags Marine World (formerly Marine World Africa USA) in Vallejo, California, U.S.A. Subjects were housed in an oval pool (18 x 12 x 5 m) with a large underwater viewing window. Observers did not feed or interact with the dolphins immediately prior to, during, or immediately after an experimental session. The dolphins did not have any previous training by humans in the production or imitation of artificial or conspecific acoustic signals.

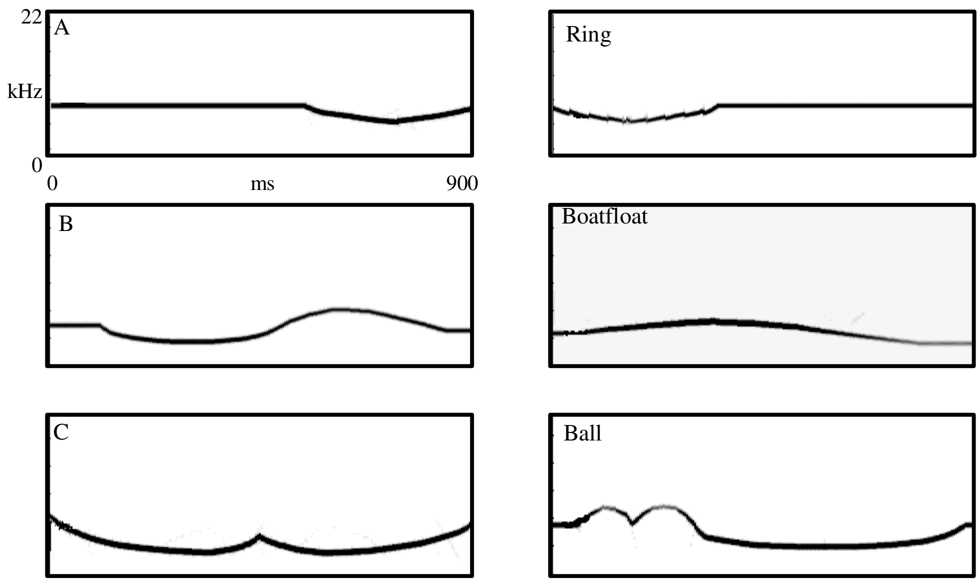

Figure 1. Spectrograms of the computer-generated whistles used in the present study (Unpaired: A, B, C; Paired: ring, boatfloat, ball).

Acoustic Stimuli

Six computer-generated whistles were designed using Cool Edit Pro Software for the PC at a sampling rate of 44 kHz. All whistles were designed to be novel and distinctive in frequency contour from each other and from the whistles extant in our subjects' vocal repertoires (McCowan & Reiss, 1995a, 1995b). Novel computer-generated whistle contours were designed to enable us to determine true imitations (including partial imitations, complete imitations, or novel combinations) of the whistles by the dolphins; all contained short tones as components not present in wild dolphin whistle repertoires but which captive dolphins have been known to incorporate into their repertoires through vocal learning (Miksis et al., 2002). The computer whistles were acoustically tapered to remove computer artifacts (start and stop clicks). Figure 1 presents spectrograms of the computer-generated whistle contours presented to the dolphins. Three computer whistles were unpaired (A, B, C) and three whistles were paired with preferred toy objects (ring, boatfloat, ball). Toys were determined to be “preferred” by long-term observations of toy use by our research group and the husbandry staff.

Acoustic Exposure

Subjects were exposed to the set of six computer whistles using a longitudinal study design across a 6-month period. A whistle was broadcast from a computer using Signalyze 3.12 Bioacoustic software into the pool through a USGS underwater transducer (output to 25 kHz) once every 2 min over a 50-min session. A toy presenter, wearing dark sunglasses and located approximately 2 m from poolside, immediately tossed the appropriate toy into the pool when a paired whistle was played and stood motionless when an unpaired whistle was played. With the exception of tossing the toy into the pool when appropriate, the toy presenter did not visually or physically interact with the dolphins in an effort not to interfere with their behavior. There were no toys or other objects in the pool prior to the session. Toys were presented sequentially and not removed prior to the end of each experimental session. Each whistle was played four times during each 50-minute session and the order in which the computer whistles were played was randomized. Three to four sessions were conducted each week between 06:00 and 19:00 h over a 6-month period for a total of 90 sessions.

