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Blindfolded Imitation in a Bottlenose Dolphin
(*Tursiops truncatus*)

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This study investigated the ability of a bottlenose dolphin to adapt a previously learned "do-as-I-do" procedure to copy behaviors of another dolphin while blindfolded (i.e., wearing eyecups). In Experiment 1, the dolphin was able to copy both vocal and motor behaviors, whether blindfolded or sighted. Hydrophone recordings showed that he echolocated during many of the motor behaviors while blindfolded. In Experiment 2, blindfolded human trainers were able to identify the same model behaviors on the basis of their characteristic sounds. While it thus remains unclear whether the dolphin recognized the motor behaviors via echolocation or via their characteristic sounds, this is the first demonstration of such flexibility in using a new perceptual route to motor imitation in a nonhuman animal.

At first glance, evidence that nonhuman animals copy each other's behaviors seems widespread throughout the animal kingdom. Many social animals perform vocal or behavioral displays synchronously (e.g., Backwell, Jennions, Passmore, & Christy, 1998; Connor, Smolker, & Bejder, 2006; Greenfield, 1994), behavioral traditions are found in some populations but not others in a number of animal species (e.g., Fragaszy & Perry, 2003; Galef, 1996; Krützen et al., 2005; Laland & Hoppitt, 2003; Rendell & Whitehead, 2001; Tomasello & Call, 1997; van Schaik et al., 2003; Whiten et al., 1999), and scientists have documented the spread of novel behaviors from one animal to the next throughout specific populations (e.g., Bonnie, Horner, Whiten, & de Waal, 2007; Fisher & Hinde, 1949; Nishida, 1987; Whiten et al., 2007).

Although it may be tempting to explain such shared behaviors in terms of imitation, more than a century of research into the mechanisms underlying such phenomena has given rise to a much more complicated picture. Importantly, behavioral mechanisms have been identified—such as social facilitation, stimulus enhancement, observational conditioning, and individuals responding to the same stimulus—that can result in one animal performing the same behavior as another, without any form of direct copying (for reviews see Galef, 1988; Whiten & Ham, 1992; Zentall, 2006). Moreover, even if one limits discussion to those instances in which one animal does copy something directly from another, there are further distinctions to be made on the basis of (a) whether the behavior in question is novel or already within the animal's behavioral repertoire (e.g., Byrne & Russon, 1998; Byrne & Tomasello, 1995; Subiaul, 2007; Visalberghi & Fragaszy, 1990); (b) whether the copying animal understands the goal or intention behind the

model's behavior (e.g., Call & Carpenter, 2002; Tomasello, Kruger, & Ratner, 1993); and (c) whether the unit of replication is the animal's behavior, the movement of the object that the animal is interacting with, or the effect that the behavior produces (e.g., Custance, Whiten, & Fredman, 1999; Tomasello, 1990; Whiten, Horner, Litchfield, & Marshall-Pescini, 2004).

The one thing all comparative psychologists seem to agree on, however, is that, whatever imitation is, humans do it best. From a very young age, humans routinely copy a wide variety of vocal and motor behaviors with extreme flexibility, including old and new behaviors, both immediately and delayed, with the ability to transfer across situational contexts (see Meltzoff, 1988, 1996 for reviews). Indeed, imitation is so fundamental to the human psyche that it is thought to provide the evolutionary and ontogenetic roots for the development of human culture, language, and theory of mind (e.g., Meltzoff, 1996; Tomasello, 1999; Tomasello, Kruger, & Ratner, 1993).

Because of imitation's purported role in human cognitive evolution, it is not surprising that the vast majority of comparative imitation literature has focused on primates. However, our understanding of the evolution of this ability can only be strengthened by broadening the scope of comparative studies. In fact, there is reason to believe that the nonhuman animal with the most developed imitative ability may not be a primate at all, but a dolphin. Anecdotal reports, field research, and experimental studies all suggest that bottlenose dolphins frequently engage in both vocal and behavioral imitation. They have been shown to copy each other's whistles (e.g., Janik, 2000; Janik & Slater, 1998; Tyack, 1986), computer-generated sounds (Caldwell & Caldwell, 1972; Reiss & McCowan, 1993; Richards, Wolz, & Herman, 1984), and both familiar and novel motor behaviors, whether spontaneously or on command (Bauer & Johnson, 1994; Herman, 2002; Kuczaj, Makecha, Trone, Paulos, & Ramos, 2006; Tayler & Saayman, 1973; Xitco, 1988).

As compelling as these results are, however, it should be noted that the study of dolphin imitation is still in its infancy. To date, there have been only a handful of peer-reviewed empirical reports on dolphin imitation, only two of which have focused on motor imitation (Bauer & Johnson, 1994; Tayler & Saayman, 1973). Clearly, much remains to be explored about dolphin imitation, including its range, flexibility, and possible role in learning cognitive and behavioral skills.

