



Research article

Bottlenose dolphins (*Tursiops truncatus*) display gaze alternation and referential communication in an impossible task

Ying Zeng^a, Luigi Baciadonna^{b,c}, James R. Davies^d, Cristina Pilenga^e, Livio Favaro^{b,f}, Elias Garcia-Pelegrin^{a,*}

^a Department of Psychology, National University of Singapore, Singapore

^b Institut de Biologie Paris-Seine, Sorbonne University, INSERM, CNRS, Paris, France

^c Department of Life Sciences and Systems Biology, University of Turin, Turin, Italy

^d Department of Psychology, University of Cambridge, Cambridge, UK

^e Zoomarine Italia, Torvaianica-Pomezia, Rome, Italy

^f CIRCE, Centro Interuniversitario per la Ricerca sui Cetacei, University of Siena, Siena, Italy

A B S T R A C T

Gaze cues play a vital role in conveying critical information about objects and locations necessary for survival, such as food sources, predators, and the attentional states of conspecific and heterospecific individuals. During referential intentional communication, the continuous alternation of gaze between a communicative partner and a specific object or point of interest attracts the partner's attention towards the target. This behaviour is considered by many as essential for understanding intentions and is thought to involve mental planning. Here, we investigated the behavioural responses of seven bottlenose dolphins (*Tursiops truncatus*) that were given an impossible task in the presence of two experimenters (a 'commanding experimenter' and a 'non-commanding experimenter'), whose attentional state towards the dolphins varied. We found that the dolphins spontaneously displayed gaze alternation, specifically triadic referential pointing, only when the human commanding experimenter was facing them. However, they ceased to alternate their gaze between the impossible object and the commanding experimenter when the experimenter had their back turned. Notably, the dolphins' behaviour differed from general pointing and gaze, as their triadic sequence occurred within a narrow time window. These findings suggest that the dolphins were sensitive to human attentional cues and utilized their own gaze cue (pointing) as a salient signal to attract the attention of the commanding experimenter towards a specific location.

1. Introduction

Gaze cues provide salient information about the status of objects or places critical to survival, including food locations, predators, and the attentional stances of both conspecific and heterospecific individuals. The emergence of gaze cues as a form of social communication could be linked to the advancement of complex social cognitive abilities in humans, such as the development of visual perspective-taking, deception detection, empathizing with others, and mental state attribution [1,2]. Observational learning about salient objects in the environment would likely not be possible without gaze following [3], which then forms the foundation for advanced social cognition. Low and high levels of gaze following each correspond to different levels of social cognition. Low-level gaze following allows one individual to co-orient their gaze in the direction of another individual. This level of gaze following allows observational learning of important information, such as the location of food sources. For example, when subject X follows the gaze direction of conspecific Y onto a prey, this type of social gaze is also called joined visual attention between subject X and the conspecific. High-level gaze following, however, is more sophisticated. The ability to take on another's visual perspective, where

* Corresponding author.

E-mail address: egarpel@nus.edu.sg (E. Garcia-Pelegrin).

subject X repositions itself to see what the conspecific Y is looking at when the target prey is blocked from its view, is also known as “geometrical gaze following” [2]. This skill lays the foundation for referential communication. Joint visual attention in its active form has been proposed to direct another’s attention to an object of interest, such as alternating gaze back and forth between a referent and a target of interest [4]. This active form of joint visual attention also requires the subject to understand that others can attend to their gaze cues.

There is considerable variability of gaze-following behaviors across species. Geometrical gaze following, the ability to take someone else’s visual perspective (when the subject reposition itself to see what others are seeing when the gaze target was blocked from its view) [5] has only been found in apes [6], monkeys [7], wolves [8], corvids [9] and starlings [10].

A recent study evidencing that paleognaths, but not crocodylians, engaged in visual perspective-taking suggests that the origin of visual perspective-taking in mammals might have developed considerably later than in birds [2]. In addition, current evidence of geometric gaze following only in a few mammalian and avian species supports the hypothesis that visual perspective-taking evolved separately across species [2]. Zeigler also noted that current research on visual perspective-taking has been fragmented such that its evolutionary origin is hard to trace [2]. Hence research on mammals belonging to other taxons, such as cetaceans, can help to disentangle whether visual perspective-taking evolved independently within mammals. Recently, Davies and Garcia-Pelegrin [11] demonstrated that bottlenose dolphins are sensitive to human experimenters’ attentional features through understanding the functionality of the eyes, which lays the foundation for visual perspective-taking.