Data Collection

Behavioral and acoustic data were collected from an underwater viewing window using a combination of one-zero, event, and continuous sampling techniques. A focal zone sampling technique, a modification of focal animal sampling (Altmann, 1974), was used to collect data on the identification and context of dolphin vocal production. For each session, two narrators observed overlapping areas of the pool to identify vocalizers, where possible (using bubblestream production), and noted the behavioral contexts of whistles (continuous sampling of vocal behavior; event sampling of context and vocalizer identity). Orientation by the dolphins to the underwater speaker, toy presenter and toy presentation was also recorded by one of the two narrators (event sampling). Behavioral contexts include a mutually exclusive list of activities by the dolphins: swimming, resting, approaching or interacting with other dolphins, and orienting to, approaching or interacting with any objects. All behavioral observations made by the narrators were recorded onto one track of audio channel; the second track simultaneously recorded the hydrophone input including the playback of computer-generated whistles and any vocalizations, including imitations, produced by the dolphins (continuous sampling). Recordings were made using a Radioshack SSM-100 stereo sound mixer and a Funai Hi-fi VHS recorder (flat frequency responses to 22 kHz). A third observer conducted one-zero sampling at 15-s intervals using a standard checksheet on toy play to quantify the amount of specific toy play by each individual in the pool. Toy play is defined as contact or interaction with an object in the pool.

Data Analysis

Imitations. All experimental recordings were analyzed for imitation events. All imitations were digitized at 44 kHz and 512-point FFT spectrograms were generated using a Hamming filter in Signalyze 3.12 Bioacoustic software. Although we did observe positive identification of the infants producing imitations in several cases, the number of these was too low to allow for any investigation of individual differences in imitations. Therefore, the four dolphins were treated as a single unit in all analyses.

Mimicry vs. Production. Mimicry was defined as imitation that occurred within 15 s of exposure to the computer-generated whistles (immediate imitation) and production was defined as imitation occurring outside of this exposure window (delayed imitation). This 15 s cutoff between mimicry and production is arbitrary but was chosen to allow for comparison with previous work (e.g., Reiss & McCowan, 1993).

Quality Rating. Partial and complete imitations were determined by auditory and visual inspection of spectrograms by two scorers and were rated on a 5-point scale ranging from poor to excellent, as defined by Reiss and McCowan (1993). Scorer ratings were validated by conducting an interscorer reliability test on a total of 106 randomly-chosen imitations of “poor” or “fair” (low quality) and “good”, “very good” or “excellent” (high quality) spectrograms . Interscorer reliabilities were 87% for visual ratings and 90% for auditory ratings. Scorers did not significantly differ at the 0.05 level in either visual or auditory ratings using the McNemar test (p = 0.59, p = 0.07 respectively). Imitation quality was also externally validated by quantitatively measuring a subset of complete imitations with high signal-to-noise ratio and correlating these measurements to quantitative measurements extracted from the computer whistle models. Measurements were conducted using a modified version of the Contour Similarity Technique (McCowan, 1995; 60 frequency points instead of 20 points were extracted from each signal) with Cool Edit Pro Acoustic software for the PC computer. A mean and standard deviation of the correlation coefficients were calculated between the whistle model and each imitation for both high- and low-quality imitations. The means and their standard deviations were then compared to the scorers' ratings using correlational analysis. This comparison indicated that visual/auditory inspection corresponded well with quantitative comparison (high quality $R^2 = 0.82 \pm 0.16$, N = 25; low quality $R^2 = 0.39 \pm 0.16$, N = 25). Thus, quality as measured by visual and auditory inspection was used in all subsequent analyses to facilitate direct comparisons with the data analyzed in Reiss and McCowan (1993).

