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OPEN Effects of experience and familiarity on visual attention and behaviours of bottlenose dolphins (*Tursiops truncatus*) in presence of humans

Alessandro Gallo^{1,2,3}✉, Robert Gojceta⁴, Martin Böye³, Alban Lemasson^{1,5,7} & Martine Hausberger^{2,6,7}

Visual attention is an intrinsic part of intra- and inter-specific interactions. Its structure (e.g. short glances vs. long gazes) depends on the species, type and expected outcome of the interaction. The outcomes of earlier repeated interactions determine the resulting valence of the relationships. Human-animal relationships rely upon species-specific cognitive abilities and attentional characteristics for associative learning and memory formation. Visual attention is crucial in cognitive processing and relationships construction, but its structure may depend on species-specific characteristics and relationships' quality. Dolphins are renowned for their cognitive abilities and in human-care settings they have regular interactions with caretakers. Dolphins' visual attention structure and laterality both differ depending on the visual stimulus to which the animal is attending (species-specific, non-biological). We hypothesized that visual attentional characteristics and associated behaviours, in a group of 9 captive bottlenose dolphins (*Tursiops truncatus*), would differ according to past experience and familiarity with humans. Human motionless tests showed a role of experience (time spent) in the facility on play and vocal production near humans regardless of familiarity. However, familiarity influenced dolphin presence near humans and visual laterality: they stayed longer and used their right eye more to glance at familiar humans. These findings provide new insights on how dolphins cognitively process stimuli according to familiarity and past experiences, as well as on how human-animal relationships evolve in captive settings.

Keywords Human-animal relationship, Inter-species communication, Play, Perceptual laterality, Cetaceans, Bioacoustics

Visual attention is an intrinsic part of intra- and inter-specific interactions in many vertebrates. Its structure may depend on the species (e.g. dogs *versus* cats¹), the type of interaction involved and its expected outcome (e.g.²), and even the type of social organization of the species (e.g. more or less tolerant³). Thus, the social affinities and bonds between interacting individuals as well as the emotional content of the interaction, influence the type and level of attention towards a given stimulus⁴⁻⁹.

Interactions are defined as an individual addressing another one, who in turn responds: they can be seen as short and sporadic events¹⁰. The repetition of interactions between the same individuals constitutes the basis for the emergence of a relationship, where individuals have positive or negative expectations on the interactions' outcome based on their memory of the former ones (i.e. their valence)¹⁰. Social cognition allows individuals to learn the individual characteristics of their interlocutor and their association with the valence (i.e. positive or negative emotion-inducing) of the outcome for themselves. It has been proposed that this same framework

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applies to interspecific interactions and relationships, in particular to the context of the human-animal relationships^{11–16}.

Interactions between humans and non-human animals occur in a large variety of settings whether under domestic, captive or wild conditions (e.g. companion or farm animals¹¹; wild animals under human care^{17–19}; or wild animals in natural conditions²⁰). Animals can show different responses depending on the perception they have of their interactions with humans, from low fear and seeking for proximity (positive valence), low fear and no seeking for proximity (neutral valence) to high fear and avoidance (negative valence)¹⁵. In fact, rough handling of animals induces fearful behaviours towards humans even outside the handling time (pigs^{21,22}; cows^{23,24}). Instead, the use of positive reinforcement or gentle handling induces behavioural indicators of proximity seeking, persisting on a long term (horses²⁵; pigs²⁶).

As mentioned earlier, building a relationship with humans implies associative learning and memories of past interactions^{12,15,27}. Animals can generalize their perception (positive or negative) from familiar humans to unfamiliar humans^{28–31}. Piglets that experienced previous positive interactions with humans (e.g. stroking or scratching) expected a positive human contact when encountering humans, and their absence provokes the emission of stress-related vocalizations³². Rhesus macaques trained with positive reinforcement procedures showed decreased aggressiveness towards familiar humans that were also generalized to unfamiliar humans³³. In horses, negative and positive reinforcement during training lead to opposite behavioural reactions outside training whether they are tested with familiar or unfamiliar humans (avoidance *versus* proximity seeking)³⁰. Moreover, when tested several months later, these same horses showed these same reactions but they were still clearer when the test person was their initial trainer, showing that they had a double memory: humans and their valence, familiar *versus* unfamiliar humans²⁵.

The ability to discriminate familiar humans on the basis of visual (e.g. dogs³⁴; cats³⁵; lambs³⁶; pigs³⁷; cows³⁸; horses³⁹), acoustic (e.g. horses^{20,27,40}; pigs³⁷; dogs⁴¹) or olfactory (e.g. horses⁴²) cues is not limited to domestic animals. Wild animals also learn to associate particular humans with their actions towards them. For example, in bird species such as magpies, mockingbirds and wild American crows, aggressive responses and alarm calls were directed only towards humans associated with negative experiences (e.g. capture, repeated nest visits)^{43–45}.

It is still more so in captive conditions where wild animals are confronted with human actions on a daily basis. Few studies have been performed on individual recognition of humans in this situation, but they show that the animals are able to discriminate familiar (e.g. the caretaker) from unfamiliar humans, based on perceptual cues such as the voice, and adapt their behaviour and direct their attention accordingly (e.g. Asian elephants⁴⁶; cheetahs⁴⁷; grey wolves⁴⁸; orangutans, gorillas and chimpanzees^{43,44}). Thus, dolphins, like horses, do not monitor visually familiar and unfamiliar humans the same way^{40,45}. Dogs direct their visual attention preferentially towards their owners before engaging in a problem-solving task⁴⁹. Familiar humans providing positive reinforcement triggered more visual attention in horses^{13,50}. Asian elephants selectively respond to acoustic signals and approach a specific human only when they hear the voice of their familiar trainer⁴⁶. Cheetahs orient their visual attention towards the loudspeaker when it broadcasts the voice of the familiar caretaker⁴⁷.

The interrelationship between the emotional valence of a stimulus and the subsequent degree of attention directed highlights the involvement of specific cognitive processes¹³, such as lateralization of brain processes⁵¹. Perceptual lateralization, and especially of visual attention, is widespread amongst vertebrates and has led to different hypotheses. For example, the theory of valence suggests that the left hemisphere (LH) would be more involved in processing positive/neutral stimuli and the right (RH) in processing the negative ones^{52,53}. Other studies suggest that LH would be more involved in global attention and RH in more sustained and detailed attention, allowing identification of individual identity, familiarity or novelty^{54–56}. Finally, it has also been proposed that the RH is involved in dealing with high arousal properties that are attention-getting^{51,57}. In the same line, unexpected (e.g. reversed vocalizations⁵⁸), novel (e.g. sound⁵⁹) or socially relevant (e.g. familiar voice^{27,60}) stimuli induce more lateralized responses compared to familiar or expected stimuli⁵⁷.

Bottlenose dolphins are very interesting animal models for investigating the link between familiarity, experience, attention and laterality. Different studies have shown that they can discriminate different humans and identify their attentional states^{61–64}. For example, familiarity with a trainer influences the frequency and type of interactions displayed by dolphins⁶⁵, which may even be motivated in engaging for physical contact with familiar humans (e.g. body rubbing)⁶⁶. Dolphins' lateral position of eyes and complete decussation of the optic nerve enhance lateralization of visual processing. The visual field is of 120–130° with the two eyes overlapping only 20–30°^{67,68}. Furthermore, as in other vertebrates, information from right eye therefore travels towards the left hemisphere (and left eye to the right hemisphere)⁶⁹. Lateralized visual responses have been observed for familiar and non-familiar objects^{56,70,71} and familiar and non-familiar humans^{72,73}. However, Hill et al.⁷⁴ did not find any visual laterality bias whether dolphins looked at a familiar or unfamiliar human. Moreover, lateralized responses have been found for unfamiliar conspecifics (i.e. biological stimulus) but not for unfamiliar objects (i.e. non-biological stimuli)⁵⁹. Therefore, these evidences provide controversial results and indicate that the salience of the stimulus could be responsible in triggering different degrees of attention/curiosity that could influence the presence or strength of visual laterality processing.

