Research Article

Prosocial Predictions by Bottlenose Dolphins (*Tursiops* spp.) Based on Motion Patterns in Visual Stimuli

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Abstract

In this study, paradigms that test whether human infants make social attributions to simple moving shapes were adapted for use with bottlenose dolphins. The dolphins observed animated displays in which a target oval would falter while moving upward, and then either a "prosocial" oval would enter and help or caress it or an "antisocial" oval would enter and hinder or hit it. In subsequent displays involving all three shapes, when the pro- and antisocial ovals moved offscreen in opposite directions, the dolphins reliably predicted—based on anticipatory head turns when the target briefly moved behind an occluder—that the target oval would follow the prosocial one. When the roles of the pro- and antisocial ovals were reversed toward a new target, the animals' continued success suggests that such attributions may be dyad specific. Some of the dolphins also directed high arousal behaviors toward these displays, further supporting that they were socially interpreted.

Recognizing and using the social information available in the interactions of other individuals is a critical cognitive skill in socially complex species (de Waal, 1986; Seyfarth & Cheney, 2003). Manipulating social variables in the laboratory, however, can be challenging, especially with nonhuman subjects that cannot generally respond to spoken instruction or narrative and for whom conspecific confederates are not an option. Fortunately, work with prelinguistic human infants demonstrates that simple animated stimuli can be used to test questions about social cognition. When the relative motion of distinctive geometric forms is animated, motion patterns can be recognized as representing animacy, goal directedness, and even social dispositions (Csibra, Gergely, Bíró, Koós, & Brockbank, 1999; Gergely, Nádasdy, Csibra, & Bíró, 1995; Hamlin, Wynn, & Bloom, 2007; Kuhlmeier, 2013). In the present study, we adapted a version of these protocols to test the reasoning ability of bottlenose dolphins (*Tursiops* spp.) about the social actions of others.

In human infants, animacy is apparently conveyed when objects are seen as self-propelled—that is, initiating motion or changing direction without contact with an external force (Mandler, 1992; Rakison & Poulin-Dubois, 2001; Spelke, Phillips, & Woodward, 1995). Further, when the relative motion of such shapes is manipulated, infants will readily interpret those shapes as persisting to a goal (for a discussion, see Gelman, 1990; Mandler, 1992). For example, after repeatedly seeing one object approach another, infants do not dishabituate if the object approaches that same target in a new location, but they do if the object takes its original path but approaches a different object (Csibra, Bíró, Koós, & Gergely, 2003; Gergely et al., 1995; Luo, 2011; Luo & Baillargeon, 2005). Thus, the target object

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is understood as the goal, and the infant treats any path to that goal as a similar (unsurprising) motion.

In 1997, Premack and Premack tested whether infants not only attribute goals to moving shapes but also assign social "value" to their interactions. In this study, a gray circle first repeatedly leaped at, but failed to enter, a slot through a wall. Then, on "helper" trials, a black circle entered and lifted the gray circle through the slot. Alternatively, on "hinder" trials, a white circle blocked the gray target from entering the slot. Twelve-month-olds dishabituated if the helper circle was later observed to forcibly collide with ("hit") the target circle, but not if it made gentle contact with ("caressed") it, and vice versa for the hinderer circle. Recent work found similar results for a target circle that repeatedly rolled up, and slid back down, a sloping "hill" (Kuhlmeier, Wynn, & Bloom, 2003). In this work, a helper square pushed the circle up the hill or a hindering triangle pushed it down the hill. Twelve-month-olds looked for different amounts of time when the target circle was seen to approach the square versus the triangle, suggesting the children made dispositional attributions (such as friendly vs. unfriendly) to the interacting shapes (see also Fawcett & Liszkowski, 2012; Hamlin & Wynn, 2011; Hamlin et al., 2007).