Only complete high-quality imitations were used for most analyses except as follows. All imitations were included for the analysis of early imitations. All complete imitations (high and low quality) were included in the data set for the analysis of imitation quality. Mixed effects logistic regression in EGRET Statistical Software was used for statistical tests on the binary outcome of imitation quality ("high" vs. "low") in relationship to contextual pairing and as a function of time in study. The random effect was designated as signal type (e.g., S1, M1, C1, ball ring, boatfloat) in order to account for this repeated measure (Agresti, 1990; Searle et al., 1992).

Behavioral Context of Imitations. Behavioral context was scored for each high-quality imitation produced by the dolphins for which contextual information was available. Due to the curvature of the tank, there were some areas that were hidden from the observer's view. If a high-quality imitation was recorded while the animals were out of sight, there would be no context for that imitation. Appropriate contexts were defined by those contexts in which one of the dolphins approached, physically interacted with, or closely oriented to (< 0.6 m) the appropriate object (i.e., the toy corresponding to the imitation produced). For example, the vocalizer produced an imitation of the signal paired with the ball and then interacted with the ball. This definition differs slightly from that used in Reiss and McCowan (1993). Because we observed the subjects through an underwater window in the present study, we were able to more clearly determine when the dolphins were approaching or orienting to specific toy objects underwater. In the study conducted by Reiss and McCowan (1993), such close examination of underwater behavior and orientation was not possible because observations were conducted from an observation tower and thus only surface or near surface behavior was readily observable. Inappropriate contexts were defined as contexts in which a dolphin approached, physically interacted with, or closely oriented to an inappropriate object (i.e., a toy not corresponding to the imitation produced). For example, the vocalizer produced an imitation of the signal paired with the ball and then interacted with the ring or produced an imitation of an unpaired signal and then interacted with any toy. Other contexts were defined as contexts in which no toy play or orientation occurred (e.g., general swimming, resting).

Toy Play. The data generated from the one-zero sampling of toy play by the dolphins were collapsed by subject (no differences were found in toy play between the subjects with the exception that infants played more frequently with toys than adults did) to reveal general trends in toy preference. The mean and standard deviation (SD) of the percentage of 15-s intervals in which toy play occurred across sessions were calculated for each toy object.

Results

Early Imitations

Figure 2 presents a composite graph of spectrograms demonstrating the initial patterns of imitation by the dolphins for one of the paired model sounds, boatfloat. As indicated in this figure, the dolphins initially partitioned the signals into smaller units (B: #2, #3). They also compressed and expanded their renditions of these signals with respect to both frequency and time (B: #1; C). This initial pattern of imitation was very similar to that found in our first study (Reiss &

McCowan, 1993), and is also similar to that seen in children during early stages of language acquisition (Bloom, 1970; Bloom et al., 1974; Kuczaj, 1982, 1987). The other signals exhibited similar patterns.

