INTERNATIONAL JOURNAL OF COMPARATIVE PSYCHOLOGY

2021, 34
Heather M. Hill
Editor
Peer-reviewed

Understanding and Assessing Emotions in Marine Mammals Under Professional Care

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In the last 30 years, concerns about animal emotions have emerged from the general public but also from animal professionals and scientists. Animals are now considered as sentient beings, capable of experiencing emotions such as fear or pleasure. Understanding animals' emotions is complex and important if we want to guarantee them the best care, management, and welfare. The main objectives of the paper are, first, to give a brief overview of various and contemporary assessments of emotions in animals, then to focus on particular zoo animals, that is, marine mammals, since they have drawn a lot of attention lately in regards of their life under professional care. We discuss here 1 approach to monitor their emotions by examining their laterality to finally conclude the importance of understanding animal emotion from a holistic welfare approach.

Keywords: behavior, cetaceans, cognition, emotions, pinnipeds

In the three last decades, we have witnessed a growing interest in animal emotions coming from public concerns for animal welfare, welfare scientists, zoologists, neuroscientists, and animal professionals working in zoos for instance. To better overtake the ongoing debate on how to define "emotions", "feelings", "moods" and "affective states" (Paul & Mendl, 2018, we suggest reading the recent paper by Kremer et al. (2020) to have a synthetic overview of the field of animal emotion. Here, we use the term "emotions" to be defined as subjective feelings of an individual during a short period of time and, in a particular situation, associated with physical and behavioral changes (Destrez et al., 2013), and described by their positive or negative valence and intensity (Leliveld et al., 2013). Understanding others' emotions is always challenging and more so in nonhuman animals. In order to understand how emotions manifest themselves in other species, scientists use various approaches and indicators, such as implementing evaluations of emotions in contemporary animal welfare assessment. For instance, Webster (2005) triangulation principle involves three main categories of measures (i.e. physiology, behavior, and cognition) that are also the three components of animals' emotional responses (Désiré et al., 2002). The aim of the present paper is first to introduce various ways to assess emotions in animals. Then, since zoo animals and more particularly marine mammals' captivity and welfare are regularly questioned and since cognition is now included in animal welfare assessment, we provide information on studies assessing emotions on those animals under professional care. We also discuss one approach to evaluate emotions by examining laterality. We end by pointing out the importance of understanding animal emotion in the framework of animal welfare.

Assessing Emotions in Nonhuman Animals

Animals' Behavioral Postures

To assess and understand emotions in nonhuman animals, behavioral postures that might be analogous to facial expressions in humans are valuable for studies of emotion. For instance, sheep (*Ovis arie*) exposed to suddenness or unfamiliarity test stimuli will negative-contrast position their ears; in a neutral state, ears are horizontal, but they point backward in unfamiliar, unpleasant, and/or uncontrollable situations (fearful situations), whereas the ears point up in controllable negative situations; sheep display asymmetric postures in very sudden situations (Boissy et al., 2011). When looking at different stimuli in the presence of their owner, domestic dogs showed a right-sided bias in the amplitude of tail wagging, and when tested alone or in the

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https://doi.org/10.46867/ijcp.2021.34.00.01

presence of an unfamiliar conspecific, dogs showed a left-sided bias (Quaranta et al., 2007). In pigs, high-frequency lateral tail movement is linked to positive emotions, whereas long-lasting ear movement is linked to a decreased welfare (Rius et al., 2018). Facial expressions are also good indicators of animals' affective state; for instance, blue-and-yellow macaws (*Ara Ararauna*) blush and fluff facial feathers in some intraspecific social interactions and interspecific interactions with their caretakers (Bertin, Beraud, et al., 2018). Similar observations were conducted on Japanese quails (*Coturnix japonica*) showing that, in these birds, variation in crown feather height and pupil area could be indicators of positive emotions (Bertin, Cornilleau, et al., 2018). When being gently groomed, horses (*Equus caballus*) show a moderately raised neck, extended immobile or twitching upper lips, and backwards pointed ears (Lansade et al., 2018).

Vocal Productions

Associations between vocal production and emotions are particularly useful in social animals as they modulate social interactions, give information about each other's intentions, and predict potential behaviors (Briefer, 2012). For instance, in horses, a snort is associated with positive situations and positive affective state postures (ears in forward or sideways positions) and is thus considered a reliable indicator of positive emotions in this species (Stomp et al., 2018). Furthermore, dogs produce vocalizations with shorter durations, wider amplitude range, and smaller frequency modulations in positive (play) contexts than in negative contexts (Goursot et al., 2018). Many social animals emit distress calls in contexts of fear such as danger, injury or illness; these particular vocalizations function to attract attention from others, to warn them of potential danger, to call for help (i.e. alarm), and/or to confuse the predator (Liévin-Bazin et al., 2018; Vannoni et al., 2005; Wu et al., 2018).

