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Extinction Reveals the Episodic Nature of Pavlovian Conditioning

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Running head: Episodic nature of Pavlovian conditioning

Key words: Pavlovian conditioning, Extinction, Partial reinforcement, Associative learning.

Acknowledgements. The author thanks Fred Westbrook and Bob Boakes for comments on an early draft of this article. The research was supported by funding from the Australian Research Council, grant DP 150101274.

Abstract. Many theories of conditioning describe learning as a process by which stored information about the relationship between a conditioned stimulus (CS) and unconditioned stimulus (US) is progressively updated upon each occasion that the CS occurs with, or without, the US. These simple trial-based descriptions can provide a powerful and efficient means of extracting information about the correlation between two events, but they fail to explain how animals learn about the timing of events. This failure has motivated models of conditioning in which animals learn continuously, either by explicitly representing temporal intervals between events, or by sequentially updating an array of associations between temporally distributed elements of the CS and US. Here, I review evidence that some aspects of conditioning are not the consequence of a continuous learning process but reflect a trial-based process. In particular, the way that animals learn about the absence of a predicted US during extinction suggests that they encode and remember these trials as single complete episodes rather than as a continuous experience of unfulfilled expectation of the US. These episodic memories allow the animal to recognise repeated instances of non-reinforcement and encode these as a sequence which, in the case of a partial reinforcement schedule, can become associated with the US. The animal is thus able to remember details about the pattern of a CS's reinforcement history, information that affects how long the animal continues to respond to the CS when all reinforcement is ceased.

Most associative models of Pavlovian conditioning describe a trial-based process in which each presentation of the conditioned stimulus (CS) that is followed by the unconditioned stimulus (US) progressively strengthens an association between the CS and US (e.g., Bush & Mosteller, 1951; Hull, 1943; Mackintosh, 1975; Miller & Matzel, 1988; Pearce, 1994; Pearce & Hall, 1980; Rescorla & Wagner, 1972; Wagner, Mazur, Donegan, & Pfautz, 1980). The most popular characterisation of this process identifies learning with an error correction algorithm that calculates on each trial the difference between some notional maximum strength (λ) that the CS-US association can take and the current strength of that association (V) based on what the animal has learned about the CS and US up to that trial. V is then updated as a proportion of this difference, as specified in the equation: $\Delta V = k \times (\lambda - V)$, where $0 < k < 1$ (Hull, 1943; Mackintosh, 1975; Miller & Matzel, 1988; Rescorla & Wagner, 1972). In effect, learning involves successive approximations of λ generated by each trial. This description of the learning process can be naturally extended to explain extinction of conditioned responding when the CS is no longer accompanied by the US. Each presentation of the CS without the US creates a negative prediction error that causes the learning algorithm to update V towards a new value of λ ($= 0$).

In these simple associative models, the trial is used as a convenient first approximation of the level at which to describe the conditioning process. However, this level of description misses important facts about learning phenomena which demonstrate that the conditioning process operates continuously both within and between trials. In Pavlovian conditioning, if the temporal interval between CS onset and the US is fixed, animals show clear evidence of timing their conditioned responses to peak close to the moment when the US should occur (at the end of the CS-US interval, e.g., Davis, Schlesinger, & Sorenson, 1989; Drew, Zupan,

Cooke, Couvillon, & Balsam, 2005; Harris, 2015; Kehoe & Joscelyne, 2005; Roberts, Cheng, & Cohen, 1989; Smith, 1968; Williams, Lawson, Cook, Mather, & Johns, 2008). Animals can even also learn about a backward temporal order between stimuli, and integrate this information across different sequences of stimuli (Savastano & Miller, 1998). Further, when the CS-US interval varies randomly from trial to trial, preventing the emergence of response timing within the trial, conditioning is still affected by the average length of each trial (Harris & Carpenter, 2011; Harris, Gharaei, & Pincham, 2011). Finally, there are many demonstrations that the acquisition and extinction of responding is affected by the time between trials, with long inter-trial intervals supporting better learning than short intervals (e.g., Barela, 1999; Barnett, Grahame, & Miller, 1995; Domjan, 1980; Gibbon, Baldock, Locurto, Gold, & Terrace, 1977; Lattal, 1999; Li & Westbrook, 2008; Morris, Furlong, & Westbrook, 2005; Sunsay & Bouton, 2008; Sunsay, Stetson, & Bouton, 2004). Animals can even learn that the likelihood of reinforcement is contingent on the length of the preceding inter-trial interval (Bouton & García-Gutiérrez, 2006; Bouton & Hendrix, 2011). These effects are entirely outside the scope of any model in which learning only operates on the whole trial as a single indivisible unit. Such evidence has motivated more elaborate associative models that allow the same, or similar, error correction algorithm to operate on a finer time scale within and between trials by treating time as a series of “micro-trials” (Desmond & Moore, 1988; Harris & Livesey, 2010; Kehoe, 1988; Killeen & Fetterman, 1988; Machado, 1997; McLaren & Mackintosh, 2002; Sutton & Barto, 1981, 1990; Vogel, Brandon, & Wagner, 2003; Wagner, 1981). The same evidence has also inspired an entirely different class of model in which temporal intervals, rather than associations, are the contents of learning, and animals make decisions to respond, or quit responding, based on information about rates of reinforcement extracted from stored memories of temporal intervals (Balsam, Drew, & Gallistel, 2010; Balsam & Gallistel, 2009;