In the present study, we hypothesized that the behaviour of dolphins, and especially visual attention structure and laterality would be influenced by familiarity with a human but also past experiences with humans overall. We used a free-swimming situation where 9 captive male dolphins could freely choose to come close to a human (familiar or unfamiliar) standing motionless at 1 m from the pool's edge (a usual situation for them). Visual discrimination in the air is possible for dolphins because of the anatomy of their eye (i.e. double-slit pupil asymmetries) that allows a comparable vision efficiency in water and in air⁶⁸. In the view of the existing literature, we expected dolphins to be more interested and interactive and to show an enhanced visual laterality for familiar humans.

Material and methods

Study site and data collection

The study was conducted in July 2023 at Attica Zoological Park (Spata, Greece). The facility consisted in a complex of four interconnected pools of different sizes housing a group of nine bottlenose dolphins (seven *Tursiops truncatus truncatus* and two *Tursiops truncatus ponticus*). They were all captive born and arrived in this facility as juveniles and adults between 2010 and 2020. The group was composed of 9 adult males aged between 12 and 30 years (20.44 ± 6.54 SD). Public visits were restricted to three time slots during the day (1.5 h each, at 11 am, 1 pm and 3 pm). Visitors were only allowed to look at dolphins while walking along the pools at a distance of 3 m from the pool's edge. Outside these time periods, the dolphins' daily schedule included four training sessions with caretakers for veterinary/research purposes (around 30 min per session). Training sessions were based on positive reinforcements which were also used for providing part of the daily feeding supply (i.e. herring, capelin, mackerel, sprat, whiting). A last time period at 5 pm was exclusively dedicated to the feeding (without any training).

Experimental tests

The tests were performed opportunistically at different times of day (between 10:00 am and 4:00 pm) and in a random order (Familiar-Unfamiliar; Male-Female humans) depending on the availability of the volunteers. A maximum of two tests in the morning and two in the afternoon were performed. Successive tests were separated by at least 1 h. Every test was carried out outside husbandry and training procedures and during times devoted to tourist visits (due to constraints of dolphins' schedule over the day), which is also a time when caretakers can stand and check on dolphins, so that the test situation corresponded to the usual situation of humans being close/standing at the pool's edge. We ensured that no tourist would walk around the test area during the tests. The tests were conducted with 18 human participants, divided into familiar and non-familiar individuals. Familiar humans (F) were dolphins' caretakers (N=9) that had, at the time of the study, at least a minimum of 5 months of daily interactions with the study group. Non-familiar humans (NF) (N=9) were individuals that had no experience with the study dolphins (notably new interns or staff of other sections of the park).

Care was taken to match each non-familiar human with a familiar one in terms of their individual characteristics, notably sex and physical size, resulting in six female F-NF pairs and three male ones. Although there is no clear evidence that clothing influences dolphins' perception of humans⁷⁴, the clothes of both F and NF humans were standardized and they were asked to wear the uniforms regularly worn by dolphins' caretakers. We thus made sure that the test situation was mimicking at best the usual situation where caretakers can stay standing immobile at the pool's edge, so that the possible discrimination of familiar humans had to rely on the humans' proper characteristics^{75,76}. Each familiar and non-familiar human member of a pair was tested at the same time and location around the pool but on different days (Supplementary Fig. 1). The tests were conducted in different locations for the different F-NF human pairs around the 4 pools that did not exactly correspond to places where trainers usually fed them (and at other precise times of day). This lowered the risks that dolphins would come in these precise locations as a result past conditioning. Each test lasted 10 min and, for the entire duration, only the human being tested and the experimenter were present at the poolside. Tests were video recorded (JVC quadproof everio R camera, fixed on a tripod at 2 m from the human being tested) as well as the comments of the experimenter who was continuously observing the ongoing activities of dolphins, and listening to the acoustic signals produced (i.e. whistles and clicks, underwater or in air). The occasions (44%) in which it was not possible to assign with certainty a recorded sound with an individual caller were not included in the statistical analysis (e.g. when two dolphins were there with the heads under water). Each test began with the human participants positioning themselves at 1 m from the pool's edge, with the experimenter standing about 2 m behind, as in other studies^{72,74,76}. Throughout the test, the human participant was asked to face the pool, remain stationary at the position and maintain a neutral behaviour (e.g. arms alongside the body, no gestures, sounds, movements or gazes towards the dolphins) (e.g. motionless human⁷⁴). Dolphins had permanent access to the four pools and were free to approach or remain away from the human during the entire duration of the test.

Data analysis

Data were analyzed by a single experimenter (A.G.) using focal continuous sampling on Pot Player software. All dolphin behaviours, whether locomotor (e.g. type of swimming), solitary (e.g. solitary play), vocal (e.g. production of whistles and clicks, Jones et al., 2020) or human-directed (e.g. tossing water or objects, pass swimming), as well as attentional behaviours (e.g. gazes) and visual laterality were recorded (Table S1 for details). Two types of visual attention towards humans were distinguished: glances (less than 1 s.) and prolonged gazes (> 1 s.) as several studies have shown that they may have a different significance⁵⁹. Also, three play situations were distinguished: play around human (i.e. playing with the object in the testing area of 1.5 m radius around the human), human-oriented play (i.e. playing with the object with the dolphin's rostrum oriented towards the human), and other types of play (i.e. passing with object in mouth or playing while passing). For vocalizations, we specified whether or not the dolphin was oriented towards the human while producing the sound. Visual laterality and its strength were measured, considering 1) the number of monocular and binocular glances and gazes (as well as the duration of gazes, measured in sec), distinguishing further between right and left eye use;²⁾ in order to assess the strength of the laterality, the absolute Laterality Index (LI) was calculated: $\left| \frac{\text{left-right}}{\text{left+right}} \right|$ (as in^{77,78}). The visual field of dolphins is 120–130° with the two eyes overlapping only 20–30°⁶⁷ and therefore their binocular vision extends in front and just below the head. Based on this characteristic, we considered that the dolphins showed binocular visual attention when their head was facing the human, as it is the only case when

the two eyes can be seen at once and monocular visual attention when only one eye was visible from the human position⁷⁹.

Only the behaviours performed within a 1.5-m radius around the pool edge closest to the human stimulus were considered for the analyses (Supplementary Fig. 2). The unit of measurements considered were all counts, except for the duration of dolphin presence around the human (minutes), gaze duration (seconds) and a ratio for LI.

Dolphins could avoid the area around the human, just pass it, or stop and exhibit various types of behaviours (human-directed or not). Dolphins came mostly alone (98%) but when 2 or more dolphins were simultaneously present in the 1.5-m radius around the humans, each of them was considered and its behaviours analyzed.

Statistical analyses

Given the type (non-normal) of data and small sample size, non-parametric statistics were used. Spearman correlation tests were calculated to investigate possible relationships between vocal production and play behaviours in the delimited area, as well as between the Laterality Index and the visual attention in the two human conditions. Wilcoxon matched-sample tests were used to compare the mean duration of dolphins' presence with familiar and unfamiliar humans, as well as the use of right or left eye to glance at the humans. Mann–Whitney tests for independent samples were used to compare group of dolphins (those which emitted clicks and those which did not) in terms of both rate of play related to human presence and rate of other types of play.

Statistical analyses were conducted on R software (R studio version 1.4.11, R Core Team 2019).