To date, related research with nonhumans has been limited, focused on the animals' detection of animacy and goal directedness. For example, like the human infants described above (e.g., Gergely et al., 1995; Luo & Baillargeon, 2005), marmosets looked longer if an agent switched which target it approached but not if it moved along a new path to its original target (Burkart, Kupferberg, Glauser, & van Schaik, 2012). Similarly, there is also evidence that nonhuman primates infer goal directedness on the basis of an object's path. Uller (2004) presented infant chimpanzees with an animated rectangle leaping over an obstacle in its approach to a target circle. As with infants (Csibra et al., 2003; Gergely et al., 1995), the apes treated this as goal-oriented behavior because they dishabituated only when the rectangle continued to leap after the obstacle was removed (see also Rochat, Serra, Fadiga, & Gallese, 2008, and Atsumi, Koda, & Masataka, 2017, for related work with macaque monkeys).

However, to our knowledge, none of the nonhuman work to date has examined the attribution of dispositional states. We tested bottlenose dolphins' capacity for such attributions by adapting the help-hinder and hit-caress protocol used by Premack and Premack (1997). Given that looking-time measures were not feasible in our setting, we used the animals' predictions about subsequent associations between the stimuli, following Fawcett and Liszkowski (2012), to determine whether they attributed social dispositions to moving, geometric forms.

Bottlenose dolphins are promising candidates for this work because they exhibit the complex sociality that may require such social attributions (see Johnson, 2015). These dolphins are collaborative foragers (e.g., Gazda, Connor, Edgar, & Cox, 2005; Gisburne & Connor, 2015), and adult males form coalitions to compete for and sequester females (Connor, Heithaus, & Barre, 1999; Wells, 2003), practices that are likely to demand that they assess others as potential collaborators. As de Waal (1986) argues, species that engage in such polyadic interactions are under selective pressure to track not only their own relationships but also the relationships between others. In addition, previous research with these animals indicates that while their primary sensory modality is audition, they can solve complex tasks using only visual stimuli (Herman, Hovancik, Gory, & Bradshaw, 1989; Pack, 2015). This includes responding to point-light displays, in which the animals recognized trainer signals on the basis of only motion information (Herman, Morrel-Samuels, & Pack, 1990). As a result, we tested whether the dolphins could spontaneously make dispositional attributions to the relative motion of simple shapes, interpreting them as conveying valenced social interactions.

Experiment 1

Method

Participants and setting. During the course of these experiments, 9 to 16 bottlenose dolphins (*Tursiops* spp.) were present in the community pool. The animals in this population ranged from 2 to approximately 37 years of age and consisted of 4 males and 12 females. The three eldest animals (C, K, and O) in this group were caught in the wild; all the rest were born at Sea World. Our experiments were all run in the evening, when the public was not present in the park and all feeding sessions were finished for the day.

For logistical reasons (because several subjects needed to be moved from the testing pool), we were able to collect data over only six sessions, within a 1-month period. Each session lasted approximately 1 hr and included testing on this and other (unrelated and nonsocial) studies. Participation in these studies was voluntary; no training or reinforcement was involved. One unique feature of our study was the ability of the dolphins to freely choose to view the stimuli. Presentations of stimuli continued for as long as any dolphin showed an interest, and we never limited a dolphin's exposure to the training or test stimuli within a testing session. This resulted in unequal numbers of trials across participants and across experiments.

At each session, a projection booth was set up that allowed us to back-project our stimuli, via a 2004
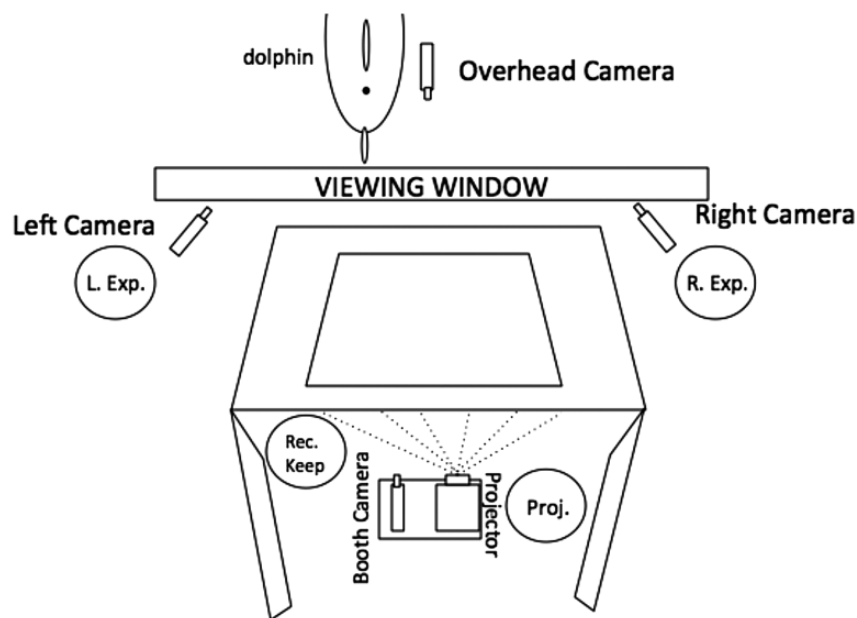
Fig. 1. Configuration of our testing setup. Dolphins viewed stimuli on a screen set up outside their tank but visible through a window. In the figure, circles indicate the locations of four experimenters (see the text for details). This figure is not to scale.