The continuous alternation of gaze between a communicative partner and a specific object during referential intentional communication [12] functions to attract the attention of the partner towards the cued target. This type of communication is considered by many as a prerequisite for understanding intentions as it is thought to represent a form of mental planning [2,13–16]. A commonly used method to assess referential communication in non-human animals is using an impossible task paradigm, in which an impossible object will be presented for the animal to retrieve in the presence of a human experimenter. This experimental approach serves as a way to naturally evoke referential communicative acts such as a two-step sequence “referential gazing” [17] or a three-step sequence “gaze alternations” [18] between the impossible object and the human target. When presented with this task, chimpanzees (*Pan troglodytes*) seem to display significantly reduced gaze alternations between the desirable food (a banana) and the experimenter after the food is delivered compared to before delivery, suggesting, that they might have recognized others as intentional beings whose perspective can differ from them [19]. These findings suggest capacities for both intentionality and nonverbal reference (hence intentional referential communication) in chimpanzees for directing the attention of a recipient, which is developed in human infants at about 10–12 months of age [20].

A variation of the impossible task paradigm incorporates the attentional stance of a human experimenter. This set-up aims to elicit differential gaze alternations conditioned on the attentional stance of the experimenter, which may highlight the subject’s understanding of the experimenter’s mental state. In an experiment where the experimenter was either forward-facing or backwards-facing, goats were found to engage in gaze alternations earlier and more frequently when the human’s attention stance was directed towards them [15]. While there is extensive research on referential communication in both domesticated and non-domesticated animals [12–16,21], studies on referential intentional communication in dolphins and other cetaceans are scarce despite their complex social lives and cognitive capacities [22]. Moreover, as captive bottlenose dolphins have gone through extensive human interactions and training, and yet they are still a non-domesticated species, investigating their reaction to impossible paradigms and their use of referential communicative gesture allows for the disentanglement of the effects of domestication and conditioning on referential communication.

Dolphins exhibit intricate socio-cognitive abilities [see 5,16–21]. The timing and contexts of motor imitative acts in dolphins are reported to parallel those of the chimpanzees, thus suggestive of a generalized capacity to socially learn through gaze cues [23,24]. This generalized capacity for social learning is consistent with research suggesting that bottlenose dolphins (*Tursiops truncatus*) can encode and recall incidental spatial and social information within remembered events which is indicative of episodic-like memory [25]. In addition, bottlenose dolphins were reported to react to uncertainty in similar tendencies as humans [26], preserve the functional aspects of the model’s behaviour in imitation tasks suggestive of goal emulation instead of simply motor imitation [23], and synchronize their actions with their partners in a cooperative task suggesting an understanding their partner’s role [27]. Furthermore, in a series of experiments manipulating attentional features, ie. head and body orientations, of human experimenters, bottlenose dolphins showed increased latency to retrieve objects, and directed less points and monitoring behaviours when the experimenter’s head and eye cued lack of attention [5,22]. However, in an experiment when body and head orientation were manipulated independently, dolphins followed the gestural signs of experimenters according to their body orientation instead of head orientation [28]. In the presence of human observers, two dolphins spontaneously pointed toward containers and frequently gazed back and forth between a human observer and a container to direct and monitor the human observer’s attention [29], which contained some of the features proposed for communicative referential behaviour. Previous experimental work on dolphin vision [30] and echolocation [31] suggest that the dolphins could both detect and discriminate the goal objects used in their study from a distance of many meters. Hence, future studies investigating dolphin’s referential gestures need not require a close proximity between the dolphins and inspected objects when defining monitoring behaviours. However, Xitco et al. [29] did not measure dolphin’s pointing and monitoring behaviours in an experimental context where the human’s attention stance varies. Given the evidence showing dolphin’s joint visual attention with their experimenters [4], it is likely that dolphin’s referential gestures to direct human’s attention would cease when the experimenter is not attending to them (signalled by head orientation). In this study, we investigated whether a sample of seven common bottlenose dolphins (*Tursiops truncatus*) exhibited behaviour suggestive of referential communication towards an experimenter on an impossible task paradigm. Alongside this, to investigate if the dolphin’s referential communication was sensitive to human attentional cues (namely head and body orientation), we also manipulated the attentional stance of one of two present