Over the past few decades, the preferred method for examining imitation in animals has been the *two-action procedure*, first introduced by Dawson and Foss (1965). In this experimental protocol, the target animal watches a demonstrator accomplish a task using one of two (or more) possible methods, before it is given the opportunity to perform the same task. If the observer accomplishes the task using the demonstrated action rather than the alternative action(s), this is taken as evidence of behavioral copying. Note that because the target action (e.g., pecking, pushing) is typically not novel to the animal's repertoire, this procedure does not provide evidence of learning a new motor behavior (i.e., what Byrne, 2002, termed "production imitation"), but rather of learning to produce a specific motor behavior in a particular context (i.e.,

"contextual imitation": Byrne, 2002; Hoppitt & Laland, 2008).

Another procedure for studying imitation that has been gaining popularity in recent years is the *do-as-I do* task, first introduced by Hayes and Hayes (1952). In this task, the animal watches a particular behavior demonstrated by a human or trained conspecific, and is then explicitly asked to perform the same behavior, using a previously established training signal or communicative symbol. As with the two-action procedure, if the animal performs the demonstrated action rather than some alternative action, this is taken as evidence of contextual imitation (and perhaps also production imitation, depending on the novelty of the motor behavior). However, unlike the two-action procedure, the do-as-I-do task (a) utilizes far more than two or three possible relevant behaviors, (b) typically does not focus on solving a problem or accomplishing a task other than reproducing the sequence of movements, and (c) arguably requires the animal to understand the *concept* of imitation (e.g., Herman, 2002, 2006; Whiten, 2000; Whiten et al., 2004; but see Hoppitt & Laland, 2008 for an alternative view). To date, this procedure has been used to study the imitative abilities of chimpanzees (Custance, Whiten, & Bard, 1995; Myowa-Yamakoshi & Matsuzawa, 1999; Tomasello, Savage-Rumbaugh, & Kruger, 1993), bonobos (Tomasello, Savage-Rumbaugh, et al., 1993), an orangutan (Call, 2001; Call & Tomasello, 1995; Miles, Mitchell, & Harper, 1996), dolphins (Bauer & Johnson, 1994; Xitco, 1988), and dogs (Topál, Byrne, Miklósi, & Csányi, 2006).

The goal of the current study was to explore the flexibility of dolphin imitation in a do-as-I-do task, by asking a dolphin to reproduce vocal and motor behaviors presented to him in a novel way. This dolphin had previously been trained to copy the behaviors of both humans and other dolphins. However, in this study we asked him to imitate the behaviors of another dolphin while wearing eyecups that completely occluded his vision. The question was whether he could flexibly adapt to the new requirements of the task and use sound—whether the characteristic sound of the behavior, or echolocation—to recognize the target behaviors with enough fidelity to accurately reproduce them. For comparison purposes, we also asked him to imitate behaviors while sighted.

Note that the behaviors tested were already within the dolphin's behavioral repertoire. We did not attempt to assess whether he was capable of acquiring novel actions (i.e., production imitation) while blindfolded, but rather specifically focused on the flexibility of his contextual imitation.

Experiment 1

Method

Subjects and testing environment

The subject was a male Atlantic bottlenose dolphin (*Tursiops truncatus*) named Tanner, who was born at Dolphin Research Center in Grassy Key, Florida, and was 7 years old at the time of testing. Tanner was selected because he already knew the prerequisite behaviors of: (1) copying the behavior of another dolphin and (2) wearing eyecups. He resided with two other male dolphins that provided the models for the behaviors: AJ, age 21, and Kibby, age 30. Tanner and AJ had previously

participated in a study of object permanence (Jaakkola, Guarino, Rodriguez, Erb, & Trone, 2010). Kibby was experimentally naïve.

The three dolphins lived in a natural seawater lagoon measuring 36.6 x 13.7 x 3.7 m deep, situated on the Gulf of Mexico. They were fed according to their normal daily routine, which typically included capelin, herring, and smelt, three times per day, approximately 33% of which they received during experimental sessions. During non-experimental sessions, they continued to participate in other training sessions, including public programs and in-water interactions with trainers and guests.

Testing set-up and materials

Two trainers sat side-by-side on the testing dock, approximately 1.5 m apart, with Tanner and one of the model dolphins stationed in front of them. Only one model dolphin was present at the testing dock during any given trial; the other model dolphin was engaged in an unrelated task at another dock with a different trainer. During blindfolded trials, Tanner wore two soft, removable, white latex eyecups (7.5 cm in diameter) that completely occluded his vision.

To record echolocation, we used an Aquarian Audio Products H2a hydrophone plugged into a SONY Handycam Vision CCD-TRV65 Hi-8 camcorder, located on a tripod behind the trainers. All sessions were also videotaped using a SONY DCR-HC38 MiniDV camcorder, located across the lagoon from the testing dock.

Behaviors

In selecting behaviors to test, we avoided high-energy acrobatics or any behavior that would entail leaving the water (e.g., dives, flips), due to safety concerns for the dolphin working without vision. Table 1 shows the final list of 31 behaviors, along with their definitions.