Gallistel & Gibbon, 2000; Gibbon & Balsam, 1981; Gibbon, Church, Fairhurst, & Kacelnik, 1988).

The importance of time in conditioning, and the theoretical developments it has required, implies that the trial, in its conventional sense, has no place in any comprehensive description of how learning arises from the continuity of an animal's experience with the world. But is this conclusion too hasty? Trial-based learning is an efficient means to establish simple contingency information about whether one event implies another—does the occurrence of the CS mean that the US will also occur?—independently of more detailed information about when one event occurs relative to another. In this review I argue that, at some level, animals do indeed parse their experience into discrete episodes in memory, and these episodes encode whether, rather than necessarily when, events occur. This is particularly important for learning about, and remembering, the non-occurrence of some event, such as the absence of an expected US. Non-occurrences cannot be identified with any specific point in time, but can only be established over the episode as a whole. In keeping with this supposition, the strongest evidence for trial-based learning comes from experiments investigating extinction or learning under conditions of partial reinforcement when trials without the US are intermixed among trials with the US.

Learning about non-reinforcement

By assuming that learning proceeds on a fine-grained (sub-trial) time scale, associative models can account for evidence that animals learn when the US occurs within a trial, but this approach faces a separate challenge to specify when animals learn about non-reinforcement. As noted by Gallistel (2009, 2011, 2012), this type of model must treat the absence of the US as an event even though, by definition, nothing has occurred. The problem of when does the

animal learn about non-reinforcement may be addressable in cases where the timing of the US is entirely predictable, such as when the interval between the CS and US is fixed. In such cases, there is an identifiable moment that the animal expects the US to occur, and that is the moment when the absence of the US is detected and learning based on a negative prediction error occurs¹. However, this reasoning doesn't work when animals have been trained with stochastic reinforcement schedules that deliver the US at a randomly varying time or on a randomly-selected proportion of trials. In Gallistel's (2012, p 69) words:

“during extinction, there is no time at which, nor any response or CS following which, a non-reinforcement can objectively be said to have occurred. The updating in response to non-reinforcement must occur at a specific moment in time, but it is in principle impossible to say whether there was in fact a non-reinforcement at that moment or not. One may wonder how it is, then, that formalized associative models explain the consequences of nonreinforcements. In most cases, the answer is that a god outside the machine (the modeler) decrees the “trials” on which nonreinforcements occur.”

This provocative rhetoric may mischaracterise the problem, in that associative models don't need to “decree” when non-reinforcement occurs. Any trial, or micro-trial, that does not include the US will generate a negative prediction error that leads to updating of the association strength. The problem is to specify the temporal unit of a trial or micro-trial. This is a problem for real-time associative models because the timing of micro-trials cannot be

¹ Objective evidence for this negative prediction error moment has been reported by Waelti, Dickinson and Schultz (2001) who recorded activity in mesolimbic dopamine neurons in monkeys while they learned that a CS signaled a droplet of apple juice (US). The dopaminergic neurons became active in response to an unsignaled US but not when the US was signaled by the CS, and, on CS trials when the US was omitted, the dopaminergic neurons were suppressed at the moment when the US should have occurred.