Results

All dolphins came at least once (total number of visits per dolphin during the study, 3.94 ± 1.34) in the delimited area around the human and stayed in the area for variable durations (total time spent in the area 5.45 ± 5.34 min, mean durations of visits/individual: 2.58 ± 0.19 min) When they were in the area, dolphins exhibited a variety of behaviours, including pass swimming (with glances towards the human: mean number 5.77 ± 6.27 per dolphin, or without glances towards the human: mean number 13.88 ± 10.57 per dolphin), gazes (mean number 1.94 ± 2.18), plays with an object (while pass swimming, around or oriented toward the human, mean number of plays 3.72 ± 4.46), and/or vocalizing (mean number of clicks: 2.11 ± 2.42 ; mean number of whistles: 2.22 ± 2.06). Apart from whistles and clicks, no other vocalization (such as burst pulses) was recorded. All glances were monocular whereas gazes could be monocular or binocular. Gazes were rare (6 out of the 9 dolphins gazed at the human and only 1 to 6 times). Dolphins mostly arrived and stayed alone in the area during the tests. The only category of intraspecies social behaviours observed in testing area were affiliative ones that occurred in 3.53% of the cases and involved a maximum of three dolphins (i.e. swimming in contact, synchronous swimming and breathing).

Experience dependent responses

Experience in the facility influenced dolphins' behaviours during the tests: the longer the time dolphins had spent in the facility, the more they played around humans in general ($r=0.71$, $p=0.03$) and vocalized while oriented towards them (Spearman, $r=0.72$, $p=0.007$) (Fig. 1a). Vocal emissions mainly consisted in whistling (whistles: $r=0.79$, $p=0.01$; clicks: $r=0.61$, $p=0.07$). Vocal production seemed highly related to the interest for humans as it was correlated with object play around the human ($r=0.68$, $p=0.04$), whether clicks ($r=0.85$, $p=0.003$) or whistles ($r=0.84$, $p=0.001$) were emitted (Fig. 1b). This was especially the case for human-oriented play ($r=0.85$, $p=0.003$), although mostly for whistles then (whistles: $r=0.70$, $p=0.03$, clicks: $r=0.54$, $p=0.13$). Click production was nevertheless mostly associated with play in human presence and not just object play overall as dolphins that produced clicks played more around humans than those that did not produce clicks (Mann–Whitney, $n_1=5$, $n_2=4$, $W=1$, $p=0.03$), which was not the case for the other types of play (i.e. passing with object in mouth or playing while passing, $n_1=5$, $n_2=4$, $W=3$, $p=0.056$) (Fig. 1c).

Effects of familiarity

There were also differences according to familiarity with the human tested, although not so much in terms of the behaviours recorded than in terms of attention. First of all, the dolphins stayed longer in the test area for the familiar than the unfamiliar human (Wilcoxon, $W=33$, $p=0.04$) (Fig. 2a). When the human was familiar, there was also a negative correlation between the degree of visual monitoring (ratio between the number of pass swimming with/without glances) and visual laterality (Laterality index of glances), whereas this was not the case for unfamiliar humans (F: $r=-0.65$, $p=0.05$; NF: $r=-0.39$, $p=0.52$). However, this correlation was strongly influenced by one individual and should therefore be considered with caution (Fig. 2b). Furthermore, only in the tests with familiar humans, dolphins showed a preferential use of the right eye over the left eye during glances towards the human being tested (F: $W=36$, $p=0.01$; NF: $W=14.5$, $p=1$) (Fig. 3). It appeared that familiarity influenced both the strength and direction of visual lateralized responses towards humans. Indeed, no specific lateralized pattern of behavioural or attentional responses was found in the presence of unfamiliar humans.

Discussion

The findings of this study reveal intriguing patterns of behaviours and perceptual laterality in relation to cognitive processing of dolphins while facing different humans. This study reveals that when attention structure is taken into account, dolphins appear to use more short glances than focused longer gazes to visually explore humans. In this free-swimming experiment, whereas all dolphins came around the passive human during the tests, the results show that the dolphins with the longest experience in the study facility were those most playful and vocal in the presence of humans, regardless of the degree of familiarity. However, dolphins clearly distinguished

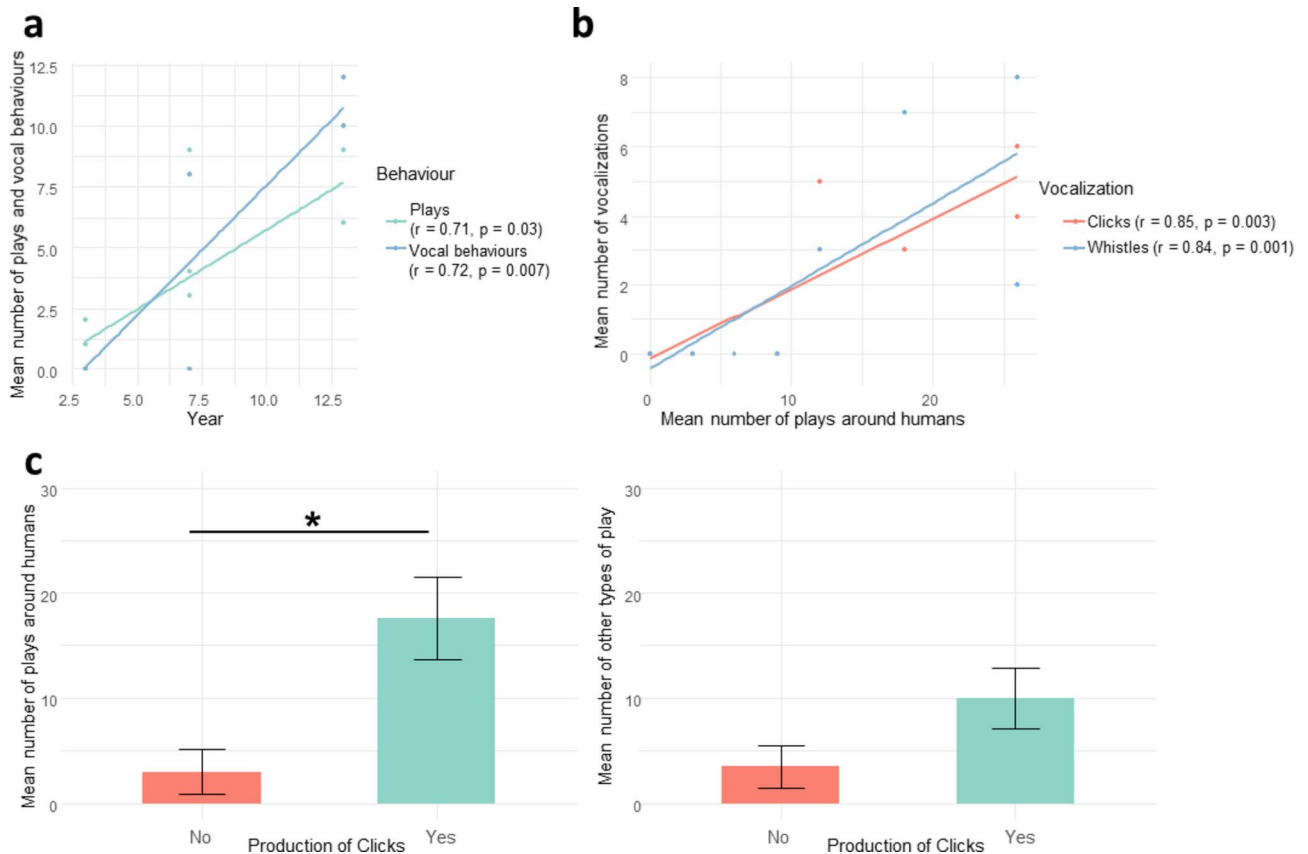


Fig. 1. (a) Impact of the experience in the study facility on dolphins' behaviours, in presence of a stationary human: Scatter plot (Mean \pm S.D.) showing the correlation (Spearman tests) between the occurrences of play behaviours (green) and vocal (blue) behaviours depending on the time (in years) spent in the facility. (b) Scatter plot (Mean \pm S.D.) showing the correlation (Spearman tests) between clicks (red) and whistles (blue) while playing around humans. (c) Bar plot (Mean \pm S.D.) showing that only for play around humans (left part of the plot) and not for other types of play (right part of the plot), dolphins that produced clicks played significantly more than those that did not produce clicks (Mann–Whitney tests, * $p < 0.05$).

familiar and unfamiliar humans, staying longer around when the human was familiar. They also showed a clear right eye preference when glancing at the familiar human but not an unfamiliar human.