MacBook laptop and video projector, onto a 1.5-m × 1.2-m white screen (see Fig. 1). The screen was centered in front of a 5-m wide, 1.4-m tall viewing window, such that the projected video was visible to the animals below the waterline. Four Canon PowerShot 960 video cameras, each with an 8 GB card that enabled about 45 min of continuous filming, recorded all sessions. One camera was trained on the projection screen from within the projection booth, capturing footage of the video being presented. One was suspended above the water at the window, providing an overhead view of the dolphins' activity at the screen. Two additional cameras were located to the right and left of the window and captured the dolphins' motions from the sides. All cameras were synchronized and then positioned before each projection session began. Synchronization was achieved by directing all four cameras at a clapboard, and in postproduction, all videos were zeroed to that same frame.

During all sessions, two observers were located at the sides of the viewing window to identify each dolphin as it approached the projection area and to indicate whether it stayed or passed by the window (see Fig. 1). These experimenters could not see what was being projected on the screen. Two other experimenters were located inside of the projection booth. One operated the projection apparatus, whereas the other, by incorporating information provided by the observers, kept track of which animals had been exposed to which stimuli and recommended which stimuli be projected

next. This was to help keep the presentations as counterbalanced as possible and ensure that animals saw test trials only after having seen familiarization trials (full exposure records are available at https://osf.io/x9wnd). The experimenters in the projection booth could not see or be seen by the animals, so no inadvertent cuing was possible.

Stimuli. Simple animations were created in Adobe Flash. For all stimuli, we generated movies in which geometrical shapes (ovals) moved about the screen (see Videos S1–S11 in the Supplemental Material available online). The ovals, all of the same size (8 in. × 3.5 in. projected), were shaded differently: Target ovals were black-and-gray striped, with a black border; friendly ovals were all white, with a gray border; and unfriendly ovals were all black, with a gray border. Dolphins do not distinguish colors but can discriminate between gray-scale images, especially when the stimuli are moving (Hanke & Erdsack, 2015). These were set against a static background of pale gray that covered all but the top 10% of the screen, which was white. This background was meant to potentially represent an underwater area below and a bright surface above. As in the work with human children (e.g., Fawcett & Liszkowski, 2012), these displays were designed to tap into basic biological motion patterns tuned to the dynamics of real-world engagement in these animals, in the hopes that they would allow the dolphins to make inferences about the future behavior of such stimuli.

Familiarization phase. During this phase, four types of animated displays were presented: help, hinder, hit, and caress. In the help and hinder segments, the target was first seen alone moving along a smooth upward diagonal path and then appeared to founder, wobbling downward like a falling inanimate or disabled animate entity would underwater. After two or three repetitions of this—each time moving toward and then falling from the "surface"—a second oval appeared from one side and approached the target.

In the help sequences, the oval designated "friendly" would move under the target and appear to lift it to the surface (see VideoS1_Help). This representation of helping is based on naturally occurring behavior in dolphins, in which they will support a struggling infant or other ailing, or dead, conspecific to the surface to breathe (e.g., Caldwell & Caldwell, 1966; Dudzinski et al., 2003). These and other types of epimeletic—or caregiving—behaviors are well documented in these social mammals (see Connor & Norris, 1982).

