Co-Orientation in Bottlenose Dolphins (*Tursiops truncatus*)

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Abstract

Humans, non-human animals, and many other species have the ability to gaze-follow. The ability to follow another's direction of attention is a social skill that can provide immediate benefits, such as gaining information about food, danger, and social interactions. In this observational study, we investigated whether bottlenose dolphins (*Tursiops truncatus*) also possess the social skill to co-orient, considering they are highly collaborative and live in complex social systems. We collected data on 7 captive bottlenose dolphins during their "free time" at the Brookfield Zoo in Chicago. We observed the extent to which the occurrence of a change of attentional orientation by the first subject predicted a change of attentional orientation by the second subject. We also observed if having a partner or witnessing a more overt behavior would influence the second subject's likelihood to follow the first's change in orientation. Our data suggest that bottlenose dolphins can follow another's attentional orientation; they can co-orient. When they had a partner, they were more likely to co-orient. However, there was no difference in their likelihood to co-orient when they witness another make an overt versus subtle behavior when co-orienting. Such comparative studies can provide insights on the evolutionary origins and adaptive functions of co-orientation.

Introduction

Social attention - paying attention to the attention of others - is an important socio-cognitive skill that can provide immediate adaptive benefits (Tomasello et al., 1998; Itakura 2004). By following a conspecific's attentional orientation, an individual can gain vital information about food, predators, or social interactions. An "attentional" orientation consists of an observable change in the orientation of the animal's sensors, such as turning to look, or to echolocate (Johnson, 2015). Gaze-following occurs if an individual perceives this change in orientation and, as a result, shifts its own attention onward the object or event to which the other is attending (Zuberbuhler, 2008).

Humans are specialized in attending to where others attend, and can manipulate the attention of others using gaze and gestures (Shepherd, 2010). Our tendency to follow gaze reflects our understanding of one another's point of view, including interests, intentions and goals. For example, if you are having a face-to-face conversation with someone and notice their eyes are looking behind you and not at you, then you may turn around to try to see what they are looking at. If you notice that they are looking towards the direction of a clock, you may assume they are expecting something, or maybe they are short on time.

Following gaze is an important communicative channel in humans. We use gaze cues in collaborative processes to predict and coordinate with others behaviors (Huang et al. 2015). Additionally, studies reveal that gaze following plays a role in language acquisition (Baldwin, 1993; Morales, 1998; Tomasello & Farrar, 1986; Shepherd, 2010). Human infants develop the ability to gaze-follow within the first year of birth, and it serves a functional role in assisting infants to respond to referential communication directed to them (Senju, 2008). An infant's ability to make the connection between the looker and the object, in conjunction with vocalizations, aids the infant's word comprehension (Baldwin, 1993). Gaze following can also aids in children's linguistic coding of psychological concepts, such as “want” and “know” (Brooks & Meltzoff, 2015).

Following the attention of another is not unique to humans. Studies on non-human primates, such as chimpanzees, orangutans, sooty mangabeys, rhesus macaques, stumptail macaques, and pigtail macaques (Tomasello et al., 1998; Itakura, 1996), reveal that they too can gaze-follow. Such gaze-following ability enables nonhuman primates to receive salient information in their environment and to engage in complex forms of social cognition (Itakura, 2004). Hare et al. (2000), for example, discovered that chimpanzees can assess what a dominant conspecific can or cannot see during a competitive foraging situation, and use that information to devise effective strategies to obtain food. Additionally, in another study, bonobos and chimpanzees' ability to infer the target of an experimenter's visual attention to familiar (previously seen) versus novel targets was tested (MacLean & Hare, 2012). They found that both bonobos and chimpanzees differentiate between these states, and further presume that the experimenter is looking at the novel target.