Experience dependent behaviours

These dolphins appeared therefore to be interested in humans overall. They played with objects and vocalized in their presence, in line with previous descriptions in the literature⁸⁰. Vocal behaviours included only clicks and whistles, whereas no burst pulse was recorded. Clicks were often produced while playing. This could just reflect object-play. However, there is also evidence that clicks can be used during affiliative interactions with conspecifics⁸¹, thus another hypothesis is that their use during the human motionless test might also constitute potential affiliative interactions with humans. The fact that clicks were associated with plays around humans and not when just passing with an object suggests that the latter explanation is more likely. Whistles were used more when the dolphins were oriented towards the humans, during or outside play sequences, as if “calling to them”. Dolphins are sensitive to certain human attentional cues (e.g. gaze direction) and adjust their response accordingly⁸². Here, the humans did not orient their attention towards the dolphins which may have triggered some vocal responses. Probert et al.⁸³ showed that the presence of trainers in the vicinity, or just the anticipation of their presence (e.g. close to the moment of public presentation)⁸⁴, were associated with increased whistles' rates in captive bottlenose dolphins as possible attention-getting or anticipatory behaviours prior to potential interactions. For example, Salmi et al.⁸⁵ have demonstrated that gorillas could produce a totally new vocalization (*Gorilla gorilla gorilla*) to catch the attention of their keepers. In the present case, although training for public presentations was not taking place anymore in the facility, the dolphins had previously been trained in this or another facility to perform behaviours on request, that currently included “special types” of loud vocalizations on command, one other hypothesis could be that they may have associated that producing some loud sounds may be rewarding. Another aspect is that the longer the animals had been in the facility, the more they were playful and vocal around humans overall. The daily interactions with humans in this facility at the time of the experiment were overall calm and positive with unfamiliar visitors just walking quietly around and caretakers feeding them through positive reinforcement training sessions. It is therefore likely that caretakers were

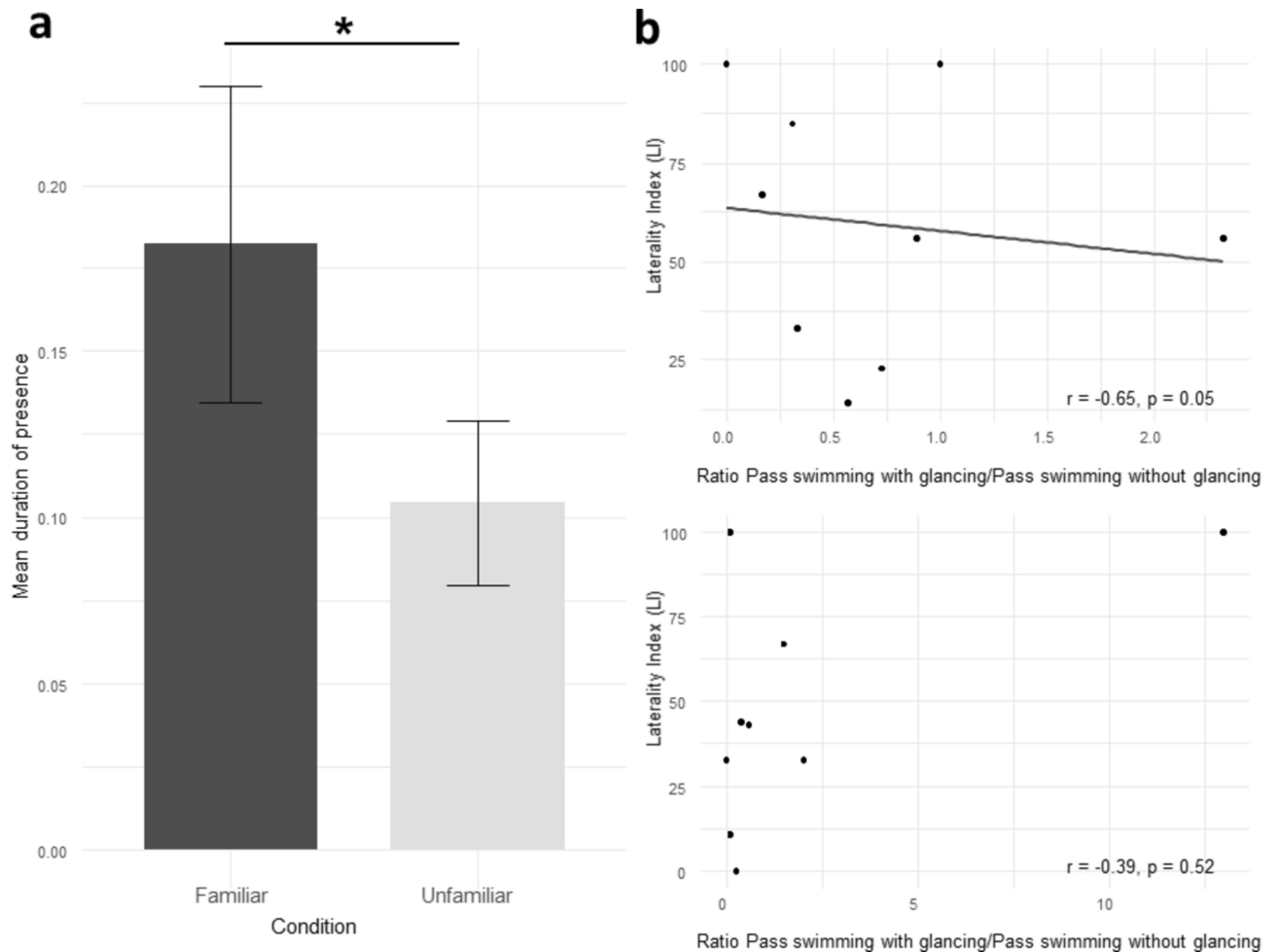


Fig. 2. Effects of familiarity on Visual attention and laterality: **(a)** Bar plot (Mean \pm S.D.) showing the duration of dolphins' presence in the area around the human during the tests according to whether the human is familiar (black) or unfamiliar (grey) (Wilcoxon test: $*p < 0.05$). **(b)** Scatter plot (Mean \pm S.D.) showing the negative correlation between the strength of laterality (Lateralization Index) and the proportion of pass swimming including glances/pass swimming without glancing towards Familiar humans (black) and the absence of correlation for Unfamiliar humans (grey): the more the dolphins monitor visually the familiar human, the less they are lateralized (Spearman correlation test $*, p = 0.05$). It is worth noting though that individual variations were high, even for the familiar human.

associated with positive memories and that dolphins may have generalized this valence to unfamiliar humans, as commonly observed in human-animal relationships^{28,29,32,86,87}. For example, horses trained with positive reinforcement respond positively to the presence of unfamiliar humans in general, but still more so in presence of their familiar trainer, even when tested 6 months later²⁵. Thus, generalization does not prevent a differential memory of familiar and unfamiliar humans, which may also explain the differences of responses observed here according to human familiarity.