Procedure

Imitations were tested under two viewing conditions: *blindfolded*, in which Tanner wore two eyecups, and *sighted*, in which he wore none. Throughout each blindfolded session, Tanner wore an eyecup on the eye facing away from the model dolphin. At the start of each trial, Tanner's trainer gave the hand signal for "imitate" in view of his uncovered eye, then placed the remaining eyecup on his second eye. The second trainer then gave a hand signal to the model dolphin, specifying the target behavior to be performed. To start trials in sighted sessions, Tanner's trainer held the eyecups against Tanner's eyes while the second trainer gave the behavior signal to the model dolphin. Then Tanner's trainer removed his eyecups and gave the signal for "imitate."

Once the model dolphin received the relevant hand signal, it performed a behavior (which was usually, but not always, the requested behavior). If Tanner performed the same behavior as the model, his trainer blew a whistle and Tanner returned to the testing dock, where his trainer removed one eyecup (in blindfolded trials) and provided him with positive reinforcements of fish and social interaction. If Tanner performed a behavior that did not match that of the model dolphin, his trainer would shake her hand in the water to call him back to the dock, where she would remove one eyecup (in blindfolded trials) and then remain neutral. The model dolphin was always rewarded if it performed the requested behavior, regardless of Tanner's response.

Occasionally, Tanner would begin his response with one behavior and then switch to another. If he performed the target behavior at any point, the trainer blew the whistle and treated that response as a success. For purposes of coding, however, only his first response on any given trial was counted.

Training. Training consisted of a single 12-trial imitation session in which Tanner wore one eyecup on the eye facing away from the model dolphin. In each trial, Tanner's trainer gave the imitate signal to his uncovered eye, then briefly touched a second eyecup to his uncovered eye and removed it. The second trainer gave a behavior signal to the model dolphin, who performed the requested behavior. Note that, unlike in later sighted trials, the hand signal for the model behavior was given at a time when Tanner could potentially see it.

If Tanner performed the same behavior as the model, his trainer blew a whistle and reinforced him as in testing sessions. If Tanner performed a non-matching behavior, the trainer either: (1) stationed him again and repeated the sequence of giving the imitate signal before touching and removing the second eyecup, while the model dolphin continued to perform the requested behavior (two times); or (2) gave Tanner the signal for the requested behavior, and reinforced him for performing it (once).

Table 1

List of model behaviors and their descriptions.

Behavior	Description
Alligator	Dolphin opens and closes jaws in a chomping motion. The upper and lower jaw may or may not touch.
Applause	Dolphin floats horizontally, ventral side up, and shakes flippers.
Bob	Dolphin bobs up and down vertically, with entire body disappearing underwater in downward motion, and roughly half its body emerging from water in upward motion.
Bubbles	Dolphin sinks underwater and blows bubbles.
Chorus	Oriented vertically, dolphin spins in a circle and makes the "talk" sound.
Chuff	Dolphin makes a quick, noisy exhale.
Clicks	Dolphin emits a clicking sound.
Foghorn	Dolphin emits a sound that is similar to a foghorn.
Giggle	Dolphin emits a sound like "ha ha ha".
Handshake	Oriented vertically, dolphin rises and offers its flippers to the person sitting/kneeling at the dock's edge.
Helicopter	Oriented downward or sideways with tail flukes protruding from the water, dolphin spins body and flukes in a circular pattern.
Inverted Splash	Oriented downward with tail flukes protruding from the water, dolphin slaps flukes on the surface several times.
No	Oriented vertically, dolphin shakes head back and forth.
Nothing	Dolphin remains at dock, vertically oriented, with head out of the water.
Peek	Dolphin swims underwater away from the dock, then reappears near the edge of the lagoon, vertically oriented, and remains in that position.
Present	Dolphin goes underwater and returns with object of his choice from the lagoon.
Razz	Dolphin emits a sound like a "raspberry".
Seagull	Dolphin emits a sound like a seagull's call.
Shark	Dolphin swims at the surface, dorsal up, moving tail and upper body in a side to side manner.
Speed	Dolphin swims very fast at the surface, dorsal up.
Spin	Oriented vertically, dolphin spins in a circle.
Spit/Razz	Dolphin brings upper and lower jaws together in the water, forcing water to splash out. (Our model, AJ, also adds the razz noise).
Splash	Oriented vertically, dolphin rises so that roughly half of its body is out of the water, and moves flippers to splash water.
Strut	Dolphin swims with head held high out of the water.
Tail	Dolphin orients downward with tail flukes protruding from the water.
Talk	Dolphin emits a high-pitched, squeaky sound.
Temper	Dolphin swims at the surface, dorsal up, slapping tail flukes on the surface of the water.
Tummy	Dolphin floats/swims horizontally at the surface, ventral side up.
Wave	Dolphin turns on side so that one flipper is out of the water, and waves it back and forth.
Whistle	Dolphin emits a whistling sound.
Yes	Oriented vertically, dolphin nods head up and down.