objectively determined. There is nothing to dictate how short a micro-trial is or how frequently they occur. In this sense, it is left to the modeller to invent a time-scale on which V is routinely updated. The issue is different for the traditional trial-based model where the non-reinforced trial is an objectively specified event spanning the period from the onset to the offset of the CS. As already noted, the fact that this type of model does not attempt to specify when *during* the non-reinforced trial V is updated, it cannot account for the effect of CS-US interval on conditioning. However, this approach may still be relevant for modelling the learning process if animals encode trials as whole episodes (in addition to encoding durations). Later, I describe evidence that animals do indeed learn about non-reinforcement in this way. That is, instead of learning continuously about the absence of reinforcement, the animal learns once per trial. As such, the challenge for the model is not to specify when non-reinforcement occurs, but to specify when the animal recognises that the trial has not been reinforced. But first, I will describe evidence that animals do learn about non-reinforcement continuously within trials, in keeping with assumptions of real-time models.

The assertion that animals learn continuously about the absence of reinforcement makes the clear prediction that long CS-US intervals should produce weaker conditioning than short CS-US intervals because long intervals contain more non-reinforced exposures to the CS. However, attempts to compare the strength of responding to CSs with different CS-US intervals is usually confounded by differences in the timing of responding across the trial when the CS-US intervals are fixed. This problem can be solved using randomly varying CS-US intervals that prevent animals from timing their responses to the CS-US interval. When animals are trained with random CS-US intervals, they respond at consistent rate across the length of the CS-US interval (Harris & Carpenter, 2011; Harris et al., 2011), rather than showing evidence for specific timing of US expectancy (Harris, 2015), which makes it

meaningful to compare the overall strength of responding between CSs that have different average CS–US intervals. Under such conditions, long CS-US intervals do indeed lead to weaker responding than short CS-US intervals (Harris & Carpenter, 2011), consistent with the assumption that the negative impact of non-reinforcement accumulates continuously across the length of a trial. Moreover, this continuous impact of non-reinforcement carries over between trials in a way that suggests that the trial itself is irrelevant to learning about non-reinforcement. Specifically, rats show no difference in how they acquire responding to a CS that is reinforced on every trial versus one that is only reinforced on some trials (e.g., one in three) if the first CS is longer than the second such that the cumulative duration of exposure is the same for the two CSs (e.g., a CS that is reinforced on one in three trials with a mean CS-US interval of 10 s has the same cumulative reinforcement rate as a consistently reinforced CS with a mean CS-US interval of 30 s, Harris, Patterson, & Gharaei, 2015). In other words, 30-s of non-reinforced exposure to the CS had the same impact on the acquisition of conditioning whether it occurred continuously within a single trial or was split across 3 separate trials (two ending without any US). This implies that non-reinforced trials *per se* have no detectable effect on conditioning. However, as is described below, this conclusion depends on how the strength of conditioning is measured. Other evidence shows that rats do indeed learn about the significance of each non-reinforced trial, even when their acquisition of responding during the CS shows no evidence for that learning.

Is extinction learning continuous?

If animals learn continuously about non-reinforcement during each trial, then a simple implication is that extinction of Pavlovian CRs should be sensitive to the total amount of non-reinforced exposure to the CS. Indeed, for a model like Rate Estimation Theory (Gallistel &

Gibbon, 2000) where extinction depends entirely on the cumulative duration of exposure, the number of individual trials has no bearing on when responding extinguishes. This means that many short exposures to a CS should produce as much extinction as a few long exposures if the cumulative duration of those exposures is matched. Several studies have tested this prediction, but only the first produced data consistent with it. That experiment, by Shipley (1974), examined the role of cumulative duration of CS exposure in the extinction of rats' conditioned fear of a tone that had been paired with shock. During the extinction session, different groups received either short (25 s) or long (100 s) presentations of the tone; the number of presentations also differed between groups such that the total duration of CS exposure was either 200, 400, or 800 s. On a subsequent test, residual fear of the tone was inversely related to total CS exposure during extinction, and rats given the same total duration of extinction exposure showed the same amount of fear, regardless of differences in the number of extinction trials or the length of each trial. However, four different labs have subsequently investigated this same issue, using appetitive and aversive conditioning paradigms, and none found that extinction is adequately accounted for by total duration of CS exposure (Drew, Yang, Ohyama, & Balsam, 2004; Golkar, Bellander, & Öhman, 2013; Harris & Andrew, 2017; Haselgrove & Pearce, 2003). In each case, the loss of responding was more closely related to the number of extinction trials than the total duration of those trials.