experimenters (the experimenter relevant to solving the task, or the ‘commanding experimenter’, vs the experimenter irrelevant to solving the task, or the ‘non-commanding experimenter’). Given the evidence reviewed, we first hypothesize that dolphins will display gaze alternations to direct the commanding experimenter’s attention towards the impossible object. Building on the first hypothesis, we also hypothesize that the dolphins will display sensitivity towards the commanding experimenter’s attentional state, based on body and head orientation cues, and thus cease to display gaze alternations when the commanding experimenter’s back is facing them.

2. Methods

Subjects and housing. Seven dolphins (three females and four males (Table 1)) participated in the study, ranging from 6 to 29 years old. The dolphins were individually identified using their distinctive physical characteristics, such as facial differences and toothrake patterns. The dolphins were housed in three adjacent pools at Zoomarine Italia, grouped into three pods. The pools were connected via gates and totalled 7667 m³, with one pool used specifically for the study. The dolphins had previously participated in other research using the same commands and were born and raised in captivity. The dolphins were trained to perform different behaviours for various reasons, including medical care and zoo performances, through food-based positive reinforcement. For testing, the dolphins were individually isolated in the experimental pool when possible but, if not (for example when testing a mother with a calf) the non-focal dolphin was kept separate and distracted by a trainer.

Procedures. Dolphins’ gaze cues were tested using a variation of the Impossible Task Paradigm, in which they were commanded to retrieve an object that was impossible to retrieve. The dolphins were previously trained (by Zoomarine staff) to retrieve an object floating in the water using a specific command consisting of two consecutive hand motions pointing with a closed fist (index finger facing upwards) in the direction of the object. A cylindrical shaped buoy was used as the floating object that was targeted to be retrieved in all trials. The object had a strong 1-m rope attached to it at one end. The buoy was placed in the water with the rope outside of the water, at the end of the pool opposite the command centre. Before the experiment, the dolphins had three trials where they experienced retrieving the floating buoy with the rope loosely wrapped around a concrete post at the edge of the pool (thus meaning the dolphin could successfully remove it, deliver it to the commanding experimenter and receive a food reward). Before each trial, the experimenter would place the buoy in the water whilst the dolphin observed. For test trials, the rope of the buoy was attached at the end to the post using a carabiner clip (outside of view of the dolphin), thus making it impossible for the dolphin to retrieve the buoy and get the food reward in exchange for delivering it to the commanding experimenter.

The dolphins were asked to retrieve an object from the other side of the pool by the ‘commanding experimenter’. Another experimenter, the ‘non-commanding experimenter’ was also present but did not give any commands, and so can be thought of as not relevant to the retrieval task. In test trials, the commander and non-commander experimenters varied their attentional states through two conditions. In the control condition, after the commanding experimenter had given the retrieval command, both the commanding experimenter and non-commanding experimenter continued facing the dolphin subject whilst it attempted to complete the task. In the experimental condition, once the command was given by the commanding experimenter, he would turn around for the rest of the trial, whilst the non-commanding experimenter remained facing the dolphin. In both conditions, the commanding experimenter and the non-commanding experimenter remained still once the command had been given: keeping their hands at their sides, and their head and eyes facing directly forward but not looking at the subject. Each trial lasted 2.5 min, the interval between trials was 7 days, and the order of conditions was counterbalanced.