Alternatively, in the hinder sequences, the "unfriendly" oval entered, moved above the target, and appeared to push it down to the floor (see VideoS2_Hinder). Wild bottlenose dolphins have, on occasion, been observed to force other smaller cetaceans down from the surface, actually drowning them in the process (Cotter, Maldini, & Jefferson, 2012). Dolphin mothers will also sometimes discipline their offspring by temporarily pinning them to the ocean floor (Herzing, 1996).

In both the help and the hinder sequences, the two ovals involved would always exit to the same side of the screen together. This was to equate their time in proximity as well as likelihood of leaving the scene together across stimuli. The sides on which the shapes entered and exited were counterbalanced across the four versions of each of the above scenarios. Plus, across all the sequences, both pairs of ovals were present on screen for the same amount of time and spent an equal amount of time in contact with one another.

In the hit and caress sequences, the target was first observed alone, moving smoothly with multiple direction changes. In the hit sequences, the unfriendly oval would enter and make abrupt, perpendicular contact with the target, which would temporarily deform the target's shape (see VideoS3_Hit). In the caress sequences, the friendly oval would enter and make repeated, gentle, parallel contact with the target (see VideoS4_Caress). In all cases, as above, the two ovals would then exit together to the same side. The sides on which the shapes entered and exited were again counterbalanced across the four versions of these sequences, and both pairs of ovals were visible overall for the same amount of time and spent an equal amount of time in contact.

Test phase. In the test sequences, a large (20 in. × 40 in., projected) black rectangle—the occluder—was added to the background. This block was centered, and its bottom was flush with the bottom of the screen (see VideoS5_Test1). Test sequences began with all three oval types—target, friendly, and unfriendly—on screen, each on an independent, direction-changing trajectory, with the target above and the friendly and unfriendly ovals on either side of the occluder. After 6 s, the friendly oval moved offscreen on one side, and then the unfriendly oval moved offscreen on the other side (with order and side counterbalanced across versions). After one more excursion to each side, the target returned to center screen above the occluder and then turned downward and disappeared behind it. After 2 s, it reappeared at the base of the occluder on the side where the friendly oval had last been seen and moved offscreen in that direction.

During projection, two trained researchers noted dolphins' exposure to each stimulus and reported the exposures to the record keeper. They did this by noting the time at which a given dolphin moved toward the projection screen and noting the time at which the dolphin left the screen or otherwise stopped attending. These time stamps were then matched with the projections that had been shown to the dolphins. For each exposure to a stimulus, we recorded whether the exposure was "direct" (meaning the dolphin viewed the screen for the entirety of the presentation of a given movie) or "passing" (meaning the dolphin swam or turned away from the screen prior to the completion of the movie). We considered only direct exposures when coding and managing data. During test trials in which animals were in the vicinity but did not watch the stimuli, we considered them distracted or inattentive; as a result, only response trials were included in our analysis.

Coding. The videos of the dolphins observing these tests (VideoS6_Response) were cropped to just the 2 s during which the target oval was hidden behind the occluder (VideoS7_RspCropped). These 2-s clips were scored by observers who were thus blind to where the friendly and unfriendly ovals had been. Our dependent measure was whether the dolphin turned its head to the right or left during these 2 s in anticipation of the target reappearing on one side or the other of the occluder. Previous work with the same animals involving the occlusion of dynamic, 2-D images (judging visible and invisible displacement; see Johnson, Sullivan, Buck, Trexel, & Scarpuzzi, 2015) showed that they would often turn to look in the direction they expected an object to reappear. In rare cases, dolphins looked in more than one direction; for all of these cases, we counted the first head turn.

Across both experiments, first-pass coding reliability was good (Cohen's κ = .634), but whenever the coders

did not agree, a third coder, also blind to condition and to the judgments of the other two coders, scored the dolphins' head movements for those segments. If these tiebreakers did not agree with either of the previous scorers of the segment, that trial was dropped from the analysis; otherwise, the majority judgment was used.