Visual attention structure and laterality

Contrarily to Thielges et al.⁷², we did not find any difference in terms of gaze duration. Hill et al.⁷⁴, in their study in three species of cetaceans, found that gaze duration had a limited sensitivity to assess discrimination of humans in a free swim situation. Actually, we found that gazes were rare and that the dolphins were mostly monitoring the humans using short (< 1 s.) glances that were always monocular. Dolphins have limited binocular vision and may therefore prefer to use monocular vision for visual exploration^{88,89}. Earlier studies looking at attention structure (i.e. glances *versus* gazes), have shown in other species with lateral (e.g. starlings⁹⁰) or frontal (e.g. monkeys³) eye positions that it may reflect different attentional states. In the context of human-animal relationships, the preferred type of attention (gazes *vs.* glances) depends on the species and human type¹ involved. In a recent study, it was hypothesized that glances would be more related to exploration behaviours or even curiosity whereas gazes would reflect a more focused attention⁵⁹. Interestingly, in this study where dolphins were presented with species-specific versus non-biological stimuli, the strength of laterality was negatively correlated with this "curiosity" (number of glances), as was also the case in the study of Lilly et al.⁹¹. Also, it has

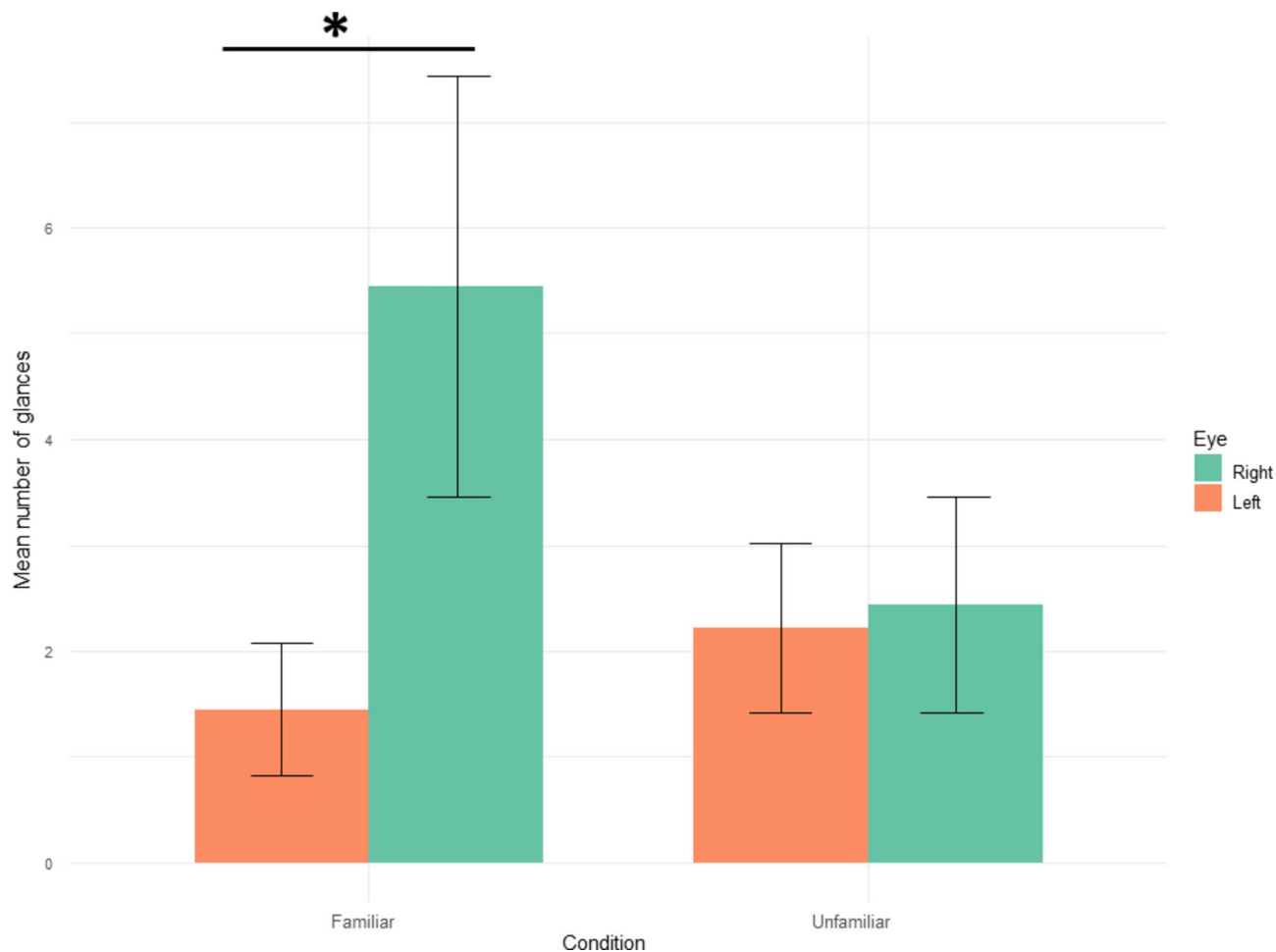


Fig. 3. Bar plot (Mean \pm S.D.) showing the use of right and left eye respectively when glancing at Familiar and Unfamiliar humans (right eye: green; left eye: orange) (Wilcoxon tests: * $p < 0.05$).

been found in wild orcas that the more explorative male orcas showed a lower laterality when confronted by a human in the wild than the more distant and focused female orcas⁹². In line with the assumption of glances being associated with exploration/curiosity⁶⁷, we also found that the visual laterality strength decreased with the proportion of pass swimming associated with glances, but only when performed close to familiar humans, thus suggesting that the more they explored visually the familiar human, maybe expecting actions from him/her, the less they were lateralized. This result would deserve further consideration though, given our low sample and individual variations.

Familiarity and visual laterality

Our study dolphins clearly discriminated familiar and unfamiliar humans, confirming earlier findings in bottlenose dolphins and other cetaceans^{72–74}. Also, they stayed longer around when the human was familiar. Earlier studies have suggested that such a difference can be explained in light of the relationship developed between the dolphins and their trainers that leads to high levels of willingness to interact⁶⁶. Our results on visual attention and familiarity however differs largely from those reported in previous studies. We found a right eye preference for the familiar human and no side preference for the unfamiliar one, contrarily to earlier studies which found a left-eye preference for both familiar and unfamiliar humans⁷² or no eye preference for either⁷⁴. This lateralized response to the presence of familiar humans may be due to dolphins' higher interest for known caretakers, in line with evidence showing that attention promotes laterality^{57,59,93}. Methodological differences can be responsible and explain some of the discrepancies between studies with humans as stimuli. Thielges et al.⁷² and Hill et al.⁷⁴ used a procedure where the person arrived from behind curtains that were hung for the experiment on the pool side. This is an unusual situation in terms of human-dolphin interactions, as dolphins are sensitive to movements⁷⁴ and the appearance of a human opening a curtain is probably different for them from a human standing passive at the poolside. In fact, in Hill et al.'s study⁷⁴ it appeared that the dolphins had the same duration of visual attention for familiar, unfamiliar humans and the sole apparatus and looked with their left eye at the apparatus when the human was not present. The experimental setup using the opening of curtains to show the human can therefore represent a novel situation for the dolphins and so the left eye bias for both categories of humans, especially for the unfamiliar human, could be explained by the predominant

involvement of RH in processing novel events more than the human recognition *per se*^{94–96}. In the present study we used a usual situation for dolphins because, when not involved in training sessions, one or more trainers stay at the poolside and monitor dolphins' behaviours and/or visitors' passages (close to the poolside). The valence hypothesis on the other hand, suggests that LH would proceed preferentially positive emotions and RH negative emotions^{52,96,97}. In the present case, dolphins had either mostly positive interactions with familiar caretakers. They may therefore have perceived their presence as a positive stimulus that they explored using their right eye (i.e. process with the left hemisphere). This would also explain why they showed no visual laterality for unfamiliar humans which may be “neutral” stimuli in terms of valence.

Further studies also showed patterns of visual lateralization in dolphins according to familiarity when attending non-human stimuli. Some of these findings were opposite to those found here: Blois-Heulin et al.⁷⁰ found that dolphins used their left eye when viewing familiar objects and the right eye for unfamiliar ones while. Siniscalchi et al.⁵⁶ found that wild striped dolphins had a higher use of right eye for unfamiliar items floating at sea. Moreover, Hausberger et al.⁵⁹ found that dolphins used more their right eye when presented with a non-biological visual stimulus and their left eye when presented with 2D images of unfamiliar conspecifics (see also⁹⁸). It is possible that dolphins process familiarity differently according to the types of stimuli (objects, conspecifics, humans, see also^{99,100}). Different studies have also reported that dolphins are more successful in visual pattern discrimination when using their right eye^{101–104}, as documented also in birds and other mammals including humans^{105–107}. This whole set of data suggests that perceptual hemispheric specialization in dolphins might be best explained by the attention getting properties of the stimulus attended^{51,57}.