Cognitive Biases

Since emotions cannot be measured directly, scientists use a posteriori measures to postulate on potential emotions felt by animals (Désiré et al., 2002); that is, scientists identify emotions on the basis of the cognitive evaluation of situations by the animal itself (Dantzer, 2002). Cognitive biases describe the effects of emotions on a subject's cognitive functioning (i.e., judgment, attention, and memory) and are adaptive (Mendl et al., 2009). In other words, they refer to how an individual's emotional state affects the way it processes information. To study cognitive bias, scientists will usually induce emotional state experimentally by imposing various stressful situations to the animals (i.e., a physical stress; Bateson et al., 2011), a chronic environmental stress (Doyle et al., 2011), or a psychological stress (Rygula et al., 2013) or by using specific pharmacological treatments (Lee et al., 2018). Cognitive bias studies have been conducted on farm and laboratory animals and on pets, as well as a few zoo animal species including three species of primates (*Macaca fuscata*, *Gorilla gorilla* and *Pan troglodytes*; Cronin et al., 2018; McGuire & Vonk, 2018) and an American black bear (*Ursus americanus*; McGuire et al., 2017). In animals, particularly zoo animals, cognitive bias tests are one of the methods used to assess their welfare (Wolfensohn et al., 2018). Judgment biases are cognitive biases where affect influences judgments about the affective value of stimuli (i.e., positive affect is associated with optimistic judgments and negative affect with pessimistic judgments; Crump et al., 2018). Judgment bias tasks have been built for mammals, birds, and insects (Crump et al., 2018). They require long training periods that could negatively impact the animals' performances. Attention bias (i.e., preferential allocation of cognitive resources towards one form of information over another; Crump et al., 2018) are good alternatives. They do not require extensive training and do not depend on interpreting pessimistic or optimistic responses. For instance, in a revised version of the emotional Stroop task, rhesus monkeys (*Macaca mulatta*) that have experienced a stressor (i.e., presumably stressful veterinary exam) slowed their responses to mildly threatening stimuli (i.e., direct gaze) compared to their speed to respond during a baseline period (Bethell et al., 2016). The authors named this response *cognitive freeze* and urged scientists to consider the response-slowing paradigm.

Anticipatory Behavior

Anticipatory behavior is defined as an activity performed by an individual in expectation of a predictable upcoming event (Spruijt et al., 2001) and is expressed by an increased activity, vigilance, and/or increased transitions between two successive behaviors (van den Bos et al., 2003). Expected events could be feeding events (Martini et al., 2018), play opportunities (Anderson et al., 2015), socio-sexual activities (Van der Harst et al., 2003), and positive and enjoyable human-animal interactions (Krebs et al., 2017). Since anticipatory behavior is linked to the reward sensitivity system (Van der Harst & Spruijt, 2007), animals experiencing negative affective states will put more incentive value on acquiring positive rewards and will more intensively anticipate their arrival. Alternatively, anticipatory behaviors can give information on the individual's motivation and the way rewards are valued. In that case, they are known to enhance positive affective states/emotions, such as excitation (Clegg et al., 2018). Even if the link between anticipatory behavior and affective state is not that simple, it is a valid method to examine the animals' perceptual processes and emotions.

Personality

Personality is defined as behavioral and physiological traits of an individual that are consistent over time and situation (Goursot et al., 2018). Personality, cognition, and emotions are intertwined. The way that animals value an event can potentially elicit an emotional response and, conversely, an animal's mood (accumulation of emotional experiences) and personality can influence the way that animal perceives an event (Baciadonna, 2017). For instance, stressful situations affect working memory performance in fearful horses (Valenchon, Lévy, Fortin, et al., 2013) and their learning performance (Valenchon, Lévy, Prunier, et al., 2013) according to the type of reinforcement and in interaction with personality (Valenchon et al., 2017). A recent study found a link between personality and problem solving abilities in young guide dogs (Bray et al., 2017). Zoo-housed capuchin monkeys (*Sapajus apella*) involved in two experiments with positive reinforcement and free-choice participation showed that the personality trait openness was positively related to individual differences in task participation: active, curious animals are willing to engage in testing, and assertiveness was negatively related to performance on tasks (Morton et al., 2013).

Assessing Emotions in Marine Mammals Under Professional Care

Zoos are adequate settings to develop research on behavior and cognition, to examine the human-animal relationship, and to assess animal welfare. Zoo animals are usually involved in medical and husbandry trainings using operant (to reward or to punish a behavior in order to enhance or extinguish its display) or classical (to elicit a reflexive response based on cue) conditioning. This makes them good candidates for experimental research to study their cognitive abilities and/or their emotions. Delphinids and pinnipeds under professional care follow these rules. Bottlenose dolphins (*Tursiops truncatus*) are the most studied cetacean species and are the most commonly found delphinid in dolphinaria. They are sociable, demonstrate complex cognitive abilities, and are easily trainable (Brando, 2010), which is valuable when setting up cognitive bias tests. California sea lions (*Zalophus californianus*) are gregarious animals living in colonies with well-known abilities in memory, attention, and abstraction (Arkwright et al., 2016; Kastak & Schusterman, 2002; Malassis & Delfour, 2015; Penel & Delfour, 2014) and, like bottlenose dolphins, are readily trainable (Schusterman, 1981).