Results

The dolphins responded to 56 test trials, and we recorded codable responses on 49 of those trials from 10 dolphins. We first asked whether dolphins looked in the correct direction more often than chance. Averaging across trials, accuracy was 69.38% (see Fig. 2). Because our outcome was binomial and because dolphins provided multiple nonindependent responses, we constructed a binomial logit model comparing trial accuracy (coded as either a 1 or a 0) with a chance value of 50%, with participant as a random factor. We found that dolphins looked in the correct direction more often than would be expected by chance alone ($b = 0.824$, $SE = 0.363$, $p = .023$).

Learning on this task was a distinct possibility—dolphins who viewed the test stimuli repeatedly had the opportunity to see that the target oval moved toward the friendly oval after it left the occluder. To test for learning, we first asked whether test accuracy was predicted by the number of tests a dolphin had completed (it was not; $b = 0.081$, $SE = 0.086$, $p = .347$). We next assessed only first-trial performance. Of the 10 dolphins, 8 showed first trial success; 1 juvenile male and 1 adult female did not. To review data and analyses, see the information posted at https://osf.io/x9wnd.

Discussion

The dolphins in this experiment anticipatorily looked to the side of the occluder where the target oval would reappear if it were following the friendly oval. This is consistent with the view that the dolphins interpreted interactions between these shapes as social and, further, predicted subsequent affiliative interaction between the prosocial shapes. These results paralleled previous research in human infants (Fawcett & Liszkowski, 2012). In that study, the infants also displayed more anticipatory looks toward the friendly shape, in expectation of the target approaching it, and showed a level of first-trial success (12/17, 70%) similar to that observed in our subjects.

While the dolphins reliably anticipated that the target oval would exit in the same direction as the friendly oval, there could be multiple ways to account for this result. If prosociality is attractive, an agent could be expected to preferentially associate with any prosocial other. Alternatively, dolphins may have tracked the relationship between particular individuals. That is, they may have learned that the target and friendly ovals had one kind of relationship (prosocial) while the target and unfriendly ovals had another (antisocial). Buresh and Woodward (2007) found that children attributed goals (in that case, one object's tendency to approach another) as specific to that individual and did not
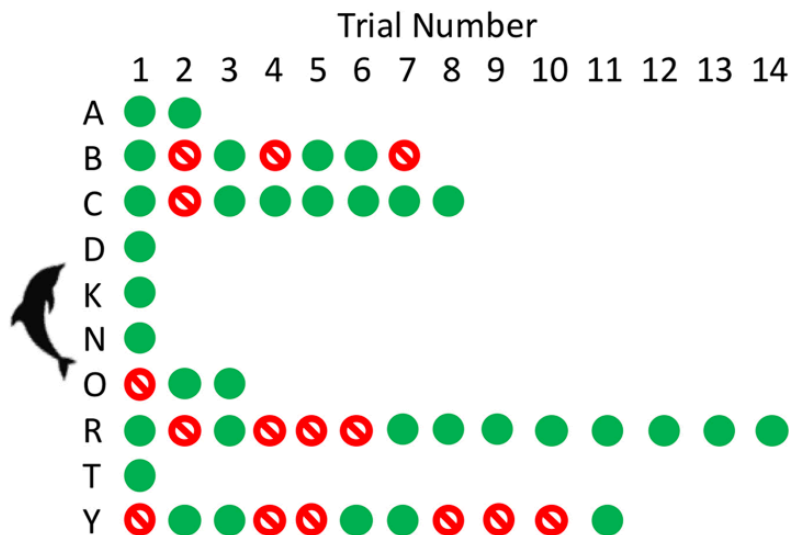

Fig. 2. Experiment 1 performance. Green circles indicate correct performance; red crossed circles indicate incorrect performance. Letters on the *y*-axis represent each of the 10 subjects included in the analysis.

generalize their expectations about that goal to a novel agent.

In Experiment 2, we aimed to discriminate between these possibilities. To do so, we introduced a new target oval and reversed the roles of the other two ovals. If the animals could switch their expectations about which oval the new target would be liable to follow, this could indicate that they were adapting their evaluations to the particular relationships being represented.

