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Looking forward to interacting with their caretakers: Dolphins' anticipatory behaviour indicates motivation to participate in specific events

Isabella L.K. Clegg[a,b,*], Heiko G. Rödel[a], Xavier Boivin[c,d], Fabienne Delfour[a,b]

[a] Laboratoire d'Ethologie Expérimentale et Comparée E.A. 4443 (LEEC), Université Paris 13, Sorbonne Paris Cité, F-93430, Villetaneuse, France
[b] Parc Astérix, F-60128, Plailly, France
[c] INRA, UMR1213 Herbivores, F-63122, Saint-Genès-Champanelle, France
[d] Clermont Université, VetAgro Sup, UMR Herbivores, BP 10448, F-63000, Clermont-Ferrand, France

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ABSTRACT

Anticipatory behaviour describes the actions taken to prepare for an upcoming event. Bottlenose dolphins (*Tursiops truncatus*) in captivity are known to display anticipatory behaviours before feeding sessions, but it is unknown whether they would anticipate non-alimentary events. Furthermore, there is no published information available for any species on whether the level of anticipatory behaviour is predictive of an animal's actual participation in the following event or reward: answering this question would bring us closer to understanding this behaviour and its related affective states. In this study, we used sound cues to condition dolphins to the arrival of toys in their pool or a positive Human-Animal Interaction (HAI) with a familiar trainer, and measured their anticipatory behaviour before each event. The protocol was validated since the dolphins performed significantly more anticipatory behaviour before the toys and HAI contexts than a control situation, by means of increased frequencies of surface looking and spy hopping. Furthermore, we found that dolphins showed more anticipatory behaviour before the HAI than the toys context (Linear Mixed Model with 1000 permutations, all $P < 0.001$). In the second part of the investigation, higher anticipatory behaviour before toy provision, HAIs, and feeding sessions was significantly correlated to higher levels of participation in the event itself (measured by time spent with humans/toys, and number of times dolphins left during feeding sessions; LMM with 1000 permutations, respectively: $\beta = 0.216 \pm 0.100$ SE, $P = 0.039$; $\beta = 0.274 \pm 0.097$ SE, $P = 0.008$; $\beta = -0.169 \pm 0.080$ SE, $P = 0.045$). Our results suggest that toys and HAIs were perceived as rewarding events, and we propose that non-food human interactions play an important role in these animals' lives. We also provide some of the first empirical evidence that anticipatory behaviour is correlated to the level of participation in the following event, supporting anticipatory behaviour as a measure of motivation, and hope that this stimulates further work regarding the use of this behaviour to assess and improve animal welfare.

1. Introduction

Anticipatory behaviour performed in expectation of predictable events has been documented in wild and captive animals (Mistlberger, 1994; Scheibe et al., 1999; Storch and Weitz, 2009), and consists of behavioural patterns that prepare the animal for an upcoming situation (Spruijt et al., 2001). Such anticipatory behaviours often manifest as increased activity, vigilance, and/or behavioural transitions (Makowska and Weary, 2016; van den Bos et al., 2003; van der Harst et al., 2003a). Studies on anticipatory behaviour have revealed links with captive animals' affective states, and thus suggest implications for welfare (see reviews by Van der Harst and Spruijt, 2007; Watters, 2014). However, although resource provision in captive environments is often highly predictable and thus anticipatory behaviour is likely to occur often (Waitt and Buchanan-Smith, 2001; Watters, 2014), there is still a lack of knowledge on how and whether anticipatory behaviour is linked to affective state in some of the less-studied species.