The training session ended with a single trial of the standard two-eyecup blindfolded imitation. For training purposes, the target behavior in this trial (i.e., "shark") was identical to the target behavior of the one-eyecup trial immediately preceding it. Because this blind imitation might therefore be considered cued, we did not count this trial.[1]

Testing design. Each testing session consisted of trials from a single viewing condition — that is, either all blindfolded or all sighted. The blindfolded condition was tested first, followed by the sighted condition. Each of the 31 behaviors was tested at least two times in each condition, spread over 19 sessions within an 11-week period, with 9 to 18 trials per session (with the exception of a single session consisting of only two trials).

The initial sessions of the blindfolded condition were carried out as part of an informal training game, without a hydrophone. In later sessions, a hydrophone was placed in the water, and trials were added to ensure at least two hydrophone trials for each behavior. Due to these added trials, and because the model dolphin did not always carry out the requested behavior for a given trial, individual behaviors were tested an unequal number of times. For purposes of analysis, only the first two imitation trials for each behavior are reported.[2] Similarly, for any analysis involving echolocation data, only the first two imitation trials with a hydrophone in the water are utilized.

Coding. The behaviors that Tanner performed were judged live by the trainers conducting the sessions, and later coded against the video. Possible coding categories included all of the behaviors tested, as well as a catch-all category for "other." Because the trainers knew the model behavior that had been requested and saw the model behavior that was actually performed, this initial imitation coding was not blind. However, an additional coder later independently coded 75% of the motor behaviors from the video, but with the half of the screen depicting the model dolphin covered. This second coder was therefore blind with respect to both the signal and model behavior. Note that it was not possible to code vocal behaviors blindly because there was no way to block out the model's sound without also blocking the sound of the imitating dolphin. Reliability between the two coders was 96% (Cohen's kappa = 0.94).

For sessions in which the hydrophone was present, we also coded for the presence of echolocation. For each trial, Tanner was counted as echolocating if: (1) echolocation clicks were heard during the model behavior; and (2) these clicks occurred after Tanner was released by his trainer (so that there was a possibility he was facing the model behavior). Note that even with these restrictions, this may be an overestimate of Tanner's echolocation frequency, as we have no way of ensuring that the echolocation clicks were not coming from the model dolphin. However, any differences in echolocation behavior between the blindfolded and sighted conditions are likely attributable to Tanner, as the context for the model dolphin did not differ between these conditions. A second coder independently coded 50% of hydrophone trials for echolocation. Reliability between the two coders was 97% (Cohen's kappa = 0.94).

Results and Discussion

Accuracy

The results of Tanner's imitation attempts for each behavior are listed in Table 2. For purposes of analysis, we divided the 31 behaviors into three types:

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[1]This one-trial experience did not serve to "train" later blind imitations of this behavior, as shown by the fact that Tanner failed to correctly imitate this behavior in the two subsequent trials of the blindfolded condition.

[2]The behavior "inverted splash" was tested only once in the blindfolded condition, because the model dolphins performed behaviors other than the requested one on each of seven other attempts. Tanner succeeded at imitating this behavior on the first trial. Since we could not assume he would have succeeded or failed in the second trial, we scored the proportion of correct imitations for this behavior at 0.75.

Motor behaviors were those that required some sort of overt bodily movement; *Vocal* behaviors were those that entailed creating a specific sound by manipulating air through the dolphin's blowhole and/or nasal sacs; *Combined* behaviors were those that consisted of both motor and vocal components. This resulted in 19 motor behaviors, 8 vocal behaviors, and 4 combined behaviors, which Tanner imitated with 41%, 75%, and 50% accuracy when blindfolded, and with 61%, 69%, and 50% accuracy when sighted, respectively. Because we coded Tanner's attempted imitations as falling into any of 32 possible categories (including the 31 tested behaviors + "other"), chance performance for any particular trial was therefore $1/32 = 0.031$. Overall, Tanner imitated each type of behavior (motor, vocal, and combined) significantly more often than would expected by chance, whether sighted or blindfolded (binomial test, p's < 0.001).

Table 2
Tanner's attempted imitations for each model behavior in Experiment 1.

Type	Model Behavior	Attempted Imitations	
		Blindfolded	Sighted
Motor	Alligator	Nothing(2)	C, Spin
	Applause	Razz, Wave	C, Tummy
	Bob	C(2)	C(2)
	Handshake	Wave(2)	Splash, Tummy
	Helicopter	C(2)	C(2)
	Inverted Splash	C	C(2)
	No	Spin(2)	C(2)
	Peek	C(2)	C, Strut
	Present	Other(2)[a]	Bob(2)
	Shark	Helicopter(2)	Shark(2)
	Speed	C(2)	C(2)
	Spin	C, Spin/Razz	C, Spin/Giggle
	Splash	C, Applause	C, Applause
	Strut	C, Giggle	C(2)
	Tail	C(2)	C(2)
	Temper	Shark(2)	C, Tummy
	Tummy	Tail, Other[b]	C(2)
	Wave	C, Strut	Applause(2)
	Yes	No, Splash	No, Razz
Vocal	Chuff	Razz(2)	Razz(2)
	Clicks	C(2)	C(2)
	Foghorn	Giggle(2)	Whistle(2)
	Giggle	C(2)	C, Whistle
	Razz	C(2)	C(2)
	Seagull	C(2)	C(2)
	Talk	C(2)	C(2)
	Whistle	C(2)	C(2)
Combined	Bubbles	Razz(2)	C(2)
	Chorus	C(2)	C(2)
	Nothing	C(2)	Giggle(2)
	Spit/Razz	Razz(2)	Razz(2)