Limitations

Some limitations of this study include sample size and a resulting non-normal distribution and a control in which dolphin baseline behavior was measured without the presence of humans of any familiarity. The sample size and non-normal distribution necessitated the use of non-parametric analyses. However, the findings of the study remain valid and comparable to other studies. Although baseline behavior in the absence of humans would strengthen the results of this study, the findings remain valid as the tests were conducted at a variety of locations around the pool that included areas that were not typically associated with training or trainers. Finally, the use of naive coders could strengthen the coding of the subtle differences in visual attention by offering greater reliability in the assessment of visual gazes versus glances.

Conclusion

The findings of the present study provide new insights on how experience can have a role on dolphins' behavioural patterns when interspecies interactions regularly occur (i.e. in human care settings). Finally, the familiarity with the stimulus had a role in determining the pattern of their visual attention structure thus providing new understandings on dolphins' cognitive processing of a stimulus.

Data availability

Raw data underlying the findings of this article will be made available by the authors on request.

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References

- Grandgeorge, M., Gautier, Y., Bourreau, Y., Mossu, H. & Hausberger, M. Visual attention patterns differ in dog vs. cat interactions with children with typical development or autism spectrum disorders. *Front. Psychol.* **11**, 2047 (2020).
- Scheid, C., Range, F. & Bugnyar, T. When, what, and whom to watch? Quantifying attention in ravens (*Corvus corax*) and jackdaws (*Corvus monedula*). *J. Comp. Psychol.* **121**, 380–386 (2007).
- Blois-Heulin, C. Variability in social visual attention in the red-capped mangabey (*Cercocebus torquatus torquatus*) and the grey-cheeked mangabey (*Cercocebus albigena albigena*). *Folia Primatologica* **70**, 264 (1999).
- Taylor, J. G. & Fragopanagos, N. F. The interaction of attention and emotion. *Neural Netw.* **18**, 353–369 (2005).
- Micheletta, J. & Waller, B. M. Friendship affects gaze following in a tolerant species of macaque, *Macaca nigra*. *Anim. Behav.* **83**, 459–467 (2012).
- Revelle, W. & Loftus, D. A. The implications of arousal effects for the study of affect and memory. In *The Handbook of Emotion and Memory* (Psychology Press, 1992).
- Cousillas, H. et al. Social experience influences the development of a central auditory area. *Naturwissenschaften* **93**, 588–596 (2006).
- Cousillas, H., George, I., Henry, L., Richard, J.-P. & Hausberger, M. Linking social and vocal brains: could social segregation prevent a proper development of a central auditory area in a female songbird?. *PLoS ONE* **3**, e2194 (2008).
- Bertin, E. & Striano, T. The still-face response in newborn, 1.5-, and 3-month-old infants. *Infant Behav. Dev.* **29**, 294–297 (2006).
- Hinde, R. A. *Towards Understanding Relationships* (Academic Press, 1979).
- Hemsworth, P. H. Human–animal interactions in livestock production. *Appl. Anim. Behav. Sci.* **81**, 185–198 (2003).
- Hausberger, M., Roche, H., Henry, S. & Visser, E. K. A review of the human–horse relationship. *Appl. Anim. Behav. Sci.* **109**, 1–24 (2008).
- Hausberger, M. et al. Mutual interactions between cognition and welfare: The horse as an animal model. *Neurosci. Biobehav. Rev.* **107**, 540–559 (2019).
- Hosey, G. A preliminary model of human–animal relationships in the zoo. *Appl. Anim. Behav. Sci.* **109**, 105–127 (2008).
- Waiblinger, S. et al. Assessing the human–animal relationship in farmed species: A critical review. *Appl. Anim. Behav. Sci.* **101**, 185–242 (2006).
- Russow, L.-M. Ethical implications of the human–animal bond in the laboratory. *ILAR J.* **43**, 33–37 (2002).
- Chang, F. T. & Hard, L. A. Human–animal bonds in the laboratory: how animal behavior affects the perspective of caregivers. *ILAR J.* **43**, 10–18 (2002).
- Kreger, M. D. & Mench, J. A. Visitor–animal interactions at the zoo. *Anthrozoös* **8**, 143–158 (1995).