Body Postures in Delphinids and Facial Expressions in Pinnipeds

When looking for emotions in dolphins, contrary to other animals, there are relatively few anatomical attributes that could serve as affective state indicators. However, pectoral, tail, head slapping, and jaw clapping along with S-shaped body postures (Dudzinski, 1998) have been associated with negative emotional situation (i.e., frustration, anger, aggression; Herzing, 1996), while pectoral rubbing (Dudzinski & Ribic, 2017) and slow-close synchronous swimming (Clegg, Rödel, Cellier, et al., 2017) with positive emotional contexts (i.e., social bonding, affiliative behavior). Circular swimming, synchronous swimming, contact swimming, and group swimming along with swimming speed seem useful to monitor emotions in dolphins (Serres et al., 2020). Circular swimming, fast swimming, and social swimming (i.e., contact, synchronous, and group swimming) increase in positive situations and decrease in negative ones. But, according to these authors, bottlenose dolphins display fast swimming in stressful situations and in intense social play, which makes this indicator ambiguous. Donut shaped bubbles have been associated to negative emotional contexts in wild dolphins (e.g., frustration, agonistic situations) and to positive emotional contexts in cetaceans under professional care (e.g., excitement, surprise, play; Delfour & Aulagnier, 1997; Hill et al., 2011; Marten et al., 1996).

For the first time, a study that investigated facial expression and behaviors of harbor seal pups (*Phoca vitulina*) when being tagged or microchipped showed that the animals reacted to those presumably painful stressors by displaying consistent orbital tightening, a decrease in looking around, and struggling behaviors, while nose bulging remained inconsistent but could potentially indicate pain (MacRae et al., 2018).

Delphinids' Vocalizations

Delphinids produce two broad categories of vocalization: amplitude-modulated clicks (or pulses) and frequency-modulated calls (whistles). Clicks can be further divided into click trains (e.g., echolocation) and burst-pulse calls depending on their repetition rate. Screams (overlapping frequency-modulated whistles: 5.8 to 9.4 kHz, 2.5 to 4 s in duration), (synchronized) squawks (broad-band burst-pulsed sounds squawk: 0.2 to 12 kHz, 0.2 to 1 s; synchronized squawk: 0.1 to 15 kHz, 0.9 to 1 s), and barks (burst-pulsed vocalization: 0.2 to 2 kHz, 0.5 to 1 s) have been associated with agonistic and aggressive interactions (Herzing, 1996). An excitement vocalization (burst-pulsed sound with overlapping signature whistle: 4 to 18 kHz, 2 to 30 s, with bubbles streaming out of the blowhole) is associated with distress or excitement in spotted dolphins (*Stenella frontalis*; Herzing, 1996). In bottlenose dolphins, burst-pulsed vocalizations have been associated with high-intensity states such as alarm and fright but also with play behavior and mother-infant interactions (Herzing, 1996). These findings suggest that vocal modulation in delphinids may be more associated with an emotional arousal dimension than a valence dimension. More specifically, spotted dolphins produce synchronized squawks and screams during intraspecific and interspecific aggression, and bottlenose dolphins emit synchronized whistles/buzz bouts, bray/buzz bouts, and buzz bouts during intraspecific aggression; these vocalizations are often mirrored with body postures (Herzing, 2015). Clicks are short transitory signals (50 to 80 μs), the inter-click interval is variable within a train, as well as between two trains, and ranges from 0.8 ms to 5 ms for a buzz (Luís et al. 2016). We demonstrated that bottlenose dolphins accelerate click emissions when approaching a target, thus displaying a classical terminal buzz that slackens off within a quarter of a second before the end of click train; then, they end the sequence by touching the object with their rostrum lower tip (Doh et al., 2018). During play-fights, juvenile and subadult bottlenose dolphins emit a short pulse burst followed by a frequency modulated whistle that prevent them from escalating into a real fight (Blomqvist et al., 2005). The authors suggest that this specific sound could be is analogous to the laugh and chuckle observed in great apes. Delphinids emit distress calls (i.e., repeated whistles) to attract conspecifics' attention and aid (Lilly, 1963), Jones et al. (2020) suggested using particular vocal behaviors as welfare biomarker for zoo cetaceans.

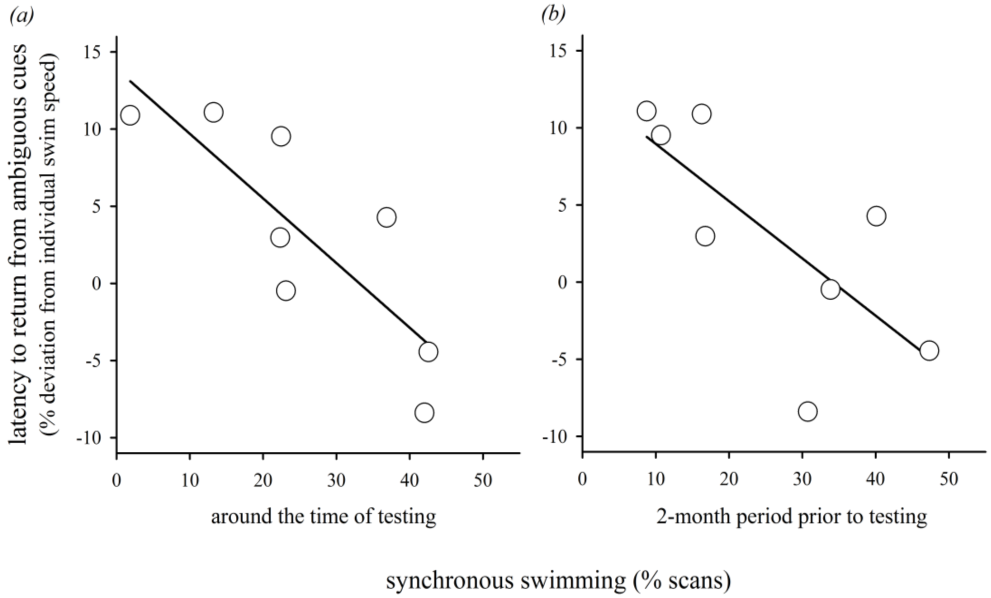
Click production is not automatic but controlled by a bottlenose dolphin, and, when succeeding in catching a prey, they emit a "victory squeal" (Ridgway et al., 2014) that might be a sign of pleasure. In contrast, captive beluga whales (*Delphinapterus leucas*) and wild narwhals (*Monodon monoceros*) decrease their acoustic activity in threatening contexts, potentially enhancing negative emotions such as fright or alarm states (Castellote & Fossa, 2006; Finley et al., 1990). More precisely, belugas produced drastically fewer vocalizations after transportation in a novel environment, which suggests that vocal production in this species may be particularly sensitive to environmental changes and may be linked with negative affective states. However, in these studies, the overall acoustic activity was investigated without necessarily distinguishing the different types of vocalizations. Further research on this topic is needed to investigate variation in duration, rate, or frequency of specific vocalizations that might be produced by animals in contexts with different levels of arousal or valence. Since the different parameters (i.e., rate, duration, amplitude, intervocalization interval) of vocal production are easily quantifiable, acoustic monitoring might be an interesting way of measuring emotions in marine mammals. However, tremendous efforts have to be made to precisely identify the emitter of the vocalizations (Lopez-Marulanda et al., 2017) and to understand the situation and the context vocalizations are produced.