While primates have been the main focus in social attention, other social species have also been found to follow another’s attentional shift. Dogs are able to utilize head-turning and glance gestures of humans as cues for finding food (Miklosi et al., 1998). They can also follow gaze or body orientation cues given by conspecifics (Hare & Tomasello, 1999). Ravens are able to follow a human experimenter’s head turn and follow the experimenter’s gaze around a visual barrier (Bugnyar et al., 2004). Horses can also use the head, eyes, and ear orientation of a conspecific to locate food (Wathan & McComb, 2014). Furthermore, studies reveal that American crows, goats, red-footed tortoises, and leopard geckos (Clucas, 2013; Kaminski et. al, 2005; Wilkinson et al., 2010; Simpson & O’Hara, 2019) also show such gaze-following abilities.

Bottlenose dolphins (*Tursiops truncatus*) live in social groups and develop social skills that support a complex society. As such, they too should be good candidates for attending to the social attention of others to coordinate their activities. They come together to collaboratively feed, so they could obtain more food easily. They also cooperate with each other to build coalitions. In male coalitions, they perform synchronous displays to fend off other coalitions from potential mates. In some populations, these dolphins develop embedded coalition structures - called “super alliances” (Conner, et al. 2000) - placing each individual in a complex social network. Additionally, they come together as a group to defend against other predators such as sharks. In order to do all of this, they have to be in tune with each other’s behavior, and in order to do that, they have to pay attention to each other. There are a few studies that reveal that dolphins may engage in shared attention by looking at or ensonifying the same target, and by “eavesdropping” on the returning echoes of another’s echolocation (Xitco & Roitblat, 1996; Gotz, Verfuss & Schnitzler, 2006). The social characteristics and skills of bottlenose dolphins may make them likely to be able to follow another’s attentional shift.

There are a few studies that have attempted to discover whether bottlenose dolphins are able to follow the attention of another. Herman et al. (1999) found that two bottlenose dolphins understand and use human’s pointing gestures to locate distant objects to the left or right of them. In his study, the experimenter would either point directly to the object followed by an action command gesture, such as “fetch”, or make a symbolic gesture of the object followed by an action command. The dolphins treated the pointing gesture similar to the symbolic gesture, and were able to obtain the correct object that was being pointed at. Pack & Herman (2004) found that the same two dolphins were successful in an object-choice task using the experimenters head turn or cross-body pointing cues. The dolphins were also successful with the task when the torso was covered in direct point, gaze, and cross-body point cues, and when the cues were given without motion, “static cues”. However, the dolphins could not not complete the task using only the experimenter’s gaze (Pack & Herman, 2004). Additionally, they could not complete the task if there was a distractor object in the path of the object that was being attended to (Pack & Herman, 2007). It is important to note that these findings are based on two dolphins that are highly trained and have participated in several cognitive experimental tasks, and may not be generalized to dolphins in the wild. Moreover, Tschudin et al. (2001) also found that some bottlenose dolphins were able to use head turn and pointing cues to retrieve an object that was being attended to by an experimenter.

Although there is some evidence that bottlenose dolphins can use head turning and pointing gestures by humans, there are not any studies in which they are called upon to use similar cues from other dolphins. In this study, we investigated whether bottlenose dolphins are able to attend to one another’s attentional shifts. In dolphins, a shift in head orientation or body orientation towards another animal or object, especially in conjunction with orienting for echolocation, can be an observable act of social attention (Johnson, 2015). We hope to learn whether a dolphin will follow another’s change of attentional orientation in a naturalistic environment.

Methodology

Subjects

The subjects are 7 captive bottlenose dolphins (*Tursiops truncatus),* in residence at the Brookfield Zoo in Chicago. There are 3 adults: 1 male and 2 females. There are 4 sub-adults: 1 male and 3 females. Three of these subjects are related: one adult is the mother to two sub-adult females. The subjects also differ in rank. In particular, the mother and the adult male, as the longest residents, are the most dominant animals, with the other adult female subordinate to them. Among the younger animals, the offspring of the mother are dominant over the other young animals, who are relatively new to this facility.

Setting

The subjects live in 4 inter-connected pools - main (MN), medical (DD), north (NH), and south (SH) - see *Figure 1* - that are connected with gate openings. There are 10 video cameras placed underwater and 3 placed above the pools. We will be focusing on the subjects in the main pool using the underwater cameras 1, 2, 7, 9, 10 and 11.