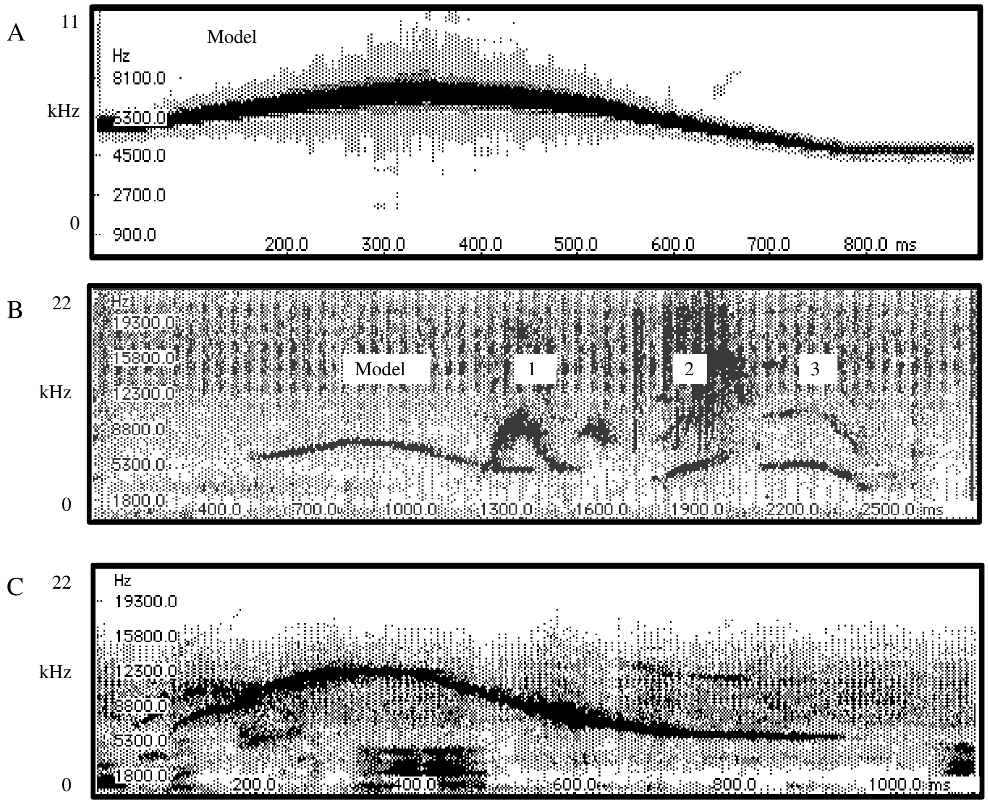

Figure 2. Spectrograms of the boatfloat whistle model and boatfloat imitations by the dolphins. (A) Close-up view of the computer-generated whistle model as generated by the computer; (B) Computer-generated whistle model recorded in the pool during a session, a complete imitation expanded in frequency and compressed in time (#1), and a partitioned imitation (#2, #3); and (C) a complete high-quality imitation expanded in frequency. Note that (A) has a y-axis that spans from 0-11 kHz and both (B) and (C) have y-axes that spans from 0-22 kHz to enhance the viewing of contour structure.

In addition, the number of exposures prior to the first imitation was similar to that reported by Reiss and McCowan (1993). The number of exposures prior to first imitation for the six signals ranged from 5 to 61 (Table 1). The average number of exposures prior to first imitation was lower for the paired than for the unpaired signals (see below and Table 1), showing that contextual pairing may have influenced the time at which first imitation occurred.

Temporal Patterns of Imitation

Types of Imitations. The amount of vocal imitation by the dolphins markedly changed as a function of time. Mimicry comprised only a small proportion (Figure 3: mimicry: 24%; production: 76%) of total high-quality imitations (N = 213) across the entire study period. The amount of imitation showed a nonlinear pattern with a maximum number of imitations occurring during the third through fifth months of the study for both mimicry and production. No differences in this pattern among the contextual pairing categories were found. Notably, mimicry was all but absent in the first two months of the study and production was substantially higher than mimicry throughout the study period. This pattern is in sharp contrast to that found in Reiss and McCowan (1993); in that study, mimicry accounted for a large proportion of imitations during the first year of the study when the infants were approximately one year of age. In fact, the pattern observed for the dolphins in this study more closely matched the pattern found during the second year in Reiss and McCowan (1993), when the young males were four to five years of age.

Table 1

Number and Averages of Exposures Prior to First Recorded Imitations and High-quality Imitations by Contextual and Signal Type.

Type		Prior exposures	Imitations
Paired		(13)	(51)
	Ring	15	36
	Boatfloat	5	67
	Ball	18	50
Unpaired		(33)	(20)
	A	17	7
	B	21	32
	C	61	21

Note: Numbers in parentheses represent the average across signal type for each contextual type; all other numbers represent the frequency of occurrence for each signal type.

