

Anticipatory behaviour in animals: A critical review

C Anderson^{†‡}, MAG von Keyserlingk[†], LM Lidfors[‡] and DM Weary^{*†}

[†] Animal Welfare Program, Faculty of Land and Food Systems, 2357 Main Mall, University of British Columbia, Vancouver, BC, V6T 1Z6, Canada

[‡] Department of Animal Environment and Health, Swedish University of Agricultural Sciences, Box 7068, SE-750 07 Uppsala, Sweden

* Contact for correspondence: dan.weary@ubc.ca

Abstract

A number of studies have investigated anticipatory behaviour in animals as a measure of sensitivity to reward or as an expression of emotional state. A common feature of many studies is that they base inferences on seemingly arbitrary measures, for example, the frequency of behavioural transitions (ie number of times an animal switches between different behaviours). This paper critically reviews the literature and discusses various hypotheses for why specific behavioural responses occur in the anticipatory period between the signal and reward in conditioned animals. We argue that the specific behaviours shown may be the result of superstitious learning and thus highly variable, leaving behavioural transitions as the only response that can be scored consistently, and that sometimes these responses may relate more to frustration than to a positive emotional state. Finally, we propose new research approaches to avoid potential confounds and improve future studies on this topic.

Keywords: animal learning, animal welfare, classical conditioning, frustration, instrumental conditioning, methodology

Introduction

Animals can use the knowledge they acquire about temporal and spatial patterns to predict when and where resources may be found and thus better exploit opportunities. In this way animals use environmental cues to *anticipate* a reward and exploit this knowledge to better direct their behaviour. However, in the anticipatory behaviour literature, it is often unclear what if any function the behaviours reported actually achieve in helping the animal acquire a reward. Researchers have drawn welfare-related inferences from the behaviours that animals display in the anticipatory period (ie between cues signalling reward availability and the time when animals access the reward), often with no clearly stated predictions for what specific behaviours will be shown and how these will be of functional benefit to the animal. This absence of theory may explain: i) why some studies rely on meta-behaviours, such as the frequency of behavioural elements or transitions (henceforth called behavioural transitions) as the outcome measure (eg van den Bos *et al* 2003); ii) the bewildering variation in anticipatory behaviours described in different situations and for different species; and iii) why authors sometimes draw similar inferences based upon divergent (and even contradictory) evidence.

The aim of the current paper is to examine the conceptual and empirical foundations of welfare-related inferences about anticipatory behaviour. In this paper, we suggest that

responses referred to in the scientific literature as ‘anticipatory behaviour’ relate to a complex combination of factors, and we suggest that although the expression of these behaviours provides some basis for inferences regarding affective arousal they provide a much weaker basis for inferences regarding affective valence (ie positive or negative). We begin with a discussion of classical conditioning, and the interpretation of behaviours that occur during the interval between a cue and the presentation of the reward. We then discuss how superstitious learning may affect the behaviours expressed. We briefly describe the methodologies used and differences in the inferences made from these studies. Finally, we discuss methodological confounds and provide suggestions for future study.

Conditioning studies

Anticipation has been described as an animal responding to a situation based on expectations about the future (Antle & Silver 2009). In a number of studies where anticipatory behaviours have been investigated in rats and farm animals, classical conditioning has been used to induce anticipation. This involves presenting animals a neutral stimulus, for example, a light, followed by an unconditioned stimulus (US), for example, food that elicits a response. Following repeated presentations, an animal will form an association between the previously neutral stimulus (conditioned stimulus; CS) and US, such that the presentation of CS

alone elicits a conditioned response (Hall 1994). For the remainder of this review, we will refer to anticipatory behaviour as behaviours that occur following a cue (CS), but prior to access to the reward; we do not address anticipation of non-positive events unless needed for comparison.

Once animals have learned to associate the US and CS, studies focused on anticipatory behaviour sometimes increase the interval between the stimuli and thus allow more time for animals to express anticipatory behaviours (eg van den Bos *et al* 2003). Other studies have used a constant CS-US interval (eg van der Harst *et al* 2003a; Anderson *et al* 2015).