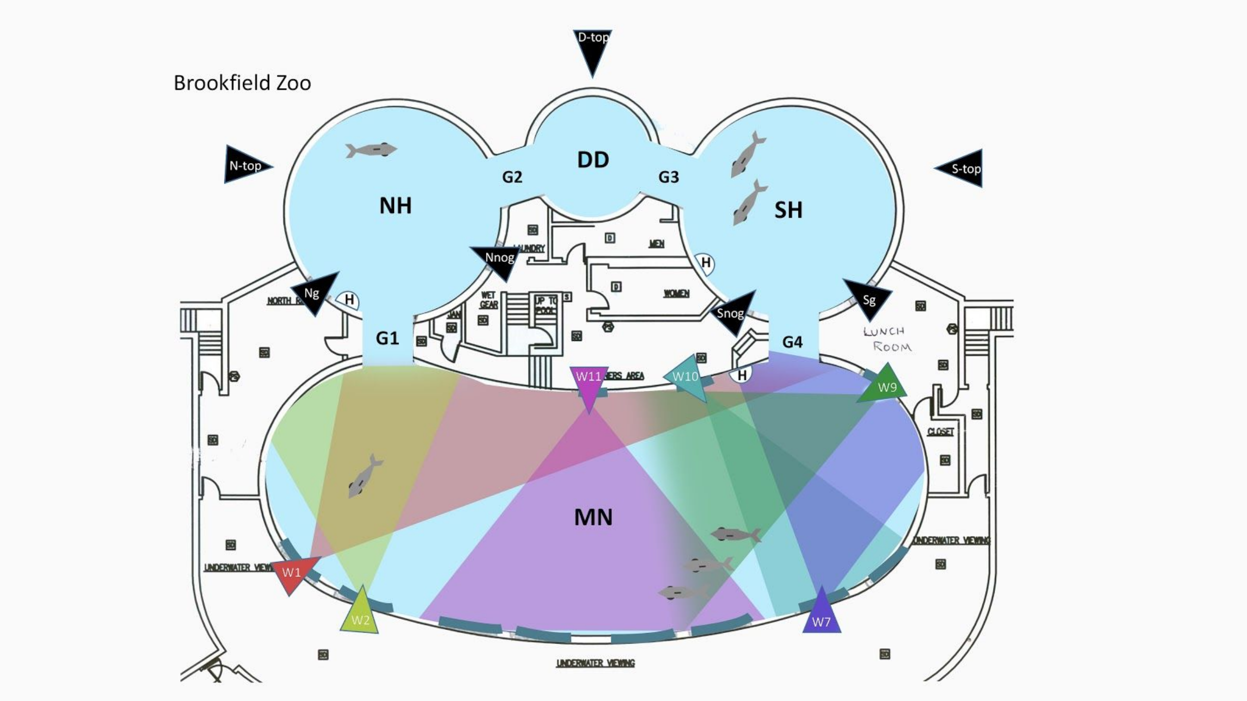

Figure 1. The layout of the inter-connected pools. The triangles indicate the camera placement. The colored triangles represent the cameras we are focusing on. The shaded areas in the main (MN) pool represent the area the cameras cover in the main pool.

Procedure

A total of approximately 20 hours of footage during the subjects' "free time" in the pools that was collected over the span of 3 days between 8 AM and 6 PM. Free time is defined as the time dolphins are not training or performing a show for the zoo. This footage was collected on February 2nd through February 4th, 2013. The focus of the footage will be on attentional behavior at Gate 1 and Gate 4 from the main pool. The total amount of footage included in the analyses presented in this paper was approximately 12 hours.

We tested the extent to which the occurrence of a change of attentional orientation by the first subject can predict a change of attentional orientation by the second subject. In particular, we compared the proportion of times the second subject changes their orientation following the first subject's change, versus the proportion of times the second subject changes when the first subject does not. We measured a shift of attentional orientation anytime the subject made a change in trajectory or in body or head orientation that allowed them to increase or decrease their perceptual access through the gate. We also recorded the type of perceptual access - Monocular, Binocular, Acoustic, None - gained from the subject's orientation, to test if differences in this may influence the orientation of the second subject.