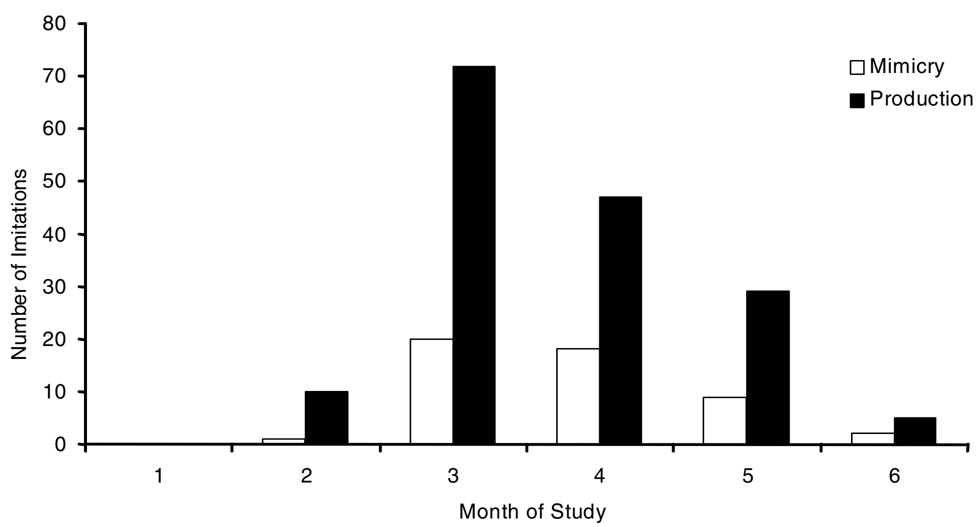

Figure 3. Amount of vocal mimicry and production of computer-generated whistles by the dolphins over the six-month study period.

Quality of Imitations. Reiss and McCowan (1993) anecdotally reported that the quality of imitations improved from the first to the second year of study for two juvenile male bottlenose dolphins. However, this observation was not directly tested because no data were analyzed on the improvement of imitations within each of the two study periods. In this study, we directly tested for changes in imitation quality as a function of time in study. Although overall improvement in imitation quality increased from the first to the last month of the study, the pattern of imitation quality across months had a nonlinear pattern (month: $\beta = 5.06$, $p < 0.001$; month^2: $\beta = -0.63$, $p < 0.001$; Figure 4). The peak of imitation quality occurred during months 3-5, the same months in which the highest numbers of imitations were found (also see below).

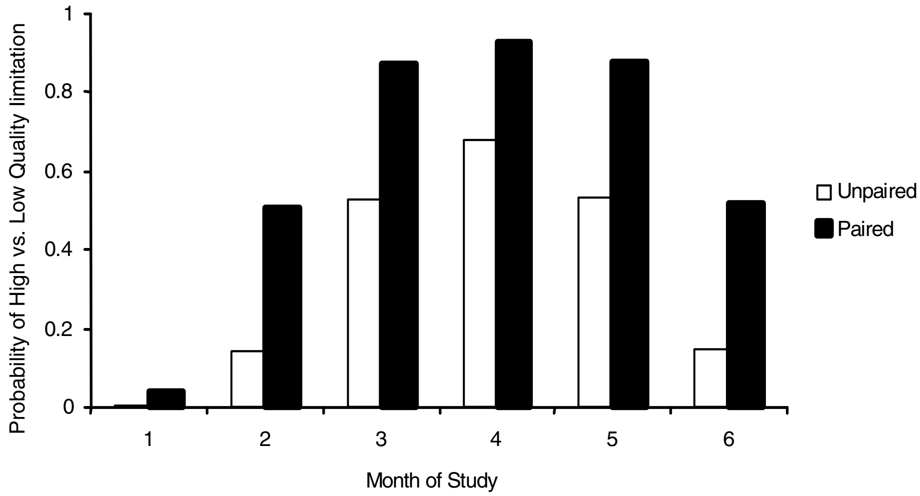

Figure 4. Probabilities generated from the logistic regression model that dolphin imitations were of high vs. low quality in relationship to contextual pairing across the six-month study period.