Anticipatory behaviour towards a positive event is adaptive since it is associated with the motivational system that directs the animal from an aversive state (e.g. hungry) to a reinforcing state (e.g. food acquisition; see Spruijt et al., 2001). Animals use a variety of environmental cues to predict when rewards will become available and thus make a contingent associations between the cue and following event (Anderson et al., 2015): such contingencies can also be experimentally induced using the Pavlovian paradigm to measure anticipatory behaviour (Folkedal et al., 2012; Krebs et al., 2017). The link between this

* Corresponding author at: Laboratoire d'Ethologie Expérimentale et Comparée E.A. 4443 (LEEC), Université Paris 13, Sorbonne Paris Cité, F-93430, Villetaneuse, France.
E-mail address: izziclegg@hotmail.co.uk (I.L.K. Clegg).

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behaviour and affective states is not linear however, since anticipation levels have been found to vary with reward sensitivity (van der Harst and Spruijt, 2007; Watters, 2014). Again, this is adaptive: a more food-deprived animal is in a more negative affective state where the reward (food) will have a higher value, and thus more anticipatory behaviour is performed (termed "incentive value" by Spruijt et al., 2001).

Thus far, anticipatory behaviour has principally been used to test whether an animal perceives a certain predictable event as a reward (or not), and what the current affective state is likely to be based on the anticipatory behaviour frequency (van der Harst and Spruijt, 2007). Anticipatory behaviour before food acquisition has been shown to be robust and stable over multiple cycles (Mistlberger, 2009; Storch and Weitz, 2009). Since anticipatory behaviour reflects a reward's value (Anderson et al., 2015; van der Harst et al., 2003b), studies have also used it to test relative values placed on certain non-alimentary events, in multiple species: for example, laboratory rats (*Rattus norvegicus*) anticipated access to sexual contact (van der Harst et al., 2003b); laying hens (*Gallus domesticus*) valued a dusty substrate more than a food reward (McGrath et al., 2016); and lambs (*Ovis aries*) anticipated opportunities to play (Anderson et al., 2015). Environmental enrichment seems to be a notable context that stimulates anticipation in various species (e.g. McGrath et al., 2016; van der Harst et al., 2003b), and such studies are applicable to improving welfare as they reveal what the animal wants in its environment (Dawkins, 2006). A few past studies with rats have successfully shown that anticipatory behaviour can predict affective states: animals in more enriched cages conducted less anticipatory behaviour than those in standard cages (Makowska and Weary, 2016; van der Harst et al., 2003a), and those who experienced social isolation anticipated food rewards and social contact significantly more than group-housed conspecifics (van den Berg et al., 1999).

However, these are the first studies using anticipatory behaviour as a measure of affective state and there are still many unknowns (Watters, 2014). There are unanswered questions on the intention behind this behaviour, in particular with regard to non-alimentary rewards: we suggest that a much needed line of research should focus on whether levels of anticipation actually correspond to the animal's participation in the reward i.e. the consummation of the anticipated goal (Watters, 2014). For example, are the animals that show much anticipatory behaviour for enrichment provision also those that interact with the enrichment the most? A few studies have presented incidental data suggesting that this might be the case: for example some anticipatory behaviours were correlated in lambs with subsequent play behaviour (but only at some points of the test, Anderson et al., 2015), and in laying hens with the latency to approach the reward (McGrath et al., 2016). In rats, dopamine antagonists reduced both anticipatory behaviour before access to sexual contact as well as the sexual behaviours themselves, but the cause and effect of this correlation, independent of pharmacological influences, was not tested (Pfaus and Phillips, 1991). While the actions of the appetitive (controlling anticipation) and consummatory systems are not always congruent, appetitive behaviour has been proposed as a facilitator for the consummation of rewards (Spruijt et al., 2001). More investigation into whether anticipatory behaviour predicts an animal's actual interaction with the reward would aid in our understanding of the association between the behavioural systems.