We defined these categories of access with dolphin anatomy in mind. Given that dolphins' eyes are laterally placed on their heads, just swimming past the gate upright gives them Monocular access to the back pool. Since they also have a limited range of binocular vision - below and in front of them - they can alter their orientation (e.g. by rolling their ventrum toward the gate) to gain Binocular access when they pass. Acoustic access refers to the subject's ability to direct their echolocation beam - emanating from their forehead - through the gate.

We collected data for every scene. A scene is defined as an instance when two or more subjects are present and pass the area of the gate. Scenes were classified into three types: "change of trajectory", "no change, with perceptual access," and "no perceptual access".

Change of Trajectory: A subject changes their current trajectory or orientation to enhance their perceptual access through the gate.

No Change, with Perceptual Access: A subject swims past the gate but does not make a change to gain better perceptual access.

No Perceptual Access: A subject passes the gate from below, but does not gain any access through it.

For every subject that reached the gate we recorded 8 things: 1) the subject's ID, 2) whether a change of orientation was made, 3) the type of perceptual access gained, 4) who was present to witness that, 5) whether the witness also made a change in orientation, 6) what type of access, if any, the witness achieved. This data allows us to assess if "attention following" occurs in these animals.

In addition, we collected data on related behaviors, to determine if they also play a role. For one, we scored if the subjects were partnered when they passed the gate. We defined a partner as another subject who is swimming synchronously and in close proximity to the first subject. We then analyzed if swimming with a partner increases the likelihood of following that animal's change of attentional orientation, especially compared to non-partnered subjects.

We also recorded any time an animal rose to the surface to breathe near the gate. When a subject takes a breath by the gate they gain perceptual access through that gate. The motion involved in taking a breath is an overt change that can act as a cue for other subjects. We analyzed if the action of breathing at the gate also influenced other subjects to change their orientation.

Additionally, we recorded when a subject rapidly realigned themselves after making their change of attentional orientation. We noticed that, at times, when a subject turns their head to gain better access, immediately after they pass the gate, they then make a rapid movement to realign their head back to its forward position. Often this rapid realignment is more obvious than the sometimes slow and gradual shift in body orientation the animals make on their long approach to the gate. While a change is involved in these events, it is often not as salient as the rapid realignment. And so, we wanted to analyze where this over motion is detected and used by other subjects to trigger a change in their orientation.

Results

Overall in the 12 hours of footage coded, we collected a total of 1,520 events - whenever at least two dolphins were present and they passed the gate. In order to examine whether the occurrence of a change of attentional orientation by the first subject can predict a change of attentional orientation by the second subject, we conducted a chi-square test for independence. We found that the first and second subject's change of orientation were *not* independent from another, X^2 *(1, N = 1,520) = 118.5, p < .001*. The second dolphin made a change of orientation 52% of the time when they were present to see the first dolphin make a change. While they only made a change 23% of the time when the first dolphin did not make a change (*Figure 2*). The second subject was more likely to change their attentional orientation when they saw another make a change.

The first and second dolphins were partners with each other in 438 of these events. We compared the proportion of times the second dolphin would change their attentional orientation after witnessing the first dolphin make a change, when the first dolphin was their partner versus when they were not by running a chi-square test of independence. We found that the second dolphin was more likely to follow a change of attentional orientation when the first change was made by their partner, X^2 *(1, N = 438) = 5.4211, p < .05* (*Figure 3*).

We also analyzed whether a subject would be more likely to change their orientation after more overt cues. The two "overt" behaviors scored were rapid realignment and breathing at the gate. We found, again using chi-square of independence, that the rapid realignment behavior did not have an effect on the second subject's likelihood to change their orientation (X^2 *(1, N = 438) = 0.12, p = 0.7*); nor did the breathing at the gate behavior (X^2 *(1, N = 418) = 0.023, p = 0.9*). Lastly, we analyzed whether a subject would be more likely to change their orientation based on the perceptual access the first subject achieved. We compared the events where the first subject only achieved visual access versus when they achieved both visual and acoustic access. We found that the type of perceptual access achieved from the first subject did not have an influence on whether the second subject would change their orientation (X^2 *(1, N = 426) = 0.998, p = 0.3*).