Extinction of responding should be accounted for entirely by cumulative CS exposure if the process responsible for extinction is uniformly continuous, that is if the rate of learning about the absence of the US is constant across the length of a trial. If, instead, the rate of learning changes within a trial, then extinction will not be directly proportional to total CS exposure. For example, if the associability of the CS declines across the length of a trial (as assumed by the real-time associative model SOP, Wagner, 1981), the first half of a CS

presentation will produce more extinction than the second half, and therefore two short trials will produce more extinction than one long trial that is matched for total time. This prediction is consistent with what most of the relevant studies have found (Drew et al., 2004; Golkar et al., 2013; Harris & Andrew, 2017; Haselgrove & Pearce, 2003).

Another reason why the rate of learning might change within a trial is if animals have learned to expect the US at a specific time after CS onset. In this case, extinction learning could increase during the trial, to peak when the trial length matches the CS-US interval. Evidence consistent with this was provided by Drew et al. (2004) who measured extinction of key-peck responses by pigeons that had been trained with a fixed 8-s CS-US interval. Extinction trials were either shorter than (4 s), equal to (8 s), or longer than (16 s or 32 s) the CS-US interval. The amount of extinction was assessed in a final test session in which all CS presentations were again 8 s so that all groups were now matched for their opportunity to respond to the CS. Drew et al. found that pigeons given 4-s presentations of the CS during extinction responded more on test than the groups given longer presentations during extinction; this was true even when the number of extinction trials was increased for the 4-s group to match their total duration of exposure to the CS. This confirms that there is less learning during the early part of an extinction trial before the expected time of US delivery. A corollary of this argument is that there should be relatively little further learning on extinction trials that extend beyond the expected time of the US. Consistent with this, Drew et al. found that pigeons given 16-s exposures showed no more extinction than those given 8-s exposures. However, where one might expect the same to be true for pigeons given very long (32 s) exposures during extinction, these pigeons showed less extinction than those given 8 or 16-s exposures. Drew et al. interpreted this result as showing that extinction is facilitated by changes in the duration of the CS from conditioning to extinction because this reduces

generalization of excitation from conditioning to extinction, but a return to the conditioning duration results in a recovery of responding.

The evidence presented by Drew et al. (2004) shows that extinction is not uniform within a trial if animals have been trained with a fixed CS-US interval, consistent with the idea that extinction learning tracks variations in the expectancy of the US. But it leaves unanswered the question whether extinction learning proceeds continuously within a trial. For example, extinction learning may occur at a discrete moment within the trial that approximates the expected time of the US, or it may accrue continuously but at an accelerating rate as the expected time of the US approaches in the trial. In the latter case, there is also a question whether extinction accrues in direct proportion to the moment by moment expectation of the US or whether there are other systematic changes in the rate of extinction learning across a trial, as predicted by a model like SOP (Wagner, 1981). Progress in addressing these issues can be made by studying the extinction of CRs that have been established with a variable CS-US interval during conditioning, so that the likelihood, and thus the expectancy, of the US is uniform across the length of the trial. Under these conditions, if extinction learning is continuous and directly proportional to US expectancy, then the amount that a CR extinguishes should be directly proportional to the total duration of CS exposure, akin to the findings reported by Shipley.

Harris and Andrew (2017) recently performed a series of experiments looking at extinction of magazine activity in rats during CSs that had been conditioned with randomly varying CS-US intervals. They confirmed what had been reported already (Drew et al., 2004; Golkar et al., 2013; Haselgrove & Pearce, 2003), that extinction was directly related to number of extinction trials and was not accounted for by the total duration of exposure to the CS. For