Cognitive Bias and Synchronous Swimming in Bottlenose Dolphins

We adapted a spatial location judgment bias test used with laboratory rats (Burman et al., 2008), domestic dogs (*Canis familiaris*; Burman et al. 2011) and domestic pigs (*Sus scrofa domesticus*; Düpjan et al. 2017). We used a go/go task to study the link between cognitive bias and social behaviors with four male and four female bottlenose dolphins (Clegg, Rödel, & Delfour, 2017). We chose to record positive social behaviors, like social play and synchronous swimming, and negative social behaviors, mainly agonistic actions outside of training sessions, and we did not experimentally induce an affective state. For the dolphins, the test consisted of touching a target with their rostrum and swimming back to their trainer with a positive target at one location being highly rewarded (big amount of fish and applause) and a less-positive target at another location being less rewarded (small amount of fish, no applause). Our results demonstrated stable individual differences in judgment biases across three testing days and showed that higher frequencies of synchronous swimming were correlated with optimistic-like judgments toward ambiguous cues (see Figure 1). Synchronous swimming is an affiliative behavior in delphinids (Sakai et al., 2010; Sakai et al., 2013), and optimistic judgments reflect positive emotional states (Mendl et al., 2009). Swimming synchronously could induce or could be induced by a particular affective state, but the nature of the link should be investigated. Spatial location judgment bias tests are easy to conduct with bottlenose dolphins, a species which is used to learning new behaviors and procedures through operant and classical conditioning.

Figure 1

Cognitive Bias Test Results Predicted by Synchronous Swimming



Note. (a) The dolphins' return latencies to ambiguous cues were predicted by frequency of synchronous swimming behavior during the 3-day test period, with the fastest dolphins to return showing the highest frequency of synchronous swimming; this same relationship was present (b) with behavioral data taken up to 2 months before the testing period, where those who were more frequently synchronous swimming also returned significantly more quickly in the subsequent cognitive bias tests. Low and negative y-axis values (i.e., short return times) correspond to optimistic-like judgments; the higher and positive, to pessimistic-like judgments. Published in Clegg, Rödel, Cellier, et al. (2017).

Personality in Marine Mammals

In bottlenose dolphins and California sea lions, personality traits have been found (Birgersson et al., 2014; Ciardelli et al., 2017); however, no study currently has demonstrated a link between these three components – personality, cognition, and emotion. Here, we have discussed studies on cognitive bias in bottlenose dolphins that highlight pessimistic and optimistic choices in these animals (Clegg, Rödel, & Delfour, 2017), as well as those linking cognitive bias with anticipatory behavior (Clegg & Delfour, 2018), but animal personality traits are missing from these studies. In the future, it would be useful to conduct research on these three related topics in order to understand better their relationship (Table 1).

Table 1

Present and Future Parameters to Consider to Assess Emotions in Marine Mammals

Evaluation of emotions in animals	Actual evaluations of emotions in bottlenose dolphins and California sea lions	Potential parameters to consider
Physical and behavioral changes (Destrez et al., 2013)	Facial expression in sea lions (MacRae et al., 2018) Cognitive bias in bottlenose dolphins (Clegg, Rödel, Cellier, et al., 2017)	Cetaceans' behaviors and postures: S posture (Dudzinski, 1998); donut-shaped bubbles (Delfour & Aulagnier, 1997; Hill et al., 2011; Marten et al., 1996); tactile behavior (Dudzinski, 2010); synchronous swimming (Clegg, Rödel, & Delfour, 2017)
A posteriori measures (Dantzer, 2002; Désiré et al., 2002)	Anticipatory behavior in bottlenose dolphins (Clegg and Delfour, 2018; Jensen et al., 2013) Human-animal relations in bottlenose dolphins (Clegg et al., 2018) Visual and behavioral lateralization in sea lions (Le Ray et al., 2017) and bottlenose dolphins (Blois-Heulin et al., 2012; Delfour and Marten, 2006; Kilian et al., 2000; Thieltges et al., 2011)	Vocal productions in delphinids (Castellote and Fossa, 2006; Herzing, 1996, 2015; Jones et al., 2020; Ridgway et al., 2014) and in pinnipeds (Schusterman and Dawson, 1968) Personality in sea lions (Ciardelli et al., 2017) and bottlenose dolphins (Birgersson et al., 2014)