Experiment 2

Method

The subjects, cameras, display protocol, and method for scoring videos were the same as in Experiment 1. However, in Experiment 2, the videos shown to the dolphins involved a new target oval (white with black spots). For this new target, the roles of the friendly (now the black oval; VideoS8_Caress2) and the unfriendly (now the white oval; VideoS9_Hit2) agents were reversed. That is, in these segments, the white oval would hinder or hit the new target, whereas the black oval would help or caress it. This design allowed us to test whether the dolphins attributed social goals in a dyad-specific way. Only the 6 of the 10 animals who had already seen and responded to the test videos from Experiment 1, involving the striped target, were included in the analysis. Once again, only the 2 s during which the target had disappeared behind the occluder were seen by the scorers, who determined whether the dolphin's head shifted to the right or the left in anticipation of its reappearance.

Results

The dolphins responded to 45 test trials. Two trials involving animals who did not participate in Experiment 1 were dropped from the analysis, and 6 trials for which we could not code the response were also excluded, leaving 37 analyzable trials.

We tested whether participants would infer that the spotted target oval would move toward the (black) oval that had behaved prosocially toward it (VideoS10_Test2). They did (chance = 50%; success rate averaged across trials = 78.38%; binomial logit model with participant as a random factor: $b = 1.29$, $SE = 0.40$, $p = .001$), and, again, binomial measures of accuracy were not predicted by the number of trials tested ($b = 0.02$, $SE = 0.08$, $p = .74$). First-trial performance was also strong, with 4 of the 6 subjects showing first-trial success (see Fig. 3). See https://osf.io/x9wnd for details.

Another noteworthy result across the two experiments was that four dolphins displayed, altogether, 27 instances of high-arousal social behaviors (open-mouth displays, bubbles, tail slaps, etc.) directed at the screen (VideoS11_Arousal). These behaviors stood in stark contrast to the reaction of the same animals in a previous study that also involved observing and predicting the movements of visual stimuli (Johnson et al., 2015). In a comparable number of trials in that study, the dolphins did not display any such high-arousal behaviors. This suggests an escalated level of socioemotional involvement in the current study.

Discussion

The dolphins' successful performance suggests that they may be sensitive to relationship-specific social behavior. Their anticipatory head moves were the opposite of those seen in Experiment 1. That is, participants predicted that the new target would approach the black oval, which had been unfriendly to the original striped target but was friendly to the new spotted target. While it is possible that the subjects did not recall the original stimuli and were only predicting that the target would follow the most recently friendly oval, a sensitivity to individual-specific information is consistent with what we know of dolphins' capacity to recognize and differentially respond to particular individuals. For example, each dolphin produces an individual-specific call—known as a *signature whistle*—that distinguishes it from others in its group (see Janik & Sayigh, 2013), and bottlenose dolphins have been documented as discriminating and remembering, for up to 20 years, such individual-specific calls (Bruck, 2013).

General Discussion

We tested whether dolphins—like human infants (Kuhlmeier, 2013)—make dispositional attributions. We presented dolphins with videos in which ovals acted prosocially (helping and caressing) or antisocially (hindering and hitting) toward a neutral target. The dolphins appeared to recognize these motions as representing pro- and antisocial behavior, and they used this information to predict that the target would preferentially associate with a prosocial other. In Experiment 2, we replicated these findings and demonstrated that such inferences may be specific to the particular dyads observed. Consistent with this, multiple dolphins also displayed a number of high-arousal behaviors during viewing—such as bubbling, tail slaps, and open mouths—indicative of socioemotional involvement. The dolphins' performance suggests that they were capable of recognizing goal-directed behavior (such as trying, helping, or hindering), attributing valence to such behaviors (e.g., friendly or unfriendly), and predicting that friendly pairs were more likely to subsequently associate than unfriendly pairs would be.
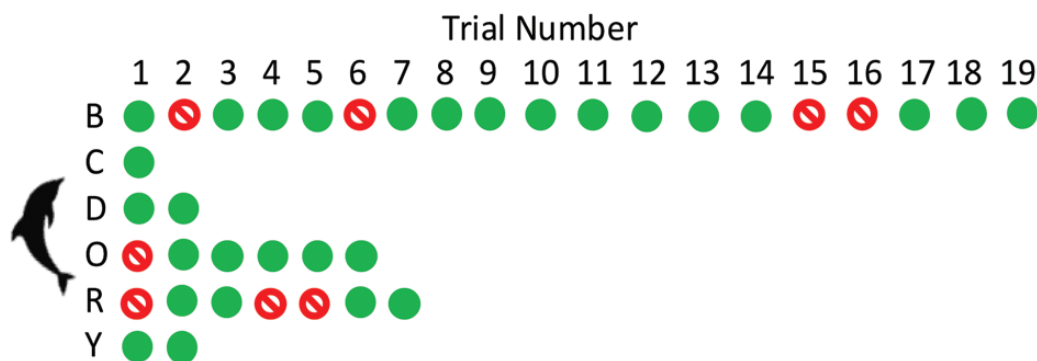
Fig. 3. Experiment 2 performance. Green circles indicate correct performance; red crossed circles indicate incorrect performance. Letters on the *y*-axis represent each of the 6 subjects included in the analysis.