Note: C = Correct. (2) = Behavior occurred on both trials.
[a]Tanner followed the model dolphin underwater, but did not return with a present. [b]Tanner swam alongside the model dolphin, but dorsal up rather than belly up.

As a more conservative estimate, we also calculated chance under the assumption that Tanner would not confuse vocal and motor behaviors. On this view, there were 20 possible categories for motor behaviors (19 tested behaviors + other), resulting in a chance level of 0.05, and 9 possible categories for vocal behaviors (8 tested behaviors + other), resulting in a chance level of 0.11. With these criteria, Tanner still correctly imitated at well above chance levels for both motor and vocal behaviors, whether sighted or blindfolded (binomial test, p's < 0.001). Note that for combined behaviors, this within-category coding assumption was not possible. Tanner could have focused on just the motor or the vocal component of the behavior, and reproduced that accurately, without receiving credit for a correct imitation. Because of this potential ambiguity with the combined behaviors, the remaining analyses of vocal and motor imitations exclude this small category of combined behaviors.

To compare Tanner's success across the blindfolded and sighted conditions, we next examined his proportion of correct imitations of each behavior, for both motor and vocal behaviors (See Figure 1). For motor behaviors, Tanner performed more correct imitations when sighted than when blindfolded, paired $t(18) = 2.08$, $p = 0.043$, two-tailed. For vocal behaviors, there was no significant difference between the sighted and blindfolded conditions, $t(7) = 1.00$, $p = 0.351$, two-tailed.
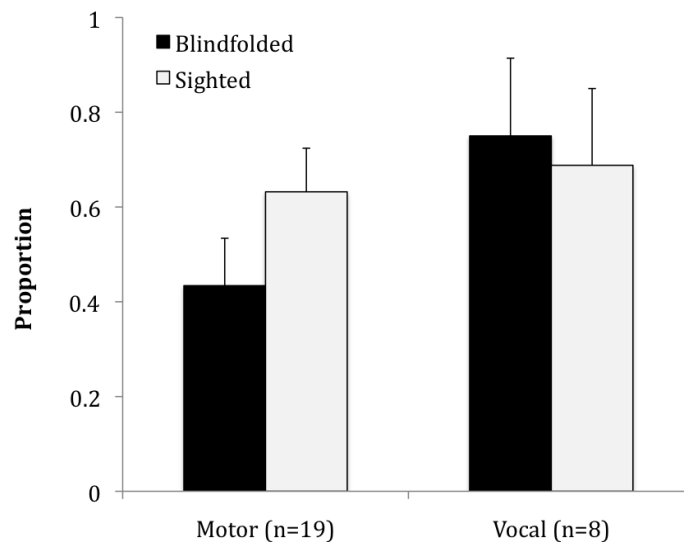

Figure 1. Mean proportion of trials of each behavior (+SE) correctly imitated in Experiment 1.

The results for vocal behaviors are unsurprising. There is no reason why blindfolding a dolphin should affect his ability to perceive and imitate sounds. However, the motor behaviors are a different story. Although, predictably, Tanner imitated more accurately when sighted, it is important to note that he also correctly imitated motor behaviors at levels far beyond chance when blindfolded. This begs the question of how he was able to accomplish this task.

Echolocation

To assess whether Tanner may have used echolocation to sense the motor behaviors of the model dolphin when blindfolded, we next analyzed his echolocation behavior. Figure 2 shows the mean proportion of trials of each behavior on which he echolocated.[3] A 2 (behavior type) x 2 (viewing condition) mixed ANOVA on these data found no main effect of viewing condition, $F(1, 24)$ $= 2.37$, $p = 0.137$. There was, however, a significant main effect of behavior type, $F(1, 24) = 8.88$, $p = 0.007$, as well as a significant interaction between viewing condition and behavior type, $F(1, 24) = 8.90$, $p = 0.006$. For motor behaviors, he echolocated significantly more when blindfolded than when sighted, paired $t(18) =$ 3.92, $p = 0.001$, two-tailed. For vocal behaviors, there was no significant difference in echolocation frequency between the blindfolded and sighted conditions, paired $t(6) = 1.55$, $p = 0.172$, two-tailed.
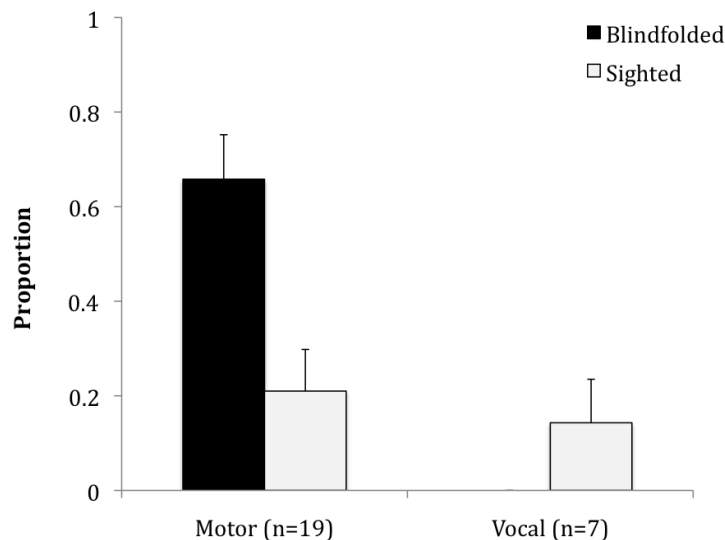