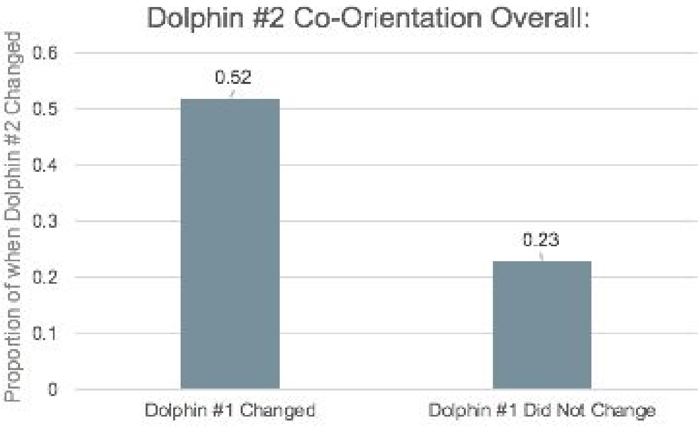

Figure 2: Co-Orientation in Overall Events. *We compared the amount of times dolphin #2 made a change of attentional orientation when it was present to see dolphin #1 make a change or not.*

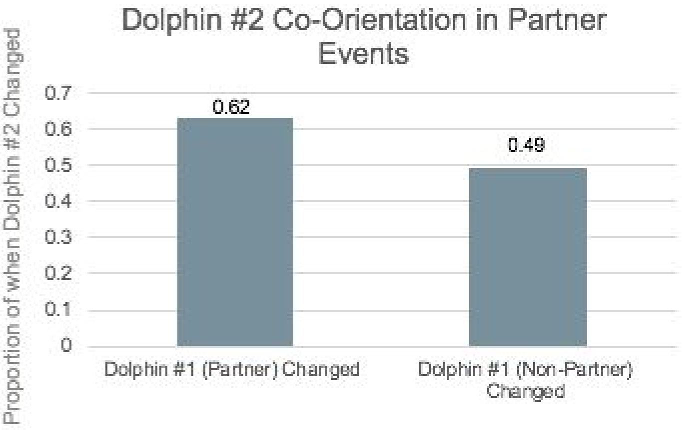

Figure 3: Co-Orientation in Partner Events. *In the events where dolphin #2 made a change of attentional orientation after dolphin #1 made a change, we compared whether the second dolphin was partnered with the first dolphin. We found that dolphin #2 followed a change 62% of the time when it was partnered with dolphin #1, while only changed 49% of the time when they were not partnered.*

Discussion

We investigated whether bottlenose dolphins (*Tursiops truncatus*) are able to attend to another's attentional shift. Our data suggests that bottlenose dolphins can follow another's attentional orientation; they can co-orient. They are more inclined to follow another's attentional orientation if the other is their partner. However, they do not need to witness another perform an overt behavior to be more inclined to co-orient; they are able to follow subtle and overt behavior equally. Their ability to follow another's attentional orientation is thus similar to how humans, non-human primates, and other species gaze-follow.

In previous experimental studies, it was found that dolphins can use human head turning and pointing gestures to co-orient (Pack & Herman, 2004). However, most of the data is based on two dolphins who were previously exposed to cognitive experiments and are highly trained, so it is unclear to what extent the study's findings can be generalized to other dolphins. Moreover, those data do not reveal if the dolphins can co-orient with each other. Another study revealed that they can listen to another's returning echoes (Xitco & Roitblat, 1996), we do not know whether they do this in a non-experimental setting. Thus, this study will be the first to investigate whether bottlenose dolphins can pay attention to a conspecific's attention.