Assessing Marine Mammals' Emotions through Behavioral Laterality

Framework

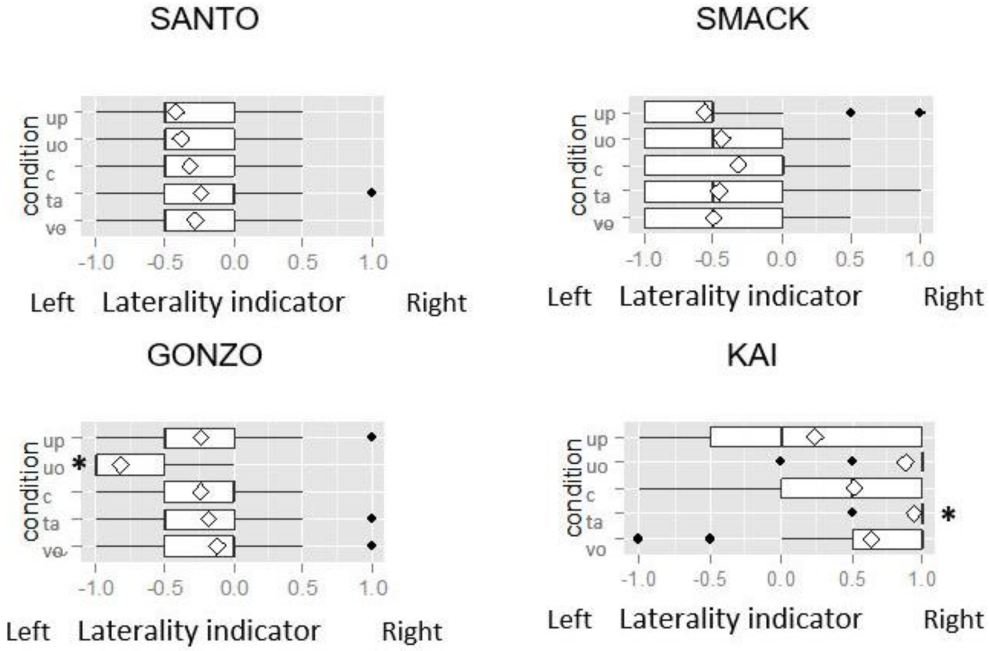
Cognitive bias tests are promising tools to assess emotional valence in animals; however, their designs currently are often time-consuming for the animal keepers (Hintze et al., 2018), and task type, training cue reinforcement, and sex of animals impact effect sizes in judgment bias tests (Lagisz et al., 2020). Thus, another way to assess emotions in animals might be to examine the cerebral processes underlying emotions. According to the emotional valence hypothesis, the right hemisphere controls negative emotions (e.g., fear and frustration), and the left hemisphere oversees positive emotions (e.g., joy; Leliveld et al., 2013). Thus, positive emotions activate the left hemisphere that is involved in controlling the right side of the body; events and situations perceived positively by the animal would then lead to a right lateral bias (Demaree et al., 2005), expressed by a right visual, motor, olfactory, and/or auditory bias (Sakai et al., 2006; Siniscalchi, 2017; Siniscalchi et al., 2016; Wells et al., 2006). The methodological approaches to study emotional lateralization in animals consist of observing the behaviors they display spontaneously in every-day situations or when placed in an experimental design where the valence of presented stimuli could be controlled by the experimenters. Moreover, associations between direction/strength of lateralization and personality have been reported in pigs and cats (*Felis catus*; Goursot et al., 2018). Pigs (*Sus scrofa*) presenting a right-side bias/left-hemisphere dominance were bolder and explored more compared to individuals with less lateralized actions or those presenting a left-side bias/right-hemisphere dominance (Goursot et al., 2018). In contrast, ambilateral dogs (i.e., equally using their right and left paw) showed stronger reactions to positive or negative emotion-inducing stimuli (associated with playfulness or aggressiveness, respectively) than lateralized dogs, suggesting that weakly lateralized animals may be less able to cope with challenge from their environment (Barnard et al., 2017). These results suggest an influence of cognitive processing on the way an animal perceives and evaluates its environment. The association of lateralization pattern(s) with personality traits may increase our understanding of individuality and emotionality in animals.

Motor Lateralization in California Sea Lions (*Zalophus californianus*)

California sea lions demonstrated a right ear bias when listening to intraspecific vocal signals (Böye et al., 2005), and they showed a swimming bias with males preferentially circling clockwise and females counter-clockwise (Wells et al., 2006). At Parc Asterix (France), we tested the influence of supposedly positive, negative, and neutral emotional situations on four adult California sea lions' motor lateralization while performing a known task (Le Ray et al., 2017). We measured the latency between the trainers' request to climb on a stool and each animal's response. We scored their uses of the left and right flipper and their head direction depending on each potential emotional context. According to hemispheric dominance, in fearful situations, we expected the sea lions to preferentially use their left flipper and left eye vision and to increase their latency to perform the asked-for behavior. In positive situations, we expected the sea lions to use their right flipper and eye vision and to show a decreased latency to respond to the trainers, latency here being a motivational indicator. The results were seemingly in accordance with the emotional valence hypothesis but large interindividual variability was observed (Figure 2; Le Ray et al., 2017). We also found what could be a sex-dependent lateralization with the three males slightly lateralized to the left and the female to the right, but further studies are needed to validate this result. A sex difference was already demonstrated in swimming direction (Wells et al., 2006). The small sample size does not allow generalization of our results; however, this finding is interesting and valuable for future research on sea lions' emotional lateralization. Emotional lateralization tests are relatively simple to set up and conduct, particularly on zoo animals like California sea lions used to being trained, which would facilitate further research on this topic.