Figure 2. Mean proportion of trials of each behavior (+SE) in which Tanner echolocated in Experiment 1. Note that data from the vocal behavior *Clicks* are not included (see Footnote 3).

The previous analysis showed that Tanner echolocated primarily when copying motor behaviors while blindfolded, which is consistent with the idea that he may have used echolocation to recognize the model behaviors in this condition. However, if this were the case, we might also expect him to perform more accurately on trials in which he echolocated than on trials in which he did not. To assess this possibility, we next examined the relation between echolocation (presence, absence) and imitation accuracy (correct, incorrect) for each motor trial in the blindfolded condition. Contrary to prediction, Tanner did not echolocate significantly more on trials in which he was correct (69.6%) than on trials in which

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[3]The vocal behavior *Clicks* was excluded from this analysis, because this behavior specifically entails producing echolocation clicks.

he was incorrect (61.5%) (Fisher exact test, $p = 0.447$).

This result leaves us with a puzzle. On the one hand, Tanner echolocated more on blindfolded motor behaviors overall. However, this echolocation did not seem to make a difference to his imitation accuracy. One possible resolution to this puzzle could occur if some behaviors produce an easily identifiable sound when performed. That is, if Tanner recognized some behaviors from their characteristic sound rather than by echolocation, we might expect the hypothesized relation between echolocation and imitation accuracy to hold true for only the subset of behaviors that were not easily identifiable by sound alone.

To investigate this issue of identifying motor behaviors by sound, Experiment 2 asked the question of humans who were deeply familiar with these behaviors. Specifically, we asked blindfolded trainers to try to identify these same behaviors on the basis of their sounds.

Experiment 2

Method

Subjects

Two female senior trainers, with 6 and 30 years of dolphin training experience, participated in this study. Neither of them had been involved with Experiment 1. The same dolphins as in Experiment 1 (AJ and Kibby) performed the model behaviors.

Testing set-up and materials

Trainers were tested individually. In each session, the participating trainer sat on the same testing dock that had been used in Experiment 1, wearing a blindfold that completely occluded her vision. The experimenter stood at the front of the dock with one of the model dolphins stationed in front of her. The other dolphins in the lagoon were engaged in unrelated tasks at another dock with different trainers. As in Experiment 1, all sessions were videotaped using a camera located across the lagoon from the testing dock.

Behaviors

The behaviors were identical to those in Experiment 1, with the exception of the "nothing" behavior, which was not tested.

Procedure

At the start of each trial, the experimenter gave a hand signal to the model dolphin, who performed the requested behavior. After listening to the behavior, the blindfolded trainer called out her guess of which behavior in the dolphin's repertoire had been performed. The trainer was not told which behaviors would be tested, or how often, and received no feedback regarding the accuracy of her guesses. The model dolphin was always rewarded if it performed the requested behavior, regardless of the trainer's responses.

Testing design. Each behavior was tested at least two times for each trainer. These trials were spread over three sessions within a 3-day period for Trainer 1, and over four sessions within a 16-day period for Trainer 2. As in Experiment 1, for any cases in which individual behaviors were tested more than twice, only the first two trials for that behavior are reported.

Coding. The responses of the blindfolded trainer were recorded live by a research assistant.

For reliability purposes, a second coder later re-coded the trainer's responses from the video, but with the picture turned off so as to remain unaware of the motor behaviors that the dolphin actually performed. Note that this coding can only be considered blind for motor behaviors, as any audio that included the blindfolded trainer's responses also included the sounds of the vocal behaviors, which the coder was familiar with. On 34% of the motor trials, the trainer's response was unable to be heard on the video, due to the camera's location (across the lagoon) and other interfering noises. For the 66% of motor trials in which the trainer's response was audible on tape, reliability between the two coders was 100% (Cohen's kappa = 1.0).