Analysis. The direction of the rostrum was used as a marker for the direction of the subject’s gaze and points. The behaviours were analyzed using BORIS v7.13 [32]. and statistical analysis was conducted with R Statistical Software (v4.2.2) [33]. Within each trial, only observations within a stipulated duration were kept. The duration of each trial was quantified as the time lapse from the onset of the first touch of the impossible object to the end of the last coded behaviour. The total duration of trials ranged from 79.8s to 103.9s (mean = 91.3s, sd = 6.9s). A cut-off time was set at the mean level of the total duration to control for the total duration without losing too much information (compared to setting at minimum level) as some subjects spent most of the time retrieving the object, leaving little time for behaviours of interest. Overall, 20 observations were removed following the criteria that for each trial, only behaviours that occurred within 91.3 s lapse following their first touch of the object were valid. The start and stop time of each trial per subject is standardized with 0s representing the onset of first touch.

Gaze alternation is operationalized as the three-step sequence starting from pointing towards the commanding experimenter, then to the object’s 3 or 9 o’clock direction, and finally back to the commanding experimenter. In the second step (i.e., when the rostrum pointed to the object’s 3 or 9 o’clock direction), the subjects can monitor the object at a distance due to lateral-sided eyes. There is some overlap in successive triadic gaze alternations observed as the last point to the commanding experimenter in previous instance

Table 1
Name, sex, and age of subjects.

Name	Sex	Age
THAI	F	9
QUINA	F	19
ZEUS	M	11
PACO	M	22
LEAH	F	19
KING	M	29
MARCO	M	23

can be the initial point to commanding experimenter in the next instance. For example, the sequence “point to non-commanding experimenter, next to commanding experimenter’s 9 o’clock direction, back to the non-commanding experimenter, next to the object’s 3 o’clock direction, back to non-commanding experimenter” is meaningful as 2 instances but there is a double count of duration due to the overlapped gaze at the boundary of the 2 instances. When there is an overlap between gaze alternations, it manifests as second gaze alternations beginning before the first gaze alternation ended. The average of the duration of the overlapped gaze is calculated and subtracted from each instance respectively. Considering the markedly different body size and ease of head orientation between dolphins and other species reviewed in the impossible task literature, the criteria of gaze alternation within 2s for goats [15] clearly is too constraining. Since the dolphin must re-orient its entire torso while keeping its gaze on the referent and target, a longer time is reasonable. For reference, the duration between the first and second instance of the two-step sequence of pointing at the container and then to the trainer is 15s in other dolphin studies showing spontaneous pointing and monitoring [29].

Two subjects (Paco and King) were removed from the analysis as there was at least one condition for the subjects where the only behaviour demonstrated was continuously attempting to retrieve the object, hence leaving missing value for other behaviours of interest. The cut-off time for a valid gaze alternation is set as the median duration (9.756 s) of the distribution of gaze alternations across conditions after removing Paco and King.

For the remaining five subjects, the missing value for gaze and gaze alternation durations in either condition was substituted as zero. However, for gaze and alternation latency (time-lapse before first gaze), the subject with missing data in either condition was removed from the relevant analysis as the missing value suggested that the lack of behaviours for meaningful comparison on latencies.

3. Results

There were no significant differences between the forward-facing and backwards-facing conditions regarding their speed of return ($V = 4$, p -value = 0.4375), suggesting that the subjects were equally motivated to approach the experimenters.

Gaze Alternations. Three types of alternating gazes were observed involving different referents. The subjects were observed either to gaze alternate towards the same experimenter (commanding or non-commanding) or gaze towards a different experimenter from what they started with (mixed) (Table 2). There were no significant differences between the control and experiment for gaze alternation frequencies towards the commanding experimenter ($V = 6$, $p = 0.1736$); the non-commanding experimenter ($V = 1$, $p = 1$); or mixed experimenters ($V = 1$, $p = 1$). Summing across experimenters, there were no significant differences between the control and experiment for gaze alternation frequencies ($V = 15$, $p = 0.0568$; Fig. 1). Importantly, although the results were not significant, three out of five subjects displayed gaze-alternating behaviours. Across all types of gaze alternations, a consistent trend is observed. Subjects who displayed gaze alternation in control conditions stopped such displays in experimental conditions when the commanding experimenter was back-facing them.

Overall, there was a reduction in the number of subjects engaging in gaze alternations across conditions for the commanding experimenter (three subjects in control, one subject in experimental), the non-commanding experimenter (one subject in control, zero subject in experimental) and mixed experimenters (one subject in control, zero subject in experimental) (Fig. 2). Due to missing paired data for latencies until the first gaze alternation (Fig. 3), no meaningful statistical analysis could be analyzed. The Chi-square test of the proportion of subjects displaying gaze alternations was also not significant ($n = 10$, $X = 1.904$, $p = 0.1680$).