Bottlenose dolphins (*Tursiops truncatus*) have been shown to display anticipatory behaviour in response to training sessions during which they receive their food (Clegg et al., 2017a; Jensen et al., 2013). Apart from food provision, there are other events occurring in the captive environment which are thought to be rewarding for dolphins, but for which there are only a few studies. Bottlenose dolphins have been shown to voluntarily interact and play with toys and other enrichment items and so seem to view them positively on the whole (Clark, 2013; Delfour and Beyer, 2012; Kuczaj et al., 2002). However, we have little to no knowledge on dolphins' actual motivation for non-food enrichment events (Clark, 2013; Delfour and Beyer, 2012). Measuring anticipatory behaviour could help in answering this question, and the results would be of interest to researchers and managers of zoo collections alike (Krebs et al., 2017; Watters, 2014). It has also been suggested that positive Human-Animal Interactions (HAIs), e.g. those involving stroking, play, voluntary contact, might be rewarding for dolphins like they are for other species (Perelberg and Schuster, 2009). Positive HAIs in domesticated species generally incite affiliation, have calming effects, and stimulate approach behaviour (e.g. Coulon et al., 2015; Handlin et al., 2011). Even for non-domesticated animals, positive HAIs can reduce stress (Hosey and Melfi, 2014; Whitham and Wielebnowski, 2013), represent gratifying events (Claxton, 2011; Hosey, 2008) and develop into strong, welfare-enhancing bonds (Hosey and Melfi, 2010). Wild and captive dolphins frequently engage in intraspecific tactile and play behaviour (Dudzinski et al., 2012; Kuczaj et al., 2013), which could tangibly be translated to inter-specific relations (Perelberg and Schuster, 2009), and case-level evidence suggests they can view humans as play partners or objects (review in Paulos et al., 2010). Mixed results from studies on dolphins' reactions to swim or touch interactions with unfamiliar guests suggest these are viewed both positively and negatively (Frohoff and Packard, 1995; Kyngdon et al., 2003; Trone et al., 2005). However, zoo animal research suggests that they significantly prefer interactions with familiar humans (Martin and Melfi, 2016; Melfi and Thomas, 2005; Mitchell et al., 1991). In the only study on HAIs with familiar humans and captive cetaceans, it was shown that outside of food-related training sessions bottlenose dolphins voluntarily chose to receive petting from their trainers in seemingly positive interactions (Perelberg and Schuster, 2009). However, no studies have used anticipatory behaviour to investigate the value that dolphins or other species place on HAIs with familiar humans. Only one related study has been published previously, using case studies with two individual zoo animals, where anticipatory behaviour increased before predictable visual, non-contact HAIs with an unfamiliar human (Krebs et al., 2017).

The lack of understanding of captive dolphin anticipatory behaviour and questions regarding their perception of certain environmental events stimulated a behavioural study to be conducted on the bottlenose dolphins at Parc Astérix (Plailly, FR). Two main questions were established: 1) Does the dolphins' anticipatory behaviour differ in relation to predictable upcoming contexts: the provision of toys, an HAI with a familiar person, versus a control context? To test this, these events would be paired with different predictor cues and anticipatory behaviour duration in the period after the cue would then be measured. We predicted that dolphins would anticipate the toys and HAI events significantly more than the control context, and that they might anticipate toys and HAIs similarly. The second question addressed a little-investigated element of anticipatory behaviour research: 2) Is the duration of anticipatory behaviour before an event correlated with dolphins' level of participation in the event itself? To answer this, anticipatory behaviour before the event was correlated with measures of interaction during it i.e. with the toys or familiar humans, and also in a third context of food provision within positive reinforcement training sessions. Based on the literature discussed above the provision of food, toys, and positive HAIs were thought to be rewarding events for the dolphins, although no *a priori* assumptions were made which might have influenced our experimental design. We predicted that animals who anticipated the signalled events the most would also participate the most during the event itself: if confirmed, these results could validate dolphins' anticipatory behaviour as a reflection of the intrinsic value they place on aspects of their environment.

2. Material and methods

2.1. Study animals and their daily routine

Our study was conducted at Parc Astérix on a group of seven Atlantic bottlenose dolphins (*Tursiops truncatus*), who were living in an outdoor pool joined to two indoor pools, with a total volume of 3790 m^3

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