Results and Discussion

Accuracy

The two blindfolded trainers performed at identical levels, each correctly identifying 55.3% of the motor behaviors, 100% of the vocal behaviors, and 66.7% of the combined behaviors. Using the same chance levels as in Experiment 1, the trainers thus identified each type of behavior (motor, vocal, and combined) significantly more often than would be expected by chance, whether chance was based on all possible behaviors, or only on within-category behaviors (binomial test, p's < 0.001).

Agreement

Because our primary interest in this study was whether motor behaviors are identifiable by sound, we next focused exclusively on motor behaviors. The performance of the two trainers was strongly correlated (Cohen, 1988) across motor behaviors, $r(19) = 0.689$, $p = 0.001$, showing that they tended to agree on the difficulty of identifying particular behaviors. The imitation performance of the blindfolded dolphin in Experiment 1 was also moderately correlated (Cohen, 1988) with the performance of each of the trainers, r's (19) = 0.377, 0.392 (p's = 0.056, 0.048, respectively). For comparison purposes, the trainers' individual guesses for the motor behaviors are presented in Table 3.

Echolocation redux

Using these data, we next returned to the issue of whether Tanner had been using echolocation to recognize the motor behaviors of the model dolphin when blindfolded in Experiment 1. Recall our hypothesis that if he was perceiving the behaviors by echolocation, we might expect him to perform better on trials in which he echolocated, but perhaps only for that subset of behaviors that were not easily identifiable by sound alone. To test this, we again examined the relation between echolocation and imitation accuracy for each motor trial in the blindfolded condition of Experiment 1, this time excluding the behaviors that the blindfolded trainers were able to identify by sound. Again, Tanner did not imitate any more accurately on trials in which he echolocated than on trials in which he did not, whether we excluded behaviors that both trainers correctly identified at least once (Fisher exact test, $p = 0.437$), or those that they both correctly identified

with 100% accuracy (Fisher exact test, $p = 0.337$).

These results suggest that Tanner was probably not identifying the motor behaviors on the basis of echolocation. Instead, it seems likely that, similar to the blindfolded trainers, Tanner identified many of the motor behaviors by their characteristic sounds and then used that behavioral identification to imitate them.

Table 3
Guesses of blindfolded trainers for each motor behavior in Experiment 2.

Model Behavior	Trainer 1	Trainer 2
Alligator	C(2)	C(2)
Applause	Strut, Wave	Peek, Tummy
Bob	C(2)	C, Tail
Handshake	Wave(2)	Strut, Yes
Helicopter	Shark(2)	C, Shark
Inverted Splash	C(2)	C, Temper
No	Spin, Splash	Applause, Yes
Peek	C, Applause	C(2)
Present	Peek, Tail	Peek, Tummy
Shark	C(2)	C(2)
Speed	C(2)	C(2)
Spin	C(2)	C(2)
Splash	C(2)	C(2)
Strut	C(2)	Shark(2)
Tail	C(2)	C(2)
Temper	C(2)	C(2)
Tummy	Tail(2)	C, Tail
Wave	Handshake, Tummy	C, Tummy
Yes	Splash(2)	Splash, Wave

Note: C = Correct. (2) = Guess occurred on both trials.

General Discussion

Previous studies have shown that dolphins are able to respond to a request to imitate by reproducing a demonstrated vocal or motor act (Bauer & Johnson, 1994; Xitco, 1988). The current study extends this result by showing that a blindfolded dolphin could immediately adapt this imitation game to use a new perceptual route to identify motor behaviors for imitation. Such flexibility in using multiple perceptual routes to motor imitation has never before been documented in a nonhuman animal.

Tanner correctly imitated 11 of 19 motor behaviors (58%) on at least one of two blindfolded trials. Due to the strict coding criteria used, this result is likely an underestimate of his imitative capacity. On trials in which he made mistakes, those mistakes tended to follow the major components of the demonstration. For example, when the model dolphin remained in place while silently opening and closing its jaws (i.e., "alligator"), Tanner also remained in place; when the model dolphin swam at the surface, slapping its tail flukes on the surface of the water (i.e., "temper"), Tanner also swam at the surface, moving his tail side to side (i.e., "shark"); and when the model dolphin dove underwater and returned with an object from the lagoon (i.e., "present"), Tanner followed the model underwater, but

returned without any object.

The question, of course, is how he was able to accomplish this feat. Because he could not have used sight to identify these motor behaviors, the obvious candidate is sound. In dolphins, this might theoretically take one of two forms. First, he may have echolocated on the model dolphin in order to perceive the form of the behavior directly. Dolphins' ability to recognize objects across the senses of echolocation and vision is well-established (Harley & DeLong, 2008; Harley, Putman, & Roitblat, 2003; Harley, Roitblat, & Nachtigall, 1996; Herman, Pack, & Hoffmann-Kuhnt, 1998; Pack & Herman, 1995; Pack, Herman, Hoffmann-Kuhnt, & Branstetter, 2002). Although their ability to recognize dynamic information across these senses has barely begun to be tested (Kuczaj, Solangi, Hoffland, & Romagnoli, 2008), it is an intriguing possibility that must be addressed.