General gaze and pointing. Individual Wilcoxon signed-rank test was conducted for gaze latencies, gaze duration and gaze frequencies. An additional Generalized Linear Model (GLM) specifying gamma and Poisson distribution was also conducted for gaze durations and gaze frequencies respectively.

Overall, there were no significant differences between control and experimental conditions in gaze latencies ($V = 8$, $p = 1$; $F = 0.14$; $p = 0.610$) (Fig. 4a), gaze durations ($V = 13$ (Fig. 4b), $p = 0.188$; $F = 3.31$, $p = 0.061$) and gaze frequencies ($V = 10.5$, $p = 0.498$; $F = 3.11$, $p = 0.073$) (Fig. 4c) towards the commanding experimenter. A significant difference was found for gaze latencies towards the non-commanding experimenter with GLM ($F = 23.62$, $p < 0.001$), however, this is not replicated with Wilcoxon signed rank test ($V = 6$, $p = 0.25$). No significant difference was found for gaze duration ($V = 6$, $p = 0.813$; $F = 2.20$, $p = 0.16248$) and frequency ($V = 4$, $p = 0.854$; $F = 1.35$, $p = 0.296$) towards the non-commanding experimenter.

4. Discussion

In this study, three out of five subjects displayed gaze alternations when the commanding and non-commanding experimenters faced the dolphin (control conditions), all of which stopped such display in experimental conditions when the commanding experimenter turned his head and body against the subjects. The proportion of subjects showing gaze alternations and the tendencies observed for the gaze alternations and the general gaze and pointing provide preliminary support for both hypotheses 1 and 2. Nonetheless, it is plausible that what appears to be referential gestures could be a general act of attending to the commanding experimenter and the object. In this case, positive reinforcement of dolphins’ pointing in past training could have conditioned them to

Table 2
Proportion of subjects displaying gaze alternation.

	No Gaze Alternation	Gaze Alternation
Control	2	3
Experimental	5	0

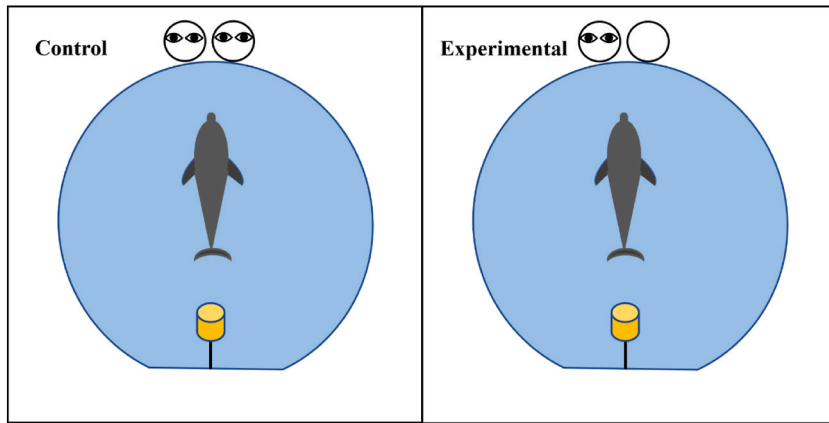


Fig. 1. Schematic representation of the two trials *Control* (left) and *Experimental* (right). In experimental trial the commanding experimenter turned his head and body away. The place where the experimenters stand is referenced as 12 o'clock in the commanding experimenter's direction.