Studies also differ in the control conditions used. The three main approaches are: i) comparing the subject's response following a CS before vs after conditioning (eg van den Berg *et al* 1999; Vinke *et al* 2004, 2006; Peters *et al* 2012); ii) comparing the behavioural expression before vs following a CS in conditioned subjects (eg Moe *et al* 2009); and iii) comparing conditioned subjects with controls that were not trained to associate the CS and US (eg van der Harst *et al* 2003b; van den Bos *et al* 2004; Zimmerman *et al* 2011; Peters *et al* 2012; Wichman *et al* 2012). For further discussion on the issue of the interval between the CS and US we refer readers to Balsam *et al* (2009).

Response measures

As others have discussed (eg Krebs *et al* 2017), anticipatory behaviours are often expressed differently in different species. For example, one study observed how seven different rodent species responded to the presentation of a ball that predicted food and found considerable variation (Timberlake & Washburne 1989). Another study compared anticipatory behaviours in rats and cats and found that rats increased the frequency of behavioural transitions during anticipation while cats showed the opposite response (van den Bos *et al* 2003). We suggest that the variation in anticipatory behaviours illustrated in Table 1 (see supplementary material to papers published in *Animal Welfare*: <https://www.ufaw.org.uk/the-ufaw-journal/supplementary-material>) is not only due to species; rather, it seems likely that these differences are also due to different researchers focusing on different behaviours (Rescorla 1988). In addition, researchers have sometimes simply recorded the frequency of behavioural transitions, making it difficult to draw conclusions regarding the specific behaviours expressed.

In contrast to instrumental conditioning, where animals must perform a specific behaviour (eg bar press) to acquire a reward, in classical conditioning the CS predicts the US independent of any behaviour that the animal performs. Given that the animal's behaviour in no way affects the outcome, there would seem to be little basis for strong predictions regarding what specific behaviours will be elicited by the CS. That said, there might be some room for cautious predictions. One such prediction can be derived from the hedonic principle (ie approach what is pleasurable and avoid that which is unpleasant; Higgins 2006). Although these associations are typically more complex (for example, see Cornwell *et al* 2014), we may predict that

during an anticipation phase the animal will stay in proximity to the expected location of a positive US. The results of several of the studies are consistent with this prediction. For example, Vinke *et al* (2004, 2006) reported that following CS, mink showed more nose-poking around the area where a US (food) would be delivered. Similarly, Wichman *et al* (2012) found that laying hens spent more time by the bowl where the US would be presented, Peters *et al* (2012) reported that horses spent more time in the area where the US was to be delivered, and Chapagain *et al* (2014) found that over four weeks of testing lambs spent more time standing facing a reward arena that they had been trained to access. Similar responses have also been found in fish (Folkedal *et al* 2012).

Makowska and Weary (2016) reported the frequency and duration of all behaviours expressed in anticipation of a novel food reward by rats housed for more than 18 months in either standard laboratory cages or semi-naturalistic environments. Rats in the two treatments expressed anticipation differently: standard-housed rats walked back and forth in the cage and reared frequently, but semi-naturalistic-housed rats ran to the area closest to the experimenter and oriented towards her. This result suggests that animals living in environments with less control may be less able to form associations between their behaviour and outcomes, and thus are more likely to show persistent behaviours unrelated to the reward.

Unfortunately, many studies fail to describe where animals spend their time in the anticipatory phase, and sometimes the experimental layout prevents animals from orienting towards the US. We encourage future studies to clearly describe where the US is presented and to measure the animals' proximity to it.

Interpreting anticipatory behaviours

Anticipatory behaviours have been suggested as a type of general indicator of welfare state (as related to reward sensitivity), and as an expression of positive emotional state (with emotions defined as mental states elicited by rewards and punishers; Rolls 2005). Below, we describe both ideas. Additionally, we discuss the relationship between anticipation and frustration and also how anticipatory behaviours may be affected by superstitious learning and by study design.