Consistent with this possibility, Tanner did echolocate on motor behaviors three times more often when blindfolded than when sighted. It is uncertain, however, whether he was using this echolocation to identify behaviors, or rather to navigate while he was performing the motor behaviors himself. We did find that overall, he was no more accurate on blindfolded trials in which he echolocated than on those in which he did not, suggesting that echolocation may not have played a significant role in identifying behaviors. However, it is important to point out that this comparison took place primarily across different behaviors. That is, there were not enough examples of individual behaviors on which Tanner echolocated on one trial but not another to test whether echolocation helped him identify *individual* behaviors. In the absence of such within-behavior comparisons, one cannot rule out the possible confounding effects inherent in comparing across behaviors. These same results might also be expected, for example, if Tanner used echolocation on behaviors that were, for whatever reason, more difficult to copy, thus obscuring any potential boost in identification conferred by echolocation.

Anecdotally, we can report that there were trials on which Tanner scanned his head from side to side toward the model dolphin, which is typical echolocation behavior, *before* he performed the behavior himself. This suggests that, in addition to whatever navigational purposes echolocation was serving, it may also have been used for perception of some model behaviors. Unfortunately, the current study doesn't allow us to tease these possibilities apart. Future research might address this question by using a delayed imitation task in which the imitating dolphin wears eyecups while perceiving the model behavior but not while performing the behavior himself, thus obviating any need to use echolocation for navigational purposes.

A second way in which Tanner may have used sound to identify motor behaviors is by recognizing the characteristic sound that the behavior produces — much like a human might recognize the sound of a handclap or a foot stomp — and then using that identification to reproduce the behavior. The results with blindfolded trainers in Experiment 2 show that such identification was possible. Of course, it must be noted that even in the absence of the requirement to reproduce the model behavior, the human identification test was not strictly analogous to the

dolphin test. Dolphins and humans have different auditory systems with different sensitivities (e.g., Au, Popper, & Fay, 2000), the sounds of the behaviors were undoubtedly different in-air than underwater, and the timing requirements of the identification were different. That is, while the dolphin responded almost as soon as the model behavior began, the trainers typically waited until the end of the model behavior before announcing their guess. Nevertheless, even with these differences, there was reasonable agreement between dolphin and humans with respect to the difficulty of identifying particular behaviors while blindfolded. At the very least, Experiment 2 demonstrated that the information for auditory identification of the motor behaviors existed in the environment, and that the dolphin might therefore have theoretically utilized such information.

In the wild, dolphins evidence several behaviors that implicate imitation as a possible mechanism — including copying each others' signature whistles (Janik, 2000), and population-specific behaviors such as sponging (Mann et al., 2008; Smolker, Richards, Connor, Mann, & Berggren, 1997), mud-herding (Hoese, 1971; Sargeant, Mann, Berggren, & Krützen, 2005), and cooperative fishing with humans (Pryor, Lindbergh, Lindbergh, & Milano, 1990). These last behaviors in particular have been cited as evidence that dolphins may possess the rudiments of culture (Rendell & Whitehead, 2001). However, because population-specific behaviors can also potentially arise from non-cultural learning mechanisms such as stimulus enhancement and environmental shaping (e.g., Galef, 1992; Tomasello, 1990), experimental studies that examine the potential cognitive mechanisms underlying these behaviors are crucial. To that end, the current study adds to the growing body of experimental literature suggesting that the dolphin's capacity for imitation, including its range, flexibility, and conceptual understanding of the task, may be unparalleled among non-human animals (Herman, 2002; Whiten, 2001).

Two final caveats are warranted. First, while the current study demonstrated a new level of flexibility in dolphin contextual imitation (i.e., using known behaviors), we made no attempt to determine whether the dolphin could extend this flexibility to copying novel behaviors as well. Indeed, whether this is even possible may depend on the method the dolphin used to perceive the model behaviors. That is, we would expect it to be extremely difficult, even for humans, to copy a novel behavior based only on its characteristic sound, unless information about the form of the behavior was somehow encoded in that sound. On the other hand, if the dolphin perceived the model behaviors through echolocation, then copying novel behaviors in this manner may theoretically be possible. Further research is needed to evaluate these possibilities.

Finally, it is worth noting that the experimental evidence for dolphin motor imitation (Bauer & Johnson, 1994; Xitco, 1988), including the evidence presented here, has come exclusively from performance in do-as-I-do tests. As noted in the introduction, this procedure specifically focuses on reproducing the form of a behavior, rather than on using imitation to accomplish a task, as in the more common two-action procedure for testing imitation. Importantly, it is not at all clear that facility with one type of imitative task should imply facility with the other. Call and Tomasello (1995), for example, reported that despite the orangutan

Chantek's easy success with copying body movements in a do-as-I-do task, he was completely unable to transfer this ability to copy a demonstrated action in a problem solving situation. It seems, therefore, that the logical next step in the study of dolphin imitation should be to explore whether their prodigious capacity for imitating actions in do-as-I-do tasks will be evident in their performance on problem-solving tasks as well.

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