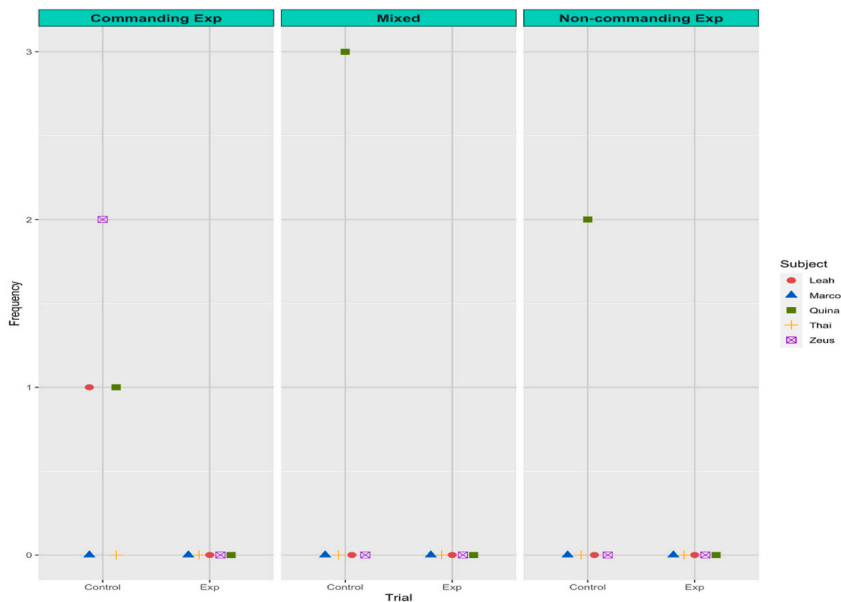


Fig. 2. Frequency of gaze alternation. Frequency of gaze alternation between impossible object and commanding experimenter/non-commanding experimenter/back and forth between both experimenters (Mixed) when the commanding experimenter is attending to the subjects (control) compared to when the commanding experimenter is not attending to the subjects (experiment).

point to the commanding experimenter in most circumstances. However, with our strict criteria controlling for gaze alternations within a set period (<9.756s) and experimental manipulation, the observed differences across conditions cannot be adequately explained by the subject's tendency to point towards the commanding experimenter due to positive reinforcement. Furthermore, it is typical for dolphins to continue swimming when they attend to objects, with either vision or echolocation [29]. Similar to other studies with dolphins [29,34], our subjects in our study remained stationary while pointing towards the commanding experimenter. More importantly, dolphins' change of body orientation to inspect the impossible object and back to the commanding experimenter were swift (<9.756s). This is unlike the small, scanning head movements that characterized dolphins' use of echolocation when they inspected the goal objects or looked toward receivers. Hence, these differences in duration and range of motion clearly differentiated our observations of referential gestures (gaze alternations) from a more general act of attending. Therefore, gaze alternations spontaneously elicited in our subjects suggest that dolphins understand that these gestures can direct the commanding experimenter's attention to the target. The subjects in our experiment have never been trained with gaze cues. Thus, associative learning is unlikely to be the cause of reduced gaze alternations in experimental conditions in this study. The cease of gaze alternations (their attempts to direct the commanding experimenter's attention) when the commanding experimenter is back-facing them suggests that dolphins understand the significance of human attention and are sensitive to the attentional state of the commanding experimenter signalled by

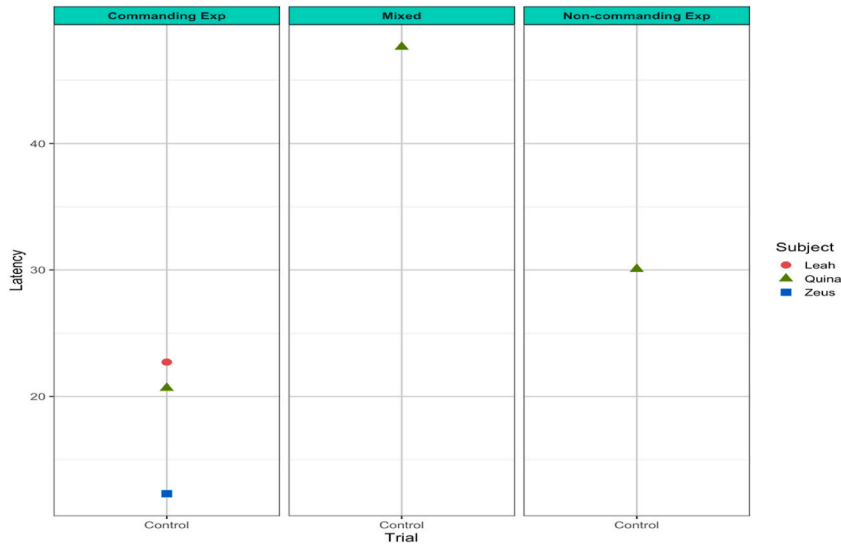


Fig. 3. Latency until first gaze alternation.