Interestingly, the only subject who consistently showed overall chance performance was the youngest animal tested—a 2-year-old male. He also demonstrated none of the arousal behaviors produced by other animals. While further research with additional juveniles is necessary to determine whether this is typical, it stands in sharp contrast to the human data in which children by their first year reliably show these effects (see Kuhlmeier, 2013).

Additional research with these animals and with humans is required to determine whether subjects primarily base their responses on an attraction to prosocial agents or a repulsion from antisocial ones. Some data suggest that human infants show a *negativity bias*, in which information on antisocial interactions may be developmentally privileged (see Vaish, Grossman, & Woodward, 2008). Hamlin and Wynn (2011), for example, contrasted the helper and hinderer roles with a neutral character that followed the same path as the others but did not directly interact with the target. In that study, 3-month-olds showed a significant preference for the neutral shape compared with the hinderer but no difference in response to the neutral shape versus the helper.

Finally, some notes on the methodology used in this study are in order. Allowing the animals to voluntarily participate in this study presented a trade-off. On the positive side, it guaranteed that the animals found the videos inherently interesting because they were free at any time to leave (as some animals did). Also, not providing extrinsic rewards removed the possibility of shaping the animals' responses. The dolphins' active engagement under these circumstances thus bolsters the argument that these displays were readily interpretable by the animals and so reveal something of the dolphins' natural social cognition. However, this approach also had its drawbacks. It was not always possible to control which animals observed which stimuli, so some dolphins provided much more data than others (see the Method section). Also, had we been able to offer systematic reinforcement, we probably could have extended the animals' participation, increasing our overall sample size, as well as the number and type of experiments that we could have run. Given the small sample in our study, we hope that others will make efforts to replicate this finding.

In any case, the dolphins' performance, despite these limitations, showed that presenting dynamic visual stimuli is a very promising method for investigating social cognition in these animals. The use of simple abstract shapes enabled us to systematically control the relevant social variables being presented. As the first research to demonstrate the ability of nonhumans to make dispositional attributions on the basis of such stimuli, this work, in conjunction with that on human infants, stands to contribute to a better understanding of the evolution of social inference based on observations of others.

Action Editor

Author Contributions

C. M. Johnson developed the study concept. J. St. Leger provided access to the subjects. C. M. Johnson, J. Sullivan, C. Buck, and J. Trexel designed the study and collected the data. C. M. Johnson and J. Sullivan created the stimuli and protocol. C. Buck and J. Trexel served as blind coders. J. Sullivan and J. Jensen compiled and analyzed the data. C. M. Johnson and J. Sullivan drafted the manuscript, and J. St. Leger provided critical revisions. All the authors approved the final version of the manuscript for submission.

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Declaration of Conflicting Interests

The author(s) declared that there were no conflicts of interest with respect to the authorship or the publication of this article.

Supplemental Material

Additional supporting information can be found at http://journals.sagepub.com/doi/suppl/10.1177/0956797618771078

Open Practices

Data and materials for this study have not been made publicly available, and the design and analysis plans were not preregistered.

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