Anticipatory behaviours as a general welfare indicator

A relationship between welfare and anticipatory behaviour may occur in several ways. Most commonly discussed in the literature is the idea that low welfare animals will experience *increased desire for and motivation to consume the reward* and thus show more behaviours during the anticipatory period (ie increased sensitivity to reward, as the reward itself holds more value for the animal). A second (seemingly contrasting) idea that low welfare animals will experience *reduced desire for and motivation to consume the reward* and thus show fewer behaviours during the anticipatory period (ie reduced sensitivity to reward, as the reward itself holds less value for the animal; in extreme cases manifested as anhedonia). A third idea is that low welfare animals may be *less able or willing to express behaviours* during the anticipatory period (perhaps due to injury; in this case the

animals still want and enjoy the reward); to our knowledge this third idea has not been addressed within the anticipatory behaviour literature and will not be discussed further.

Most studies have focused on the first idea, predicting that animals with reduced welfare will be more sensitive to reward and thus express more anticipatory behaviour. Examples include rats housed in enriched versus standard cages (van der Harst *et al* 2003b; Makowska & Weary 2016) and mink showing low versus high levels of stereotypies (Hansen & Jeppesen 2006). As a type of validation of this approach, studies have compared the responses to rewards presumed to be of high versus low value, with the idea that an animal will express more behaviours in anticipation of a greater reward (van den Berg *et al* 1999; van der Harst *et al* 2003a).

Several of these studies have used the frequency of behavioural elements or behavioural transitions as a measure of reward sensitivity (van den Berg *et al* 1999; von Frijtag *et al* 2002; van der Harst *et al* 2003b, 2005; Vinke *et al* 2004, 2006). In one study, male rats were conditioned to anticipate transfer to an enriched cage, sexual contact with a female, transfer to a standard cage or transfer to their home cage (van der Harst *et al* 2003a). The number of transitions among 32 different behaviours was used to compare treatments; animals waiting to transfer to an enriched cage, or for sexual contact with a female, engaged in many more transitions than did rats awaiting transfer to a standard cage; the authors concluded that the increased number of transitions was evidence of higher motivation to access the reward.

One promising method for assessing mood states in animals is judgment bias testing (Mendl *et al* 2010). To our knowledge, only one study to date (Clegg & Delfour 2018) has specifically tested how anticipatory behaviours relate to performance in a judgement bias test. This study found that bottlenose dolphins that showed more anticipatory behaviour also showed a more pessimistic response bias in a judgement bias test.

The second idea, that low welfare animals will experience reduced desire for and motivation to consume the reward, is sometimes combined with the first to suggest that reward value can vary in an inverted 'U-shaped' function with mood, resulting in reduced anticipatory behaviour at both high and low mood states (van der Harst & Spruijt 2007; Watters 2014). The inverted 'U' function suggests that the indicator (anticipatory behaviour) peaks at 'medium-welfare' but is expressed less when welfare is good or bad. According to this perspective, the dolphin results may suggest that the welfare of the animals varied from good to medium (explaining the positive relationship between anticipatory behaviour and the degree of pessimistic bias), but that the animals did not experience the very poor welfare states associated with anhedonia.

If anticipation is experienced as emotional episodes, repeated presentations of a positive or negative US may be expected to alter an animal's mood (Mendl *et al* 2020). For example, rats that experienced social defeat showed anhedonia associated with low mood, but after multiple rewarding trails (in which a CS was paired with a positive

outcome), these animals began to behave normally (van der Harst *et al* 2005). Thus, mood changes can be induced as a result of positive conditioning, increasing the difficulty in drawing inferences about the effect of mood on anticipatory behaviours that result from conditioning.

Anticipation is commonly assumed to represent the appetitive, or wanting phase of positive emotions, and this anticipation phase is believed to be pleasurable (Spruijt *et al* 2001; Mendl *et al* 2010). From this perspective, behaviours that occur during the anticipatory phase might be considered indicative of pleasure. Studies on ultrasonic rat 'laughter' (Panksepp & Burgdorf 2003) give some support to this interpretation (Heyse *et al* 2015).

There is also some evidence of dopamine release during anticipation (for reviews, see Berridge 1996 and Spruijt *et al* 2001), but elevated levels of dopamine are not necessarily associated with the experience of pleasure (Wise 2008). A more correct interpretation of the role of mesolimbic dopamine is likely 'wanting' (Berridge 2007), a state that is not necessarily positive.