Bottlenose dolphins are social animals that cooperate and collaborate with each other. Through collaboratively feeding, building coalitions, and partaking in group defense, they have the social skills to coordinate with each other. This coordination requires paying attention to each other, so it would make sense that they are disposed to co-orienting. After observing their behavior during their free time, as predicted, we found that they do indeed co-orient. Additionally, as predicted, they are particularly inclined to co-orient with their partner. When they have a partner, they are synchronously and closely moving together, so they are more in tune with each other than with other animals. For this reason, we believe they are more likely to notice and follow their partner's orientation.

To our surprise, we found that they are not more likely to co-orient if the first subject made a particularly overt behavior to gain better perceptual access. Since they are collaborators, they may pay attention to each other's behaviors more often than we know, so they could observe subtle behaviors as equally as they observe more overt behaviors. Perhaps they are even more in tune with each other than we predicted.

Although we know that bottlenose dolphins co-orient with each other, many open questions remain. A limitation in our study is that due to the captive nature of these animals, they may not be completely representative of wild dolphin behavior. However, this study is still a large step towards ecological validity from previous studies. Additionally, we do not know the functionality of co-orientation nor how they use the information. We can assume they are gaining information about who is the back pool or information about other individuals behavior or social interaction, but we have not yet systematically studied this. Additionally, we do not know whether they understand when another is following their attentional orientation, let alone, whether they can show or point-out things to each other, similar to the way humans do.

Co-orientation is a universal benefit in social animals, but in humans it underlies critical cognitive human achievements, such as language learning, apprenticeship, and complex collaboration. To understand how these skills may have evolved, we would typically turn to non-human primates as a model. However, non-human primates differ from us in ways that may be critical here - that is, in terms of how little they depend on collaborative action. Since, unlike non-human primates, bottlenose dolphins regularly engage in collaborative foraging and are socially networked into embedded alliance, they may be able to serve as a model that can fill in the "primate gap", and provide new insights into human evolution of social attention. Future research should be aimed towards investigating the functionality of co-orientation of bottlenose dolphins, to contribute to our understanding of the contexts in which such behavior may have proved adaptive.

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Appendix

Table 1: Summary of Event Types.

Overall Events	1,520
Partner Event	438
Rapid Realignment Events	438
Breathing Events	418

Table 1. In total we recorded 1,520 events. Within this total we have 438 partner events, 438 rapid realignment events, and 418 breathing events.

Table 2: Overall Events Data

	Dolphin #2 Changed	**Dolphin #2 Did Not Change**
Dolphin #1 Changed	228	210
Dolphin #1 Did Not Change	253	829

Table 2. We recorded an event as when two or more dolphins were present and they passed the gate. We scored whether the first subject and the second subject made a change of attentional orientation towards the gate or not.

Table 3: Partners Events

	Dolphin #2 Changed	**Dolphin #2 Did Not Change**
Dolphin #1 (Partner) Changed	55	32
Dolphin #1 (Non-Partner) Changed	173	178

Table 3. In the events where the first subject made a change of attentional orientation, we recorded the amount of times the second subject did or did not make a change when they were or were not partners with the first subject.

Table 4: Rapid Realignment Events

	Dolphin #2 Changed	**Dolphin #2 Did Not Change**
Dolphin #1 Changed (w/ R)	31	31
Dolphin #1 Changed (w/o R)	197	179

Table 4. In the events where the first subject made a change of attentional orientation, we recorded the amount of times the second subject did or did not make a change when they witnessed the first subject do a rapid realignment behavior or not.

Table 5: Breathe Events

	Dolphin #2 Changed	**Dolphin #2 Did Not Change**
Dolphin #1 Changed (w/ B)	62	55
Dolphin #1 Changed (w/o B)	157	144

Table 5. In the events where the first subject made a change of attentional orientation, we recorded the amount of times the second subject did or did not make a change when they witnessed the first subject breathe at the gate or not.

Table 6: Perceptual Access Events

	Dolphin #2 Changed	**Dolphin #2 Did Not Change**
Dolphin #1 Changed & Achieved Visual Access	189	168
Dolphin #1 Changed & Achieved Multi-Access	32	37

Table 6. We recorded the amount of times the second subject made a change of attentional orientation and when they did not make a change after witnessing the first subject change and achieve either visual access only, or multi-access (visual and acoustic).