Figure 2

Flipper Laterality In California Sea Lions (Zalophus calfornianus) during Positive, Neutral and Negative Emotional Situations



Note. Means of the flipper laterality indicators depending on the conditions. Published in Le Ray et al. (2017). up = unfamiliar person; uo = unfamiliar object; c = control; ta = tactile enhancement; vo = vocal enhancement.

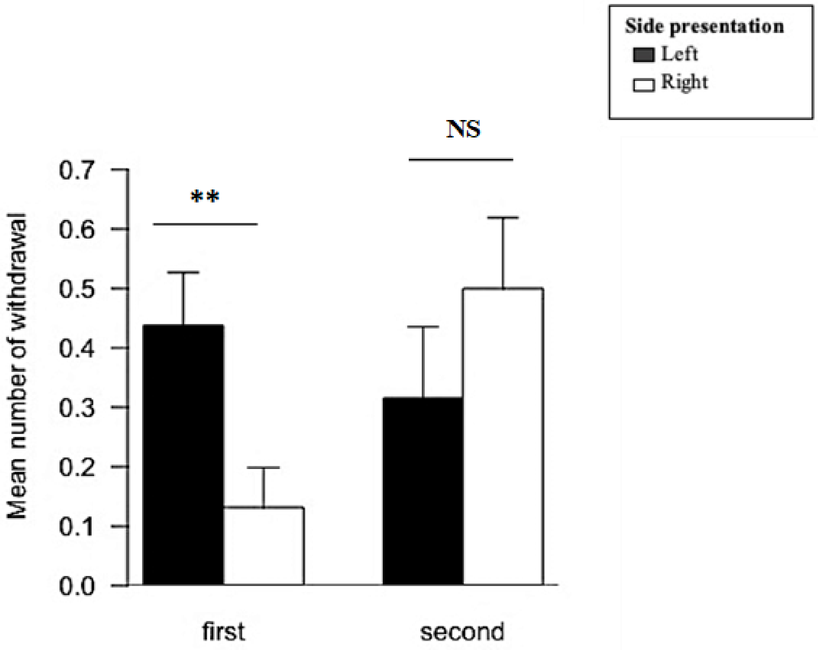
Visual and Motor Lateralization in Bottlenose Dolphins

Across odontocete species, visual and behavioral asymmetries have been found in feeding (Karenina et al., 2016), breaching (Casagrande et al., 2013), and social behaviors (Sakai et al., 2006). Bottlenose dolphins appear to be particularly suited to the study of visual laterality because of their anatomical characteristics. Their eyes are positioned laterally with a complete crossover of optic fibers in the optic chiasma. This particularity suggests that preference in use of one or the other eye would potentially indicate a hemispheric dominance (Kilian et al., 2000). Previous studies on bottlenose dolphins under human care showed a left eye dominance for visual spatial tasks (Kilian et al., 2000) and, when looking at human beings, whatever their degree of familiarity (Thieltges et al., 2011). Considering non-human stimuli, dolphins processed unfamiliar objects preferentially with their right eye and familiar objects preferentially with their left eye (Blois-Heulin et al., 2012). However, no study has investigated the influence of emotionality on bottlenose dolphins’ visual laterality.

We tested the influence of emotion-inducing stimuli on bottlenose dolphins’ visual laterality and behavior. Dolphins were exposed to various stimuli with positive or negative emotional valence introduced to their left or right visual hemi-field. Our results showed that dolphins displayed more emotional reactions, for instance, by being more distant (i.e., staying physically farther away) toward negative stimuli when they were presented in their left hemifield (Figure 3; Charles et al., in press). These preliminary findings offer interesting insight for further studies on larger populations with respect to odontocetes’ visual laterality and emotions. Since it can be quickly and readily measured using direct observations, examining emotional lateralization appears to be a promising tool to assess animal emotions and offers a new approach to understanding these brain processes in animals.

Figure 3

Mean Number of Withdrawals According to the Presentation Order and the Side Presentation of the Stimuli