Administration of β -endorphin in rats results in a dopamine release in the nucleus accumbens and increases locomotor activity (Spanagel *et al* 1991). In several studies, increased locomotion was found following a CS signalling a positive US (see Table 1; <https://www.ufaw.org.uk/the-ufaw-journal/supplementary-material>). Peters *et al* (2012) measured locomotor activity in horses following a CS signalling a reward and found increased duration and frequency of these behaviours. Similarly, Hansen and Jeppesen (2006) found that mink increased 'normal locomotion' following a CS associated with food. In laying hens, Moe *et al* (2013) found more steps after a CS signalling food. Anderson *et al* (2015) also found more walking in lambs conditioned to access an opportunity to play. However, not all studies showed similar responses; Zimmerman *et al* (2011) reported more steps in laying hens following both a neutral CS and a CS signalling a negative US (being sprayed with water), but not following a CS signalling a positive US (mealworms). In summary, there is some evidence of increased locomotion during the anticipatory phase; increased locomotion is consistent with dopamine release, presumably as dopamine activity is associated with approach motivation (Di Canio *et al* 2001; Schultz 2007), but there is no strong basis for the inference that this reflects a positive emotional state. Some researchers have incorporated behaviours such as "solitary walking, running, climbing" into their ethograms (Vinke *et al* 2004), but other studies only report a count of behavioural elements or transitions (eg van den Berg *et al* 1999; van der Harst *et al* 2005). Even with better measures of locomotion, drawing strong inferences is problematic as animals move for reasons other than high dopamine levels.

A number of researchers have suggested that some behaviours exhibited during anticipation for a reward are indications of positive emotions, regardless of context. For example, Zimmerman *et al* (2011) found that laying hens anticipating a positive reward expressed more comfort behaviours

(including wing flapping, feather ruffling and preening) compared to hens anticipating a negative event or a control group, and suggested that such responses may reflect positive emotions not contingent with US. The authors acknowledged, however, that preening was sometimes associated with frustration, and could also be interpreted as displacement behaviour. Other studies have shown that rats emit 50 kHz ultrasonic vocalisations during anticipation for rewarding brain stimulation (Burgdorf *et al* 2001) and for play (Knutson *et al* 1998). Such vocalisations in rats are commonly interpreted as indicative of positive affect (Knutson *et al* 2002), but these have also been recorded during negative events (Vivian & Miczek 1993; Tornatzky & Miczek 1995; Niel & Weary 2006) making inferences difficult.

Anticipation versus frustration

The behaviours that occur between the CS and US may be associated with frustration (Moe *et al* 2009; Zimmerman *et al* 2011; Peters *et al* 2012). As Moe *et al* (2009) put it: “prolonged CS-US interval may be experienced as a lack of reinforcement in a situation that was consistently reinforced previously, and therefore induce frustration”. Amsel (1992) describes frustration as “an aversive state that results from non-reward, reduced reward or delayed reward in the presence of a history of reward”. Kuhne *et al* (2013) argue that behaviours can occur out of context and at altered frequencies and durations in response to frustration associated with the lack of an expected reward. Increased locomotion has been observed in laying hens initially trained to associate a CS with a food reward that was then withheld (Zimmerman & Koene 1998), boars trained to be manually ejaculated but then the manual help was stopped (Bishop *et al* 1999), lambs trained to place their muzzle into a hole to access a food reward but then the food reward was reduced or removed (Greiveldinger *et al* 2011), hens prevented access to a previously accessible water bowl (Haskell *et al* 2004), and goats prevented access to a previously accessible food bowl (Gygax *et al* 2013). Collectively, these results suggest that increased locomotion is associated with frustrating situations. If frustration is considered a state elicited when unable to access what you are motivated for (Manning & Stamp Dawkins 1998), then the examples described in Table 1 (<https://www.ufaw.org.uk/the-ufaw-journal/supplementary-material>), in which animals were required to wait between the CS and US, would seem to qualify.

Results from a number of studies show that behavioural transitions, commonly associated with anticipation, also increase with frustration. For example, Yayou *et al* (2009) show that ewes prevented from feeding (while watching other ewes feeding) expressed more than double the frequency of behaviours (212 behavioural elements during 60 min of observation versus just 100 elements expressed by control ewes). Kuhne *et al* (2013) reported increased frequencies of behaviours in hens during extinction trials (ie when the US no longer followed the CS). In combination, these results indicate that increased locomotion and behavioural transitions can also indicate frustration.