Latency until first gaze alternation between impossible object and commanding experimenter/non-commanding experimenter/both experimenters (Mixed) when the commanding experimenter is attending to the subjects (control) compared to when the commanding experimenter is not attending to the subjects (experiment).

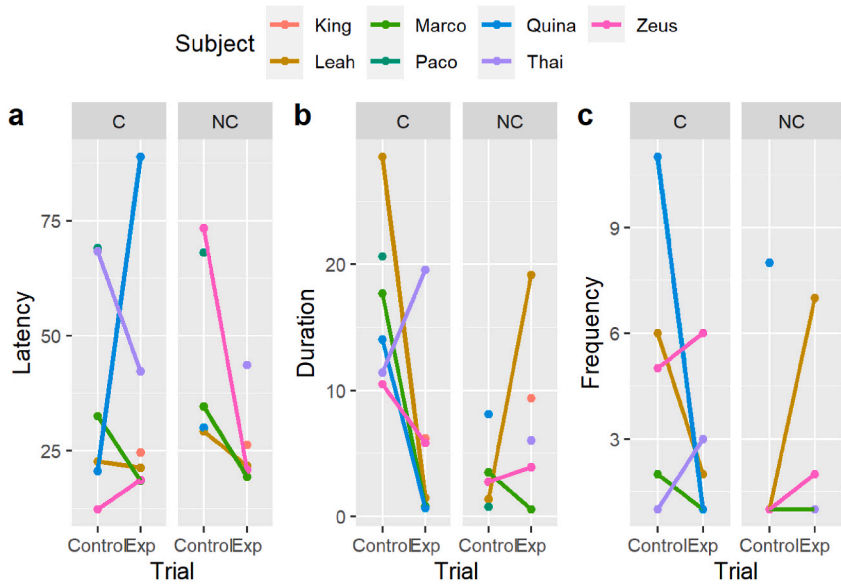


Fig. 4. General gaze and pointing.

Latency (in seconds), duration (in seconds) and frequency of gaze and pointing behaviours for commanding experimenter (C) and non-commanding experimenter (NC) when the commanding experimenter is attending to the subjects (control) compared to when the commanding experimenter is not attending to the subjects (experiment).

their head and body orientation, which supports the conclusion reported by Davies and Garcia-Pelegrin [11].

Dolphins have significantly distinct sensory abilities in the visual and auditory domains compared to other species investigated in the impossible task literature. Bottlenose dolphins engage in both monocular and binocular vision, however, reports suggest that dolphins generally use monocular vision [35–39]. For monocular vision, dolphins’ eyes are laterally positioned, typically providing the animal with over 200° of visual access to its surroundings [40]. In contrast, primates, with their forward-facing eyes, have a visual field encompassing about 90° on each side of the midline, about 50° above, and 60° below, the point of focus [41]. In addition, non-primate animals have undeveloped facial musculature [42] and therefore, whenever they direct their gaze, they need to move their entire head [3]. Besides a wider visual field that makes head orientation less necessary, dolphins have fused cervical vertebrae which limits their

head movement [43]. These differences in morphological structure and eye morphology imply a fundamental difference in gaze alternations in dolphins compared to other species, which required a different experimental setup to elicit the operationalized gaze alternations than the typically used for this paradigm [6–10].

The complex and flexible communications system in cetaceans encompasses vocal, visual, tactual, and chemical signals [22]. Bottlenose dolphins produce several different whistle types and sounds [44,45] and their calls are highly varied and used differently across social groups and were suggested to underlie their referential identity-labelling system [46]. Although dolphins do not possess forward-facing eyes which helps to indicate head orientation (and is hypothesized to be a pre-requisite for the evolution of conspecific gaze following [47]), they possess echolocation, which is intricately linked to head orientation. In the wild, dolphins use echolocation to discriminate and recognise objects [48], which is crucial for foraging [49] and conspecific gaze following [50]. By listening to the echoes returning from a target being inspected through echolocation by another dolphin, the “eavesdropping” dolphin can identify the target [51]. Hence, the adaptive fitness of attending to conspecific’s echolocation is likely to result in selective pressure for adaptation to understand conspecific’s head orientation. Johnson and colleagues [50] argued that similar alignment of head orientations with conspecifics not only gives them access to echoes, but allows them to experience, and learn the functional significance of such co-orientation. Indeed recent studies showed that dolphins [50], as well as penguins [52] and ibis [53], all of which possess lateralized eyes, do display conspecific gaze-following.