example, when responding to two identically-conditioned CSs was extinguished using either five 20-s trials or 20 5-s trials (thus matching cumulative duration), responding to the 5-s CS extinguished within fewer sessions than did responding to the 20-s CS (see Figure 1A). The most striking finding, however, was that length of trial had no detectable impact on extinction. Thus, when the data from the two CSs was plotted to match them on number of extinction trials, there was no difference in the rate of extinction despite the four-fold difference between the CSs in the duration of each trial (Figure 1B). In another experiment, a five-fold difference in CS duration failed to produce any increase in extinction when number of extinction trials was held constant (Figure 1C). In their final experiment, Harris and Andrew trained rats with two CSs that were 40-s long and included a food pellet delivered at a random time during each CS presentation (rather than at CS offset, as done in the preceding experiments). Responding to these two CSs was then extinguished by an equal number of non-reinforced presentations that were short (10 s) for one CS and long (40 s) for the other. Each extinction session included a single 40-s presentation of the short CS so that responding could be measured across the full length of that CS in order to be compared with responding to the long CS. Despite the four-fold difference in the length of each extinction trial, and thus the total CS exposure, once again there was no difference in the rate of extinction for the two CSs (Figure 1D). Therefore, not only is extinction not linearly related to the length of CS exposure, but at least in these data the amount of extinction did not scale at all with trial length. Harris and Andrew concluded that extinction learning is not in any sense continuous across a trial but occurs at a single point in the trial, even when the timing of the US is unpredictable.

----- Figure 1 about here -----

Extinction as trial-based learning

The conclusion reached by Harris and Andrew (2017) raises an important question. Why should extinction learning, at least in their conditioning procedures, occur at a single discrete time rather than continuously throughout the trial? Extinction might occur at a discrete time after conditioning with a fixed CS-US interval if there is a specific moment in the trial when the animal expects the US to occur. However, in all of Harris and Andrew's experiments, the CS-US interval varied randomly, which should create a uniform expectancy of the US across the length of each extinction trial (an assumption that was confirmed by the uniformly elevated levels of magazine activity the rats showed across the length of each trial). If extinction is the direct product of US expectancy, or even the consequence of non-reinforced responding as suggested by Rescorla (2001), then it should accrue continuously across the length of each trial. That was clearly not the case.

The reasoning behind the claim that extinction should be continuous assumes that each moment in the trial generates an independent prediction error, as if the animal is repeatedly expecting the US and repeatedly learning that it is absent. For that to be appropriate, the probability of the US at any time point during the trial should be independent of every other point within the same trial, which would mean that multiple USs could be delivered within a single trial (and some trials might not include any USs). However, that was not true of the experiments presented by Harris and Andrew (2017). In those experiments, as for most experiments on Pavlovian conditioning, the US was delivered only once per trial. If the animal learned to expect only one US per trial, then even though that expectation might be sustained over the full length of a trial, the animal should learn that each extinction trial constitutes only one instance of a US being predicted but failing to occur. This implies that

animals learn two things about a CS-US association: they learn the probability that the US will occur on each trial, as a discrete event, and they learn the probability of the US occurring at each moment in time when the CS is present.

If there is a single time point during the trial when animals learn that an expected US has not occurred, when is that moment? Logically, if the animal can reliably estimate when the US should have occurred, then extinction might be tied to that time. For example, if, as is often the case, delivery of the US coincides with termination of the CS, then extinction learning might occur at the very end of each extinction trial, even when the timing of the US relative to onset of the CS is variable. In this case, extinction would only depend on the number of trials (or number of CS terminations) rather than the length of those trials. However, in Harris and Andrew's (2017) final experiment, described above, the US occurred at a random time during the 40-s CS, such that neither the onset nor offset of the CS provided specific information about the timing of the US. One possibility is that extinction learning occurs at a random time during each trial, consistent with the random timing of the US during conditioning in the experiments by Harris and Andrew. Nonetheless, one should still see an effect of trial length on extinction because long trials will have a greater probability than short trials of including a randomly timed extinction moment. Therefore, the only time points that are not affected by trial length are the start and end of the trial, since every trial, no matter how long, has a single start and a single end. Since the animal could not know at the start of the trial whether the US was going to occur or not, it must be at the end of the trial that the animal detects the discrepancy between what it expected and what occurred. Logically, the end is the only part of the trial when the animal can in any sense know that the US has not occurred on that trial.