Whether the animal experiences anticipation or frustration may vary in relation to time after the CS when the US is provided. During the period immediately after a reward is signalled, but before the reward is normally provided, animals may experience positively valenced feelings of anticipation, but as the delay increases beyond the time when the US is expected, positive feelings may diminish and be replaced by frustration. If the behavioural response is associated with both anticipation and frustration, then total or instantaneous recordings of these behaviours will not allow for strong inferences. More direct behavioural, physiological or neurological measures of frustration may be helpful. In a study on lambs, Anderson (2016) found that vigilance towards where the reward would be presented was higher when the CS-US interval reached 1 min (following 15 repetitions with continuously increasing CS-US intervals) compared to the first, second and third minute, in a test lasting 3 min. Measures of how behavioural responses change over time may be helpful, but few studies to date have published a detailed time course of the behavioural responses during a trial.

Some studies on frustration have made specific predictions as to which behavioural responses are associated with the mental state. For example, studies on frustration have predicted and reported increased frequency of gavel-calls (Zimmerman & Koene 1998; Zimmerman *et al* 2000), aggression (Carlstead 1986; Haskell *et al* 2004), and redirected behaviours and displacement activities (Kuhne *et al* 2013), all believed to be associated with negatively valenced emotions. We call for increased use of specific, validated measures that better distinguish frustration from anticipation in animals.

Superstitious learning

In some experimental settings, animals may be exposed to situations where there is no behaviour that could improve access to the reward, for example, rats trained to associate a bell with being moved to an enriched cage (van der Harst *et al* 2003a). In such cases, it may be helpful to consider the animal’s perspective of the training regime. Specifically, how does the animal come to realise that the behaviours it performs around the time that the US is delivered are not causally related to this event? The animal may test various models of association and then try to assess which of these are best supported by their own experience. During this testing phase, the animal may (wrongly) associate certain behaviours with the delivery of the US.

In studies where a food reward has been presented using a regular schedule, a number of studies have shown that behavioural responses coincide with scheduled food presentation (eg Staddon & Simmelhag 1971; Staddon & Ayres 1975), perhaps because animals come to believe that the food presentation is associated with this behaviour. Skinner (1948) points out that “whenever we present a state of affairs which is known to be reinforcing at a given drive, we must suppose that conditioning takes place, even though we have paid no attention to the behaviour of the organism in

making the presentation". In other words, at an early stage in a classical conditioning protocol, a subject may receive the US at the time it is performing a specific behaviour, and thus come to associate the reinforcement with the behaviour. Such responses should be mostly expressed early in conditioning and should decline over repetitions given that the responses are not reinforced. The specific behaviours should also vary between subjects and likely even between conditioning events within a subject, which may explain the considerable variation in the anticipatory behaviours listed in Table 1 (<https://www.ufaw.org.uk/the-ufaw-journal/supplementary-material>). Perhaps animals simply express behavioural responses that they assume to be contingent with reward; in other words, the animals have unintentionally been trained to associate a behaviour with the reward. Taken to its conclusion, perhaps there is no 'true anticipatory behaviour' expressed by animals in all contexts; rather, the behaviours are simply those that happen to have been expressed around the time the US was presented. Examining differences in methodology between studies may provide insights into the aetiology of different anticipatory behaviours. We encourage researchers to document specific behavioural responses, when these were first observed during training, and how the frequency of these responses change over time. We predict that these behaviours will become less frequent with continued training, as the association between the behaviour and the US is extinguished.

The effect of study design

In cases where there is no clear behaviour that animals can express to affect the outcome, there is also no clear behavioural response that can be used to determine if the animal has learnt to associate the CS and US. According to Dickinson and Balleine (1994), goal-oriented responses require an instrumental contingency between behaviour and outcome. Using classical conditioning, it may be more difficult to assert that the subject has formed an association between the CS and US.