In addition to gaze following, dolphins appear sensitive to static and dynamic human pointing and gaze (accomplished with head directions) cues [4]. However, although they were successful at understanding pointing cues and human gaze accomplished with head-turning, gaze with eyes only resulted in chance performance. This is consistent with the idea that sensitivity to head orientations in joint attention to the echoes reflecting off an object provides a general foundation for the dolphin’s joint visual attention to human head orientations [4]. In the laboratory, however, dolphin’s communication with experimenters is constrained to the use of gaze and pointing. Xitco et al. [29] argued that dolphin referential pointing may not be frequently expressed between conspecifics because it is rarely needed. Given the complex social structure and flexible communication system of dolphins, it is likely gaze alternations in human interactions emerged as a result of their flexibility in social learning that allows them to readily learn the attentional state of humans through head and or body orientation and adopt the communication channel that the receiver can understand, in this case pointing.

Lastly, domestication is commonly believed to have resulted in enhanced intentional referential communicative interaction of animals with humans [13–16] as communicative behaviours that facilitated human-animal interactions are supposedly more likely to be selected in animals with long histories of human dependency. However, intentional referential communicative gestures in the impossible task paradigm have been observed not only in domestic companion animals such as dogs (*Canis familiaris*) [21], horses (*Equus caballus*) [16], and animals domesticated for production such as goats (*Capra hircus*) [15], but also in animals that have never been domesticated, such as wolves (*Canis lupus*) [54], and kangaroos (*Macropus rufus*) [12]. In addition, both wolves and dogs with extensive socialization with humans showed similar levels of pointing gestures in referential communication [54]. Furthermore, no significant correlation was found between the proportion of wolf blood in dogs and their probability of looking back towards humans [21]. These results cast doubt on the role of domestication as the main cause of enhanced communicative interactions of animals with humans. Instead, it is likely that a combination of conditioning, positive socialization, and responsiveness to visual stimuli from conspecifics might be more important than domestication for referential communication with humans [12]. In the present study, bottlenose dolphins’ referential communicative acts seemed to arise from their understanding of the functional significance of head/body orientation as a consequence of their sensitivity to the head/body orientation of conspecifics when echolocating. Given the preliminary evidence for visual perspective-taking in dolphins and the body of evidence of visual perspective taking in apes [6], monkeys [7] and wolves [8], it is likely that visual perspective-taking arose independently across species within mammals.

While the present study faces the typical constraints often encountered when conducting cognitive research in zoological facilities [55] such as a small sample size, lack of repeated testing, and lack of complete information about the subject’s rearing, these can be addressed by recruiting more subjects through multi-site collaboration to reduce the influence of confounding factors such as training histories. Despite negative results, the results presented here evidence that some dolphins alternated gaze back and forth when the commanding experimenter was facing them, which provides further support to the vast array of complex sociocognitive abilities that dolphins appear to possess.

Ethics statement

The project was reviewed and approved by the University of Cambridge Animal Welfare Ethical Review Body and conducted under a university non-regulated procedure license (OS2022/01).

Data availability

The data and code used in this study is available following this link: https://osf.io/udty4/?view_only=29dfce3305794869a09c97bc7c7a2c2d.

CRedit authorship contribution statement

Ying Zeng: Writing – original draft, Formal analysis. **Luigi Baciadonna:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization. **James R. Davies:** Writing – review & editing, Methodology, Investigation, Data curation. **Cristina**

Pilenga: Writing – review & editing, Resources. **Livio Favaro:** Writing – review & editing, Resources. **Elias Garcia-Pelegrin:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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