If extinction learning does occur at the end of a trial, might we see something in the behaviour of the animal after the termination of the trial that speaks to this fact? To answer this question, Harris and Kwok (2018) conducted a series of experiments that measured rats' magazine activity both during and after presentations of two CSs that signalled delivery of food at a random time during the CS. One of the CSs was consistently reinforced (CRf), being paired with food on 7 out of 8 trials in each conditioning session (the one non-reinforced trial was included so that magazine activity during and after the CS could be measured without contamination by the presence of the US). The other CS was partially reinforced (PRf), being paired with food on 7 out of 24 trials. Presentations of this CS were much shorter than the CRf CS (20 s versus 60 s) so that their total reinforcement rates were matched (one US per 60 s). The rats responded at the same rate during the two CSs, just as we had reported previously in similar experiments (Harris et al., 2015). Despite this, there was a marked difference in how responding during the CSs extinguished—responding during the PRf CS persisted much longer than responding during the CRf CS, confirming the existence of a Partial Reinforcement Extinction Effect (PREE, Jenkins, 1950; Mackintosh, 1974). That is, the rats learned more about the absence of the US on each extinction trial of the more consistently reinforced CS, even though their expectancy of reinforcement, as shown by their magazine activity, appeared to be the same during the two CSs. However, if extinction depends on a post-trial process to recognise that an expected US was absent, then we should see differences between the two types of trials in post-trial responding. That is what Harris and Kwok observed. Throughout the conditioning sessions, when the rats were responding at equally high rates during the PRf and CRf CSs, they responded significantly more after non-reinforced trials with the CRf CS than after non-reinforced trials with the PRf CS (Figure 2). The implication of this result is that rats continued to expect the US after offset of the CRf CS but showed less expectation after

offset of the PRf CS. This difference could explain why responding to the CRf CS extinguished more quickly than to the PRf CS.

----- Figure 2 about here -----

Partial reinforcement and extinction

In the analysis above, I have argued that extinction learning occurs at the end of a non-reinforced trial because this is the first moment at which the animal can know that an expected US has not occurred, particularly under conditions when the CS-US interval was variable so that the US was equally likely to occur at any time during the CS. If extinction on any given trial depends on retrospective recognition that a US has been missed, then it should be sensitive to how reliably the CS has been reinforced in the past. That is, if a CS has been conditioned on a consistent reinforcement schedule where every trial included a US, then the animal should know that each occurrence of the CS (trial) will bring a US, and thus every extinction trial represents a missed US. However, if the US had only occurred on some trials during conditioning (i.e., under partial reinforcement), then the animal should only expect the US to occur on some trials and should only detect that a US has been missed on some extinction trials. In other words, responding should take more trials to extinguish after partial reinforcement than after continuous reinforcement. As mentioned in the preceding paragraph, there is a wealth of evidence showing that extinction is slower after partial reinforcement than after consistent reinforcement.

The PREE is an important test for any account of extinction. According to a simple associative account, consistent reinforcement should establish a stronger association than partial reinforcement, and therefore responding to the partially reinforced CS should extinguish more quickly. The PREE shows that the opposite is usually true. Indeed, even when

comparing between partial reinforcement schedules, the leaner the reinforcement rate during training, the greater the resistance to extinction (e.g., Bacon, 1962). While the PREE is somewhat problematic for associative theories, RET offers a relatively straightforward account of the phenomenon. According to RET, PRf leads to slower extinction because the rate of reinforcement is lower under the PRf schedule than a CRf schedule, and therefore it takes longer (more cumulative CS exposure) to acquire evidence that the reinforcement rate has decreased after PRf (Gallistel & Gibbon, 2000). As noted already, RET incorrectly predicts that the amount of extinction in general will be explained by cumulative CS exposure rather than by number of extinction trials. However, it makes several other testable predictions about the PREE.

One of RET's predictions is that the PREE can be eliminated—a CRf and PRf CS will extinguish equally quickly—if the length of each extinction trial is extended for the PRf CS (Gallistel & Gibbon, 2000). For example, if a CRf CS has been reinforced on every trial and a PRf CS has been reinforced on one in every 4 such trials, then it should take 4 times as much extinction exposure to the PRf CS to establish that the reinforcement rate has changed. However, this prediction has not been supported under direct test (Bouton, Woods, & Todd, 2014; Chan & Harris, 2017). Another prediction by RET is that the PREE should be eliminated if, during conditioning, the total reinforcement rate of the PRf CS is matched to that of the CRf CS. For example, if the length of each conditioning trial of a CRf CS is three times longer than the length of each conditioning trial of a PRf CS reinforced on one third of trials, then the two CSs will have the same total rate of reinforcement despite a difference in how consistently they were reinforced per trial. Several groups have conducted experiments to test this prediction, and all have failed to support it (Bouton et al., 2014; Chan & Harris, 2017, 2019; Harris & Kwok, 2018; Haselgrove, Aydin, & Pearce, 2004). In each case, responding to

the partially reinforced CS took longer to extinguish than responding to the consistently reinforced CS. These findings highlight the fact that, just as extinction appears to occur once per trial rather than continuously within a trial, extinction is also sensitive to the likelihood of reinforcement per trial during conditioning rather than the rate of reinforcement per unit time.