There are methodological biases that may affect attention toward CS. Pavlov (1927) describes an investigatory reflex (the 'what-is-it?' reflex; p 12) in response to changes in the animal's environment. According to Pavlov, this reflex was believed to depend on the perceived quality of the CS with the animal spending more time investigating the stimulus when needed. When a CS signals a predictable US, this orienting response should eventually decline (Kaye & Pearce 1984; Pearce & Kaye 1985), because once a strong CS-US association has developed less attention to the CS is required (Pearce 2008).

The method of reaching a CS-US interval may also affect the responses during the anticipatory period; all studies of anticipatory behaviour require at least some 'anticipatory' interval between the CS and US (Clark & Squire 1998), but the duration of this interval, and how it is achieved, may introduce confounds. A generally accepted procedure when studying anticipatory behaviour is to gradually build up the CS-US interval during which anticipatory responses can be

observed. The gradual increase in the CS-US interval has sometimes been slow (eg an increase of 1 s on every alternative session), and at other times more rapid (as much as 1 min from one repetition to the next; van den Bos *et al* 2003; Moe *et al* 2009). Longer intervals provide more time for responses to be observed but animals may perceive a long interval as an omission inducing frustration (Amsel 1992).

Some studies have trained subjects using a constant CS-US interval (eg 50 repetitions with a 3.5-s CS-US interval; Moe *et al* 2009) before gradually increasing the interval; by initially pairing the CS and US closely in time the association is easier to learn. Other studies employ a long CS-US interval from the outset; in one experiment by van der Harst *et al* (2003a), pair-housed rats were conditioned to anticipate an enriched cage following a CS-US interval of 10 min. In another experiment described by the same authors, single-housed rats were conditioned to anticipate an enriched cage but this time the CS-US interval was gradually increased from 0 to 10 min over 17 days. These rats showed almost double the number of behavioural elements compared to the rats in the previous design, perhaps because rats in the second study formed a stronger association between the CS and US. To avoid such confounds we recommend that studies use short initial intervals until animals achieve a strong association; once the association is established the CS-US interval may be increased to allow more time for expression of behaviours, although authors must acknowledge the potential for frustration.

The manner in which the animals are initially presented the CS may also be of importance. Suddenness, unpredictability, unfamiliarity and novelty are known to induce fear (Gray 1987; Forkman *et al* 2007) and affect behaviour (Boissy *et al* 2011). Thus, the behavioural response to an initial CS presentation, used as a baseline in some studies (eg van der Harst *et al* 2003b; Vinke *et al* 2004, 2006), may be related to fear. Imfeld-Mueller *et al* (2011) found that heart rate increased during the first CS presentation in pigs, but not during subsequent presentations. This result is consistent with the idea that animals were habituating to the CS, while also learning to associate CS with US. Therefore, to use the response to the initial CS presentation as a baseline measure may be problematic.

Animal welfare implications and conclusion

Anticipatory behaviours are highly variable with behavioural transitions appearing to be the only response that can be scored consistently. The observed differences in anticipatory behaviours may be caused by experimental design and superstitious learning; there is no basis for strong inferences regarding the expression of these behaviours and positive emotions. A more reasonable interpretation of differences in responses between conditioned and unconditioned subjects relates to a state of *wanting* in the conditioned subjects, acknowledging that this state is not necessarily experienced as pleasurable. Even though the state of wanting may not be pleasurable, it is of value to know how much animals want access to different resources (such as enrichment for laboratory animals). In this context, measures of these behaviours may be useful, although for

the reasons we have argued above these are likely to be less sensitive and specific than operant responses that animals have been specifically trained to perform.

Given that reward sensitivity is expected to increase and then decrease as the animal's welfare worsens, it is difficult to unambiguously interpret changes in reward sensitivity. Anticipatory behaviours used to assess reward sensitivity are unlikely to meet the criterion of Murphy *et al* (2014); ie that indicators of animal emotions should be sensitive enough to capture subtle differences between emotional responses. That said, the relative simplicity with which these responses can be measured means that they may provide a reasonable starting point for some studies.

We suggest that future research documents specific behaviours, how these behaviours change in relation to when the CS and US are normally presented, and how the behavioural responses change over the course of continued training. These data will help identify superstitious behaviours and may help disentangle anticipation and frustration. We also urge future studies to include behaviours that are validated as unambiguous indicators of positive versus negative emotional states.

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