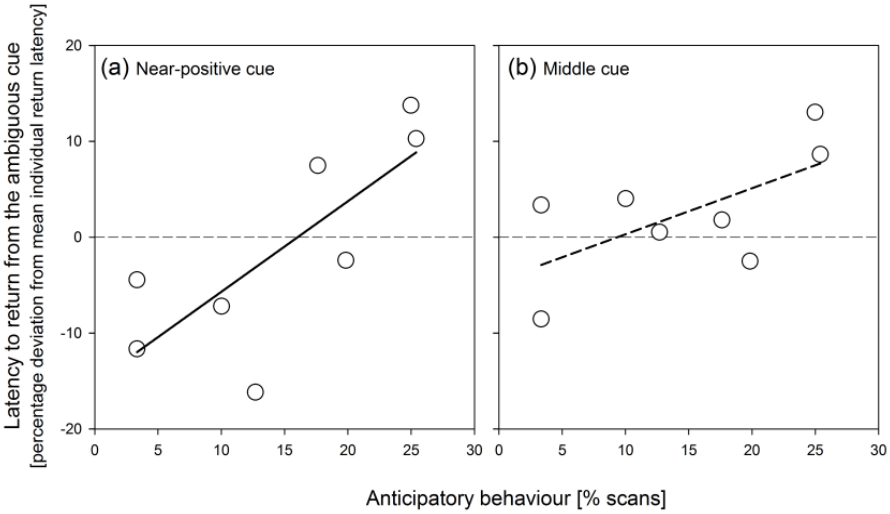
Note. Error bars represent standard error. ** = $p < 0.01$; *** = $p < 0.001$ (post-hoc tests).

Anticipatory Behavior in Relation to Cognitive Bias, Interactions with Familiar Trainers, and Behavioral Lateralization in Bottlenose Dolphins

Dolphins that show a higher frequency in anticipatory behavior made more pessimistic judgments in a spatial location judgment bias test (Clegg & Delfour, 2018). This result supports previous findings linking higher reward sensitivity with negative affective states (Spruijt et al., 2001; Figure 4). Under professional care, bottlenose dolphins display anticipatory behaviors before feeding sessions, so we wanted to know if they would anticipate nonalimentary events. Experimentally, we conditioned dolphins with sound cues to the arrival of toys or a positive human-animal interaction with a familiar trainer, then we measured anticipatory behavior (i.e., surface looking and spy hopping) before these two situations. Dolphins performed significantly more anticipatory behavior before the two experimental contexts than before a control situation, and they displayed more anticipatory behavior before interacting with their trainer than before the toy-presentation context (Clegg and Delfour, 2018). Moreover, higher anticipatory behavior was significantly correlated to higher levels of participation in the event itself. Interacting with familiar trainers and getting an object to play with were positively perceived: they were rewarding events. To explore the perceptual process underlying anticipatory behaviors in bottlenose dolphins, we investigated the visual asymmetry spontaneously expressed at the water surface during surface-looking behavior. We calculated a visual laterality index based on the number of times that dolphins spontaneously looked at the platform from where trainers usually arrive with their left or right eye. Preliminary results showed a right eye bias at group level, and almost all dolphins (N= 4 of 5) presented a right eye bias at the individual level (Figure 5; Charles et al., in press).

Figure 4

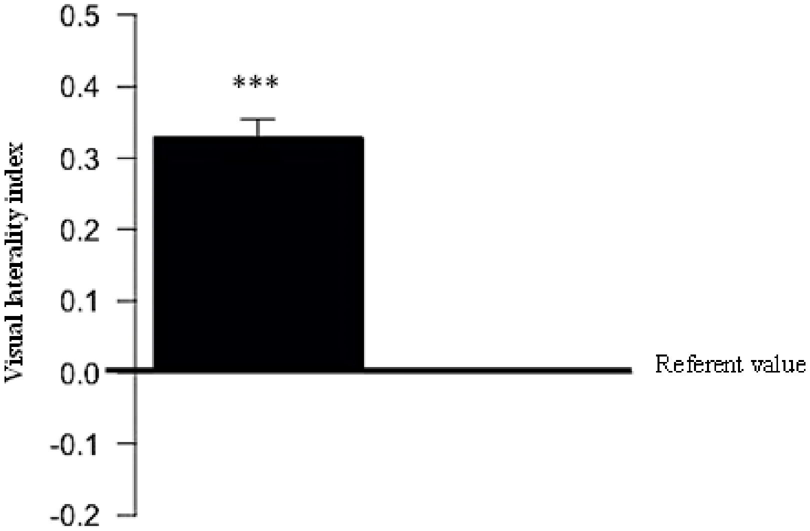
Cognitive Bias Test Results Predicted by Anticipatory Behavior



Note. (a) The dolphins' relative return latencies to the near-positive cue were predicted by the frequency of anticipatory behavior toward the training sessions during the third day test period: Those slowest to return (pessimistic-like judgment) also showed significantly highest frequencies of anticipatory behavior, and this same relationship was present (b) with respect to the middle cue, although the association was a statistical tendency only. High and positive y-axis values correspond to a pessimistic-like judgment; the lower and negative, to optimistic-like judgments. Anticipatory behavior in relation to upcoming training sessions was the combined frequencies of two behaviors: surface-looking, and spy-hopping. Published in Clegg and Delfour (2018).

Figure 5

Visual Laterality Index During Surface Looking Behavior (Monocular Vision)



Note. Positive values indicate preference for the right eye, and negative values indicate preference for the left eye. Bars represent standard error. Levels of significance: *** = $p < 0.001$ (linear mixed-effects model).

Brain asymmetry is influenced by the motivational system engaged by the stimulus, with the left hemisphere controlling behaviors towards appetitive stimuli (Spielberg et al., 2008). Our results, in accordance with previous work (Clegg & Delfour, 2018), suggest that dolphins perceive their session/trainers as motivational stimuli, but further studies are needed to explore this hypothesis more completely. Finally, since the right eye/left hemisphere follows a top-down process (Rogers, 2014), anticipatory behaviors may be driven by dolphins' internal state, such as their hunger or stress level, or by their expectations (e.g., influenced by their previous session). This last hypothesis underscores the necessity to consider interindividual differences when assessing animals' emotion and welfare, which might be expressed by differences in laterality strength. Since these behaviors are associated either to positive or negative emotions depending on their frequency, further studies, including assessment of cognitive and behavioral indicators, are needed to quantify more precisely excessive levels of anticipatory behaviors.