While RET appears to be mistaken in its emphasis on time, rather than trials, as the unit of extinction learning, it has offered some useful ways of describing how events are processed during extinction. For RET, an animal updates its estimate of the reinforcement rate of a CS each time that an expected US is missed (Gallistel & Gibbon, 2000). The decline in responding is directly linked to the number of missed USs. This notion that extinction occurs when the animal recognises it has missed an opportunity for reinforcement is consistent with the arguments developed here that extinction is trial-based rather than continuous because each trial is an opportunity for reinforcement. It easily explains why, for example, a lower per-trial rate of reinforcement produces greater resistance to extinction (Bacon, 1962).

This description of the extinction process generates an interesting and very specific prediction. It says that if a CS has been reinforced on every n th trial during conditioning, then during extinction the animal will only learn about the absence of expected reinforcement every n trials. Therefore, responding to this CS will take n times as many trials to extinguish than will responding to a consistently reinforced CS. One way to test this prediction is to give the partially reinforced CS n times as many extinction trials as the consistently reinforced CS, which should eliminate the difference in responding across extinction sessions. This was the approach taken in recent experiments by Bouton et al. (2014) and Chan and Harris (2017). Bouton et al. compared responding across a single session of 48 extinction trials between a

consistently reinforced group and a partially reinforced group, for the latter group the CS had been reinforced on one in four trials. As expected, rats in the partial group responded more across the extinction session than did rats in the consistent group. However, when they compared the first 12 extinction trials for the consistent group with responding on every fourth trial (totalling 12 trials) for the partial group, there was no difference in mean response rate. Chan and Harris made an equivalent demonstration. They trained one group of rats with two CSs, one reinforced on every trial and the other on one in three trials, before extinguishing responding to both CSs concurrently. Evidence for a PREE was eliminated if each extinction session contained three times as many trials of the partially reinforced CSs as trials of the consistently reinforced CS.

While the results reported by Bouton et al. (2014) and Chan and Harris (2017) are consistent with the prediction that a schedule that reinforces one in n trials will slow extinction by a factor of n , those particular findings rely on null results which weakens any conclusions that can be drawn from them. A stronger test of the prediction would involve comparing between a consistently reinforced CS and a partially reinforced CS, under identical extinction conditions, and measuring the number of trials taken for responding to extinguish in each case. This number should be n times larger for the partial CS than the consistent CS.

Chan and Harris (2019) have recently conducted a series of experiments to compare rates of extinction after consistent and partial reinforcement. In two of these experiments, two groups of rats were trained with a CS that was either consistently reinforced (Group CRf) or partially reinforced (Group PRf). For both groups, the CS was reinforced using a variable CS-US interval and the mean duration of the CS differed between the groups such that the total rate of reinforcement was equated between the groups. This ensured that acquisition

of responding to the CS was well matched between the two groups, and therefore extinction would be measured over the same range of the response scale for the two groups. This was crucial to make any precise comparison between the groups in the rates of extinction. After 20 conditioning sessions, responding to the CS was extinguished in both groups using an identical schedule of CS presentations. The PRf group responded significantly more across the extinction phase than did the CRf group, confirming the existence of a PREE. Two methods were then used to identify when responding began to decrease across trials in the extinction sessions². The data obtained using these two methods supported the same conclusion. In one experiment, the PRf group was trained with a CS reinforced on 1 in 3 trials, and it took almost exactly 3 times as many trials to commence extinction as did the CRf group. In another experiment, the PRf group was trained with a CS reinforced on 1 in 5 trials, and it took almost exactly 5 times as many trials to commence extinction as did the CRf group. In a third experiment, Chan and Harris compared two PRf groups, one trained with a CS reinforced on 33% of trials and the other with a CS reinforced on 66% of trials. They found that the 33% group took almost exactly twice as many trials to extinguish as the 66% group, consistent with the two-fold difference in their reinforcement rates. Collectively, these experiments provide clear evidence that the rate of extinction is directly linked to the rate of reinforcement, consistent with the idea that extinction learning occurs whenever the animal recognises that it should have received a US but none occurred.

The strength of the evidence just described can be quantified using Bayesian methods to calculate the likelihood, given