19. Cassini, M. H. Behavioural responses of South American fur seals to approach by tourists—a brief report. *Appl. Anim. Behav. Sci.* **71**, 341–346 (2001).
20. Proops, L., McComb, K. & Reby, D. Cross-modal individual recognition in domestic horses (*Equus caballus*). *Proc. Natl. Acad. Sci.* **106**, 947–951 (2009).
21. Pedersen, L. J., Damm, B. I. & Kongsted, A. G. The influence of adverse or gentle handling procedures on sexual behaviour in fearful and confident sows. *Appl. Anim. Behav. Sci.* **83**, 277–290 (2003).
22. Brajon, S. et al. Persistency of the piglet's reactivity to the handler following a previous positive or negative experience. *Appl. Anim. Behav. Sci.* **162**, 9–19 (2015).
23. Breuer, K., Hemsworth, P. H., Barnett, J. L., Matthews, L. R. & Coleman, G. J. Behavioural response to humans and the productivity of commercial dairy cows. *Appl. Anim. Behav. Sci.* **66**, 273–288 (2000).
24. Waiblinger, S., Menke, C. & Fölsch, D. W. Influences on the avoidance and approach behaviour of dairy cows towards humans on 35 farms. *Appl. Anim. Behav. Sci.* **84**, 23–39 (2003).
25. Sankey, C., Richard-Yris, M.-A., Leroy, H., Henry, S. & Hausberger, M. Positive interactions lead to lasting positive memories in horses, *Equus caballus*. *Anim. Behav.* **79**, 869–875 (2010).
26. Rault, J.-L., Waiblinger, S., Boivin, X. & Hemsworth, P. The power of a positive human-animal relationship for animal welfare. *Front. Vet. Sci.* <https://doi.org/10.3389/fvets.2020.590867> (2020).
27. d'Ingeo, S. et al. Horses associate individual human voices with the valence of past interactions: a behavioural and electrophysiological study. *Sci. Rep.* **9**, 11568 (2019).
28. Hausberger, M. & Muller, C. A brief note on some possible factors involved in the reactions of horses to humans. *Appl. Anim. Behav. Sci.* **76**, 339–344 (2002).
29. Fureix, C., Jegou, P., Sankey, C. & Hausberger, M. How horses (*Equus caballus*) see the world: humans as significant “objects”. *Anim. Cogn.* **12**, 643–654 (2009).
30. Sankey, C. et al. Reinforcement as a mediator of the perception of humans by horses (*Equus caballus*). *Anim. Cogn.* **13**, 753–764 (2010).
31. Krueger, K. Behaviour of horses in the “round pen technique”. *Appl. Anim. Behav. Sci.* **104**, 162–170 (2007).
32. Tallet, C. et al. Behavioural and physiological reactions of piglets to gentle tactile interactions vary according to their previous experience with humans. *Livest. Sci.* **167**, 331–341 (2014).
33. Minier, D. E. et al. Human-directed contra-aggression training using positive reinforcement with single and multiple trainers for indoor-housed rhesus macaques. *Appl. Anim. Behav. Sci.* **132**, 178–186 (2011).
34. Mongillo, P., Bono, G., Regolin, L. & Marinelli, L. Selective attention to humans in companion dogs, *Canis familiaris*. *Anim. Behav.* **80**, 1057–1063 (2010).
35. McCune, S. The impact of paternity and early socialisation on the development of cats' behaviour to people and novel objects. *Appl. Anim. Behav. Sci.* **45**, 109–124 (1995).
36. Boivin, X., Nowak, R., Després, G., Tournadre, H. & Le Neindre, P. Discrimination between shepherds by lambs reared under artificial conditions. *J. Anim. Sci.* **75**, 2892–2898 (1997).
37. Tallet, C., Rakotomahandry, M., Guérin, C., Lemasson, A. & Hausberger, M. Postnatal auditory preferences in piglets differ according to maternal emotional experience with the same sounds during gestation. *Sci. Rep.* **6**, 37238 (2016).
38. Munksgaard, L., de Passillé, A. M., Rushen, J. & Ladewig, J. Dairy cows' use of colour cues to discriminate between people. *Appl. Anim. Behav. Sci.* **65**, 1–11 (1999).
39. Stone, S. M. Human facial discrimination in horses: can they tell us apart?. *Anim. Cogn.* **13**, 51–61 (2010).
40. Sankey, C., Henry, S., André, N., Richard-Yris, M.-A. & Hausberger, M. Do horses have a concept of person?. *PLoS ONE* **6**, e18331 (2011).
41. Adachi, I., Kuwahata, H. & Fujita, K. Dogs recall their owner's face upon hearing the owner's voice. *Anim. Cogn.* **10**, 17–21 (2007).
42. Lampe, J. F. & Andre, J. Cross-modal recognition of human individuals in domestic horses (*Equus caballus*). *Anim. Cogn.* **15**, 623–630 (2012).
43. Smith, J. J. Human-animal relationships in zoo-housed orangutans (*P. abelii*) and gorillas (*G. g. gorilla*): The effects of familiarity. *Am. J. Primatol.* **76**, 942–955 (2014).
44. Leinwand, J. G., Fidino, M., Ross, S. R. & Hopper, L. M. Familiarity mediates apes' attentional biases toward human faces. *Proc. R. Soc. B Biol. Sci.* **289**, 20212599 (2022).
45. Xitco, M. J., Gory, J. D. & Kuczaj, S. A. Spontaneous pointing by bottlenose dolphins (*Tursiops truncatus*). *Anim. Cogn.* **4**, 115–123 (2001).
46. Li, L.-L., He, R., Pansini, R. & Quan, R.-C. Prolonged proximity to humans ensures better performance of semi-captive Asian elephants at discriminating between human individuals by voice. *Front. Ecol. Evol.* **10**, 963052 (2022).
47. Leroux, M., Hetem, R. S., Hausberger, M. & Lemasson, A. Cheetahs discriminate familiar and unfamiliar human voices. *Sci. Rep.* **8**, 15516 (2018).
48. Gammino, B., Palacios, V., Root-Gutteridge, H., Reby, D. & Gamba, M. Grey wolves (*Canis lupus*) discriminate between familiar and unfamiliar human voices. *Anim. Cogn.* **26**, 1589–1600 (2023).
49. Horn, L. et al. Domestic dogs (*Canis familiaris*) flexibly adjust their human-directed behavior to the actions of their human partners in a problem situation. *Anim. Cogn.* **15**, 57–71 (2012).
50. Rochais, C. et al. Visual attention, an indicator of human-animal relationships? A study of domestic horses (*Equus caballus*). *Front. Psychol.* **5**, 108 (2014).
51. Rogers, L. J. & Andrew, R. *Comparative Vertebrate Lateralization* (Cambridge University Press, 2002).
52. Rogers, L. J. Relevance of brain and behavioural lateralization to animal welfare. *Appl. Anim. Behav. Sci.* **127**, 1–11 (2010).
53. Davidson, R. J. Cerebral asymmetry and emotion: Conceptual and methodological conundrums. *Cogn. Emot.* **7**, 115–138 (1993).
54. Andrew, R. J. The differential roles of right and left sides of the brain in memory formation. *Behav. Brain Res.* **98**, 289–295 (1999).
55. Vallortigara, G. & Andrew, R. J. Differential involvement of right and left hemisphere in individual recognition in the domestic chick. *Behav. Processes* **33**, 41–57 (1994).
56. Siniscalchi, M., Dimatteo, S., Pepe, A. M., Sasso, R. & Quaranta, A. Visual lateralization in wild striped dolphins (*Stenella coeruleoalba*) in response to stimuli with different degrees of familiarity. *PLoS ONE* **7**, e30001 (2012).
57. Hausberger, M. et al. A crucial role of attention in lateralisation of sound processing?. *Symmetry* **11**, 48 (2019).
58. Ghazanfar, A. A., Smith-Rohrberg, D. & Hauser, M. D. The role of temporal cues in rhesus monkey vocal recognition: orienting asymmetries to reversed calls. *Brain. Behav. Evol.* **58**, 163–172 (2002).
59. Hausberger, M. et al. When perceptual laterality vanishes with curiosity: A study in dolphins and starlings. *Laterality* **26**, 238–259 (2021).
60. Basile, M. et al. Socially dependent auditory laterality in domestic horses (*Equus caballus*). *Anim. Cogn.* **12**, 611–619 (2009).
61. Tomonaga, M. & Uwano, Y. Bottlenose dolphins' (*Tursiops truncatus*) theory of mind as demonstrated by responses to their trainers' attentional states. *Int. J. Comp. Psychol.* <https://doi.org/10.46867/IJCP.2010.23.03.03> (2010).
62. Tomonaga, M., Uwano, Y. & Saito, T. How dolphins see the world: A comparison with chimpanzees and humans. *Sci. Rep.* **4**, 3717 (2014).
63. Xitco, M. J., Gory, J. D. & Kuczaj, S. A. Dolphin pointing is linked to the attentional behavior of a receiver. *Anim. Cogn.* **7**, 231–238 (2004).