Effects of Contextual Pairing on Imitation

Number of Exposures and Imitations. Table 1 presents the number of exposures prior to first imitation, the number of high quality imitations for each computer signal and their averages for each contextual type. For almost all comparisons, the number of exposures required before imitation was fewer and the number of imitations was greater for the signals that were paired with toy objects than those that were unpaired.

Quality of Imitations. Both unpaired and paired signals showed the same temporal pattern of imitation quality over the course of the study (see *Temporal Patterns of Imitations* above). However, imitations of paired signals were significantly more likely to be of high quality than imitations of unpaired signals (Figure 4, paired vs. unpaired ($N = 240$): $\beta = 1.82$; $p < 0.001$, Odds ratio = 6.17).

Behavioral Concordance. Imitations of the paired signals were evaluated for behavioral context and concordance. In contrast to Reiss and McCowan (1993), behavioral concordance between *productions* of computer-generated whistles and appropriate object play was poor to marginal, ranging from 45-58% (Table 2). Behavioral concordance for mimicry was not evaluated as dolphins were likely to orient to the paired objects when they were presented with the signal and thus concordance would be artificially high. However, the dolphins produced *imitations* (both mimicry and production) in appropriate contexts more often than in either inappropriate or other contexts for each signal type. In fact, inappropriate contexts accounted for little of the variation observed (Table 2). In addition, because productions of computer signals could have incidentally coincided with toy play if dolphins were continuously interacting with a particular toy, we also evaluated these data in relationship to the percentage of toy play for each object across sessions. Analysis of toy play across sessions revealed that while the dolphins preferred to interact with the ball toy object over all other objects presented to them, they only did so in an average of 17% of the intervals across sessions (Table 2).

Table 2
Behavioral Concordance of Productions of Computer-generated Whistles Paired with Toy Objects and the Average Percentage of 15-s Intervals in which Toy Play for each Toy Object Occurred Across Sessions.

Signal type	Appropriate	Inappropriate	Other	Average (SD) % of 15-s intervals in which toy play occurred
Ring	17 (55)	4 (13)	10 (32)	6 (14)
Boatfloat	23 (45)	10 (20)	18 (35)	7 (15)
Ball	22 (58)	5 (13)	11 (29)	17 (25)

Note: Values in parentheses represent percentages. Values outside of parentheses represent the frequency of occurrence.

Discussion

The results from this experimental study of vocal imitation in dolphins corresponded well with those originally reported in Reiss and McCowan (1993). The dolphins spontaneously imitated the computer-generated whistles without explicit training and showed similar patterns of initial mimicry and production. Imitations were initially fragmentary or partial components of the exemplars, sometimes matched in frequency and time, and frequently expanded and compressed with respect to both frequency and time. Acoustic exposure alone was sufficient for imitation to occur by the dolphins, but contextual pairing clearly influenced both the extent and quality of imitations of the model sounds.

Significance of Results

Two independent studies by our research group suggest that dolphins acquire new signals into their repertoires by producing partial imitations of the signals and frequently breaking up the signals into components during early stages of acquisition. These dolphins also produced expansions and compressions of the computer signals as well as exact matches in both frequency and time. The data from both studies further suggest that relative whistle contour, not absolute whistle contour, is the most salient feature in dolphin whistle communication. Dolphins in both studies transposed the contours in the frequency domain, and expanded and compressed the signals in both time and frequency parameters. The present study also found that the quality or integrity of vocal imitations, based upon contour structure, increased with additional exposure to the signals, similar to the anecdotal results reported by Reiss and McCowan (1993). The present and previous results on dolphin whistle communication (McCowan et al., 1999; McCowan & Reiss, 1995a, 1995b; Reiss & McCowan, 1993) show striking parallels to those found in studies of birds and humans. Finding such close parallels in three phylogenetically distinct groups of vocal learners suggest evolutionary convergence in the process of vocal learning.