Zoo Animals: Experimental Procedures to Measure Their Emotions and Their Welfare

Direct observations of an animal's laterality seem to be a reasonable option to study emotions in animals during intraspecific and interspecific interactions. Visual laterality index and/or right/left flipper uses are quite simple to implement and calculate when conducting standardized observations of the animals, and their results should then be discussed according to various contexts (e.g., new behavior training, heavy medical examination, transport, etc). In the short term, asymmetries in eye or body side used in particular situations may be a good indicator of emotions currently experienced by the animals. In the long term, consistency in lateralization preferences may be indicative of the overall affective state of the animal and potentially may be linked to personality. Dolphins' laterality could be easily implemented on already existing welfare evaluation tools such as the Dolphin-WET developed by the European Association Aquatic Mammals Welfare Committee (Tallo-Parra et al., 2019).

We also have provided empirical evidence that anticipatory behavior is correlated to the level of participation in a following event, indicating that it is a measure of motivation (Clegg & Delfour, 2018). We suggest that anticipatory behavior is a potential tool to assess and improve animal welfare. Interestingly, anticipatory behavior could be measured using focal follows on animals during their free time (Jensen et al., 2013) or during an experimental procedure (Clegg & Delfour, 2018). Anticipatory behavior can also be included in a protocol to assess the animal welfare. One male silverback gorilla and one young male red panda (*Ailurus fulgens*) were selected for their known positive social interactions with their caretakers and tested in an experiment where the sound of a buzzer announced the arrival of an animal management staff four minutes later to positively interact with the animal (Krebs et al., 2017). The study focused on the behaviors that the two animals displayed after the buzzer sounded and before the arrival of the familiar human. The results showed that the male gorilla and male red panda displayed anticipatory behavior with some species-dependent differences: the gorilla sat and waited, while the red panda increased its activity (Krebs et al. 2017). This study is interesting on many levels: it shows that it is possible to assess one aspect of animal welfare using this simple procedure of observation. The behaviors that the animals displayed after the buzzer sounded rely on the animal's perception of the reliably signaled event and how it perceives its own welfare. This experiment shows that anticipatory behavior is species dependent and might also depend on an animal's motivation and personality.

Moreover, in this procedure, human-animal interaction is considered as a reward for the animal, so this statement can be individually validated for each animal involved in the test (i.e., human-animal interaction might not be rewarding for all animals). Nonetheless, this experiment showed that the concept can be generalized and tested in many zoo animal taxa. Moreover, this kind of cognitive research can be enriching itself for the animals, as has been shown for a group of 11 chimpanzees (*Pan troglodytes*) who displayed repeated interest and motivation with subtle variations depending on their personality traits to participate in the research (Herrelko et al., 2012).

In order to avoid poor welfare and to promote good welfare for an animal, the first step is to measure welfare objectively. However, we should keep in mind that we will never be able to completely and accurately measure this subjective and transitional state. Welfare is a holistic, all-encompassing phenomenon that should be assessed using multidimensional measures (Boissy et al., 2007; Yeates & Main, 2008). The main categories of these different measures are behavior, physiology, and cognition, which are the three components of emotional responses (Désiré et al., 2002; Paul et al., 2005). According to Webster's triangulation principle, the three components of welfare measures are points on a triangle, and the true center is the animal's actual welfare (Webster, 2005). The measures could be epidemiological measures (e.g., mortality, reproductive success), disease prevalence, body-condition scoring, stress hormone levels, excessive aggression, affiliative behavior, play, abnormal and stereotypic behaviors, indicators of basic (e.g., fearful, playful, rage) and more complex (e.g., contentedness, depression) emotions, and the parameters we already discussed (Clegg, Van Elk, & Delfour, 2017). These measures should also be resource- (Veissier et al., 2008) and animal-based (Roe et al., 2011). Then, according to the animal's personality and its physiological, behavioral, and cognitive needs, actions could be taken to improve its welfare and well-being, but again the results of those actions should be objectively assessed and monitored in short and long terms.

Conclusion

Unlike most of, if not all, terrestrial mammals, marine mammals do not show major or obvious facial and bodily expressions in relation to their affective states. So, it is necessary to find other measurable indicators: their behavioral displays, vocal production, and cognitive processes are good parameters to consider as potentially related to their affective state. Additionally, to be more precise in the determination and description of their emotions, personality traits are important factors to include in these studies. Our current modern societies express much concern about animal welfare and well-being, which require and insist their animal needs are considered. Thus, an increase in research and understanding of the sentience of these animals is needed to protect them; being able to recognize marine mammal emotions is part of this laudable and important process.

Acknowledgments

We would like to thank the curator, Birgitta Mercera, and the Parc Asterix for allowing us to work at the Delphinarium with their animals. Thanks to the trainers' team for their involvement and active participation for all projects. We thank Kathleen Dudzinski for providing language help and proofreading.

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Financial conflict of interest: No stated conflicts.
Conflict of interest: No stated conflicts.

Submitted: *November 12th, 2020*
Resubmitted: *January 1st, 2021*
Accepted: *January 21st, 2021*