64. Trone, M., Kuczaj, S. & Solangi, M. Does participation in Dolphin–Human Interaction Programs affect bottlenose dolphin behaviour?. *Appl. Anim. Behav. Sci.* **93**, 363–374 (2005).
65. Frohoff, T. G. & Packard, J. M. Human interactions with free-ranging and captive bottlenose dolphins. *Anthrozoös* **8**, 44–53 (1995).
66. Platto, S. & Serres, A. A quantitative assessment of trainers–dolphins’ interactions in the absence of food reward. *Animals* **13**, 1651 (2023).
67. Mass, A. M. & Supin, A. Y. Adaptive features of aquatic mammals’ eye. *Anat. Rec.* **290**, 701–715 (2007).
68. Rivamonte, L. A. Bottlenose dolphin (*Tursiops truncatus*) double-slit pupil asymmetries enhance vision. *Aquat. Mamm.* **35**, 269–280 (2009).
69. Morgane, P. J., Jacobs, M. S. & Galaburda, A. Evolutionary morphology of the dolphin brain. In *Dolphin Cognition and Behavior* (Psychology Press, 1986).
70. Blois-Heulin, C. et al. Visual laterality in dolphins: importance of the familiarity of stimuli. *BMC Neurosci.* **13**, 1–8 (2012).
71. Yeater, D. B. et al. Do belugas (*Delphinapterus leucas*), bottlenose dolphins (*Tursiops truncatus*), & pacific white-sided dolphins (*Lagenorhynchus obliquidens*) display lateralized processing when presented with familiar or novel objects?. *Int. J. Comp. Psychol.* <https://doi.org/10.46867/ijcp.2017.30.00.02> (2017).
72. Thielges, H., Lemasson, A., Kuczaj, S., Böye, M. & Blois-Heulin, C. Visual laterality in dolphins when looking at (un)familiar humans. *Anim. Cogn.* **14**, 303–308 (2011).
73. Yeater, D. B., Hill, H. M., Baus, N., Farnell, H. & Kuczaj, S. A. Visual laterality in belugas (*Delphinapterus leucas*) and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) when viewing familiar and unfamiliar humans. *Anim. Cogn.* **17**, 1245–1259 (2014).
74. Hill, H. M. et al. Responses to familiar and unfamiliar humans by belugas (*Delphinapterus leucas*), bottlenose dolphins (*Tursiops truncatus*), pacific white-sided dolphins (*Lagenorhynchus obliquidens*): a replication and extension. *Int. J. Comp. Psychol.* <https://doi.org/10.46867/ijcp.2016.29.00.09> (2016).
75. Murayama, T., Usui, A., Takeda, E., Kato, K. & Maejima, K. Relative size discrimination and perception of the ebbinghaus illusion in a bottlenose dolphin (*Tursiops truncatus*). *Aquatic Mammals EBSCOhost*. vol. **38** 333 <https://openurl.ebsco.com/contentitem/10.1578%2FAM.38.4.2012.333?sid=ebsco:plink:crawler&id=ebsco:10.1578%2FAM.38.4.2012.333> (2012).
76. Tomonaga, M. et al. Which person is my trainer? Spontaneous visual discrimination of human individuals by bottlenose dolphins (*Tursiops truncatus*). *SpringerPlus* **4**, 1–7 (2015).
77. Bisazza, A., Facchin, L., Pignatti, R. & Vallortigara, G. Lateralization of detour behaviour in poeciliid fish: The effect of species, gender and sexual motivation. *Behav. Brain Res.* **91**, 157–164 (1998).
78. Cousillas, H., Henry, L., George, I., Marchesseau, S. & Hausberger, M. Lateralization of social signal brain processing correlates with the degree of social integration in a songbird. *Sci. Rep.* **10**, 14093 (2020).
79. Johnson, C. M., Ruiz-Mendoza, C. & Schoenbeck, C. Conspecific ‘gaze following’ in bottlenose dolphins. *Anim. Cogn.* **25**, 1219–1229 (2022).
80. Miller, L. J., Mellen, J., Greer, T. & Ii, S. K. The effects of education programmes on Atlantic bottlenose dolphin (*Tursiops truncatus*) behaviour. *Anim. Welf.* **20**, 159–172 (2011).
81. Gallo, A. et al. Study of repertoire use reveals unexpected context-dependent vocalizations in bottlenose dolphins (*Tursiops truncatus*). *Sci. Nat.* **110**(6), 56 (2023).
82. Davies, J. R. & Garcia-Pelegrin, E. Bottlenose dolphins are sensitive to human attentional features, including eye functionality. *Sci. Rep.* **13**, 12565 (2023).
83. Probert, R. et al. Vocal correlates of arousal in bottlenose dolphins (*Tursiops* spp.) in human care. *PLoS One* **16**(9), e0250913 (2021).
84. Probert, R., James, B. S., Elwen, S. H. & Gridley, T. Vocal cues to assess arousal state of bottlenose dolphins (*Tursiops* spp.) involved in public presentations. *J. Zool. Bot. Gard.* **4**, 711–727 (2023).
85. Salmi, R., Szczupider, M. & Carrigan, J. A novel attention-getting vocalization in zoo-housed western gorillas. *PLoS ONE* **17**, e0271871 (2022).
86. Dairy calves’ discrimination of people based on previous handling | Journal of Animal Science | Oxford Academic. <https://academic.oup.com/jas/article-abstract/74/5/969/4639132>.
87. Baragli, P., Gazzano, A., Martelli, F. & Sighieri, C. How do horses appraise humans’ actions? A brief note over a practical way to assess stimulus perception. *J. Equine Vet. Sci.* **29**, 739–742 (2009).
88. Supin, A. Ya., Popov, V. V. & Mass, A. M. Vision in aquatic mammals. In *The Sensory Physiology of Aquatic Mammals* (eds. Supin, A. Y. et al.) 229–284 https://doi.org/10.1007/978-1-4615-1647-7_4 (Springer US, 2001).
89. Delfour, F. & Marten, K. Lateralized visual behavior in bottlenose dolphins (*Tursiops truncatus*) performing audio–visual tasks: The right visual field advantage. *Behav. Processes* **71**, 41–50 (2006).
90. Pougault, L. et al. Experimental tests for measuring individual attentional characteristics in songbirds. *Animals* **11**(8), 2233 (2021).
91. Lilley, M. K., de Vere, A. J. & Yeater, D. B. Laterality of eye use by bottlenose (*Tursiops truncatus*) and rough-toothed (*Steno bredanensis*) dolphins while viewing predictable and unpredictable stimuli. *Int. J. Comp. Psychol.* <https://doi.org/10.46867/ijcp.2020.33.03.01> (2020).
92. Chanvallon, S. et al. Spontaneous approaches of divers by free-ranging orcas (*Orcinus orca*): age- and sex-differences in exploratory behaviours and visual laterality. *Sci. Rep.* **7**, 10922 (2017).
93. Andrew, R. J. & Watkins, J. A. S. Evidence for cerebral lateralization from senses other than vision. In *Comparative Vertebrate Lateralization*, 365–382 (2002).
94. Zucca, P. & Sovrano, V. A. Animal lateralization and social recognition: Quails use their left visual hemifield when approaching a companion and their right visual hemifield when approaching a stranger. *Cortex* **44**, 13–20 (2008).
95. Rogers, L. J. Brain lateralization and cognitive capacity. *Animals* **11**, 1996 (2021).
96. MacNeilage, P. F., Rogers, L. J. & Vallortigara, G. Origins of the left & right brain. *Sci. Am.* **301**(1), 60–67 (2009).
97. Crow, T. J. the cerebral torque and directional asymmetry for hand use are correlates of the capacity for language in homo sapiens. *Behav. Brain Sci.* **28**, 595–596 (2005).
98. Sakai, M., Hishii, T., Takeda, S. & Kohshima, S. Laterality of flipper rubbing behaviour in wild bottlenose dolphins (*Tursiops aduncus*): Caused by asymmetry of eye use?. *Behav. Brain Res.* **170**, 204–210 (2006).
99. Peirce, J. W., Leigh, A. E., daCosta, A. P. C. & Kendrick, K. M. Human face recognition in sheep: lack of configurational coding and right hemisphere advantage. *Behav. Processes* **55**, 13–26 (2001).
100. Guo, K., Meints, K., Hall, C., Hall, S. & Mills, D. Left gaze bias in humans, rhesus monkeys and domestic dogs. *Anim. Cogn.* **12**, 409–418 (2009).
101. Von Fersen, L., Schall, U. & Güntürkün, O. Visual lateralization of pattern discrimination in the bottlenose dolphin (*Tursiops truncatus*). *Behav. Brain Res.* **107**, 177–181 (2000).
102. Yaman, S., Von Fersen, L., Dehnhardt, G. & Güntürkün, O. Visual lateralization in the bottlenose dolphin (*Tursiops truncatus*): evidence for a population asymmetry?. *Behav. Brain Res.* **142**, 109–114 (2003).
103. Kilian, A., Fersen, L. V. & Güntürkün, O. Left hemispheric advantage for numerical abilities in the bottlenose dolphin. *Behav. Processes* **68**, 179–184 (2005).
104. Kaplan, J. D., Goodrich, S. Y., Melillo-Sweeting, K. & Reiss, D. Behavioural laterality in foraging bottlenose dolphins (*Tursiops truncatus*). *R. Soc. Open Sci.* **6**, 190929 (2019).

105. Fink, G. R. et al. Neural mechanisms involved in the processing of global and local aspects of hierarchically organized visual stimuli. *Brain* **120**, 1779–1791 (1997).
106. Hopkins, W. D. Hemispheric specialization for local and global processing of hierarchical visual stimuli in chimpanzees (*Pan troglodytes*). *Neuropsychologia* **35**, 343–348 (1997).
107. Tommasi, L. & Vallortigara, G. Encoding of geometric and landmark information in the left and right hemispheres of the Avian Brain. *Behav. Neurosci.* **115**, 602–613 (2001).

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Author contributions

AG, MH and AL conceived the study; AG performed the experiments; AG, MH and AL conducted the statistical analyses and drafted the manuscript, RG and MB provided logistical support for the data collection. All the authors revised the final version of the manuscript and approved the submission.

Declarations

Ethical statement

Under current animal experimentation legislation in the countries involved in our study, no ethical clearance is required for purely observational research. In our case, the animals are observed without modification of their daily routine, without any attempt to engage with them, and without restriction of their movement. Furthermore, as the humans, who all took part in the study voluntarily with an informed consent obtained from all subjects, were only filmed from behind so that they cannot be identified and as no data was collected on them, our work does not fall under the European Union General Data Protection regulation for human rights to privacy.

Competing interests

The authors declare no competing interests.

Additional information

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