Importance of Context on Vocal Imitation

A critical issue in understanding vocal development and learning is the importance and efficacy of environmental input within a social context. The importance of these factors has been well demonstrated in studies of human language development (Goldstein et al., 2003; Locke, 1993; Locke & Pearson, 1992), and in studies investigating the acquisition of natural calls (Adret, 1993a, 1993b; Baptista & Petrinovich, 1986; Bell et al., 1998; Deecke et al., 2000; Smith et al., 2000; Todt et al., 1970) and of artificial codes in nonhuman animals (chimpanzees: Savage-Rumbaugh, 1986; Savage-Rumbaugh & Rumbaugh, 1978; birds: Pepperberg et al., 2000; Pepperberg & Neapolitan, 1988).

Environmental input also appears important for whistle acquisition in dolphins. In our first experimental study (Reiss & McCowan, 1993), the results indicated that the number of acoustic exposures required to elicit the imitation of model sounds was substantially lower than that reported in other studies, in which dolphin were trained to imitate model sounds on command (Richards et al., 1984; Sigurdson, 1989). The methods employed in Reiss and McCowan (1993) incorporated both social interaction and contextual saliency, which may have promoted imitation. Another potentially important factor was that Reiss and McCowan's (1993) study the dolphins had both control and choice in obtaining the acoustic stimuli and corresponding contingencies (e.g., objects or an activity). In the present study, we specifically tested whether contextual information was necessary for imitation and acquisition. Acoustic exposure alone was sufficient for imitation to occur. The dolphins imitated computer whistles that were both unpaired and paired with toy objects. However, whistles that were paired with objects were imitated after fewer exposures and produced more frequently than those that were unpaired. Furthermore, paired signals were produced with higher quality by the dolphins earlier in the vocal imitation process than signals that were unpaired. These data suggest that acoustic signals that are paired with specific events are more salient or significant to the dolphins than unpaired signals and that contextual salience promotes vocal imitation and acquisition, as in humans and birds.

Relative Levels of Mimicry and Production

The different methods used in Reiss and McCowan (1993) and the present study could account for differences found in the relative amounts of mimicry vs. production of computer-generated whistles in these two studies. In Reiss and McCowan (1993), the dolphins had both direct control over exposure to acoustic models and choice in obtaining specific acoustic stimuli and the corresponding contingencies. In the present study, the dolphins had no control or choice over exposure or contingencies; the computer whistles were broadcast once every 2 min. This difference in experimental design could account for the higher rate of mimicry during the first year of our original study (Reiss & McCowan, 1993). In some avian species, for example, stimulus control over exposure to recorded song can influence the vocal imitation process (see Baptista & Gaunt, 1997).

Behavioral Concordance

We previously found concordance between dolphin productions of computer signals and appropriate behavioral activities (Reiss & McCowan, 1993). In the present study, concordance was marginal, never exceeding 58% (see Table 2). The discrepancies in results could be due to a number of factors. First our category termed appropriate may have been limited in revealing true behavioral concordance. Referential signals by their very nature do not necessarily occur simultaneously with the activity to which they refer. Therefore our other category may contain additional data on appropriate contextual use by the dolphins, missed by our highly conservative definition of appropriate context. In addition, in our first study subjects were given control over the experiment and a well-defined linear set of contingencies (e.g., visual form→computer signal→toy object) which we suggested might have promoted the spontaneous development of associations between the toy objects and computer signals by the dolphins (Reiss & McCowan, 1993)

In conclusion, this study supports the results of previous studies on vocal imitation and learning, and confirms that dolphins exhibit an organized process of vocal imitation and acquisition similar to that observed in humans and birds. This study has also presented new evidence demonstrating that dolphins imitate new signals to which they are acoustically exposed but that they acquire and retain such signals earlier and with better integrity if the signals are paired with contextual events. Data on the behavioral concordance of acquired signal use were equivocal. Systematic playback experiments will be required to resolve alternative hypotheses on the possibly referential nature of dolphin whistles. In addition, imitation studies should be conducted with adult subjects, housed separately from infants, to determine if vocal learning shows a critical or sensitive period as found for many species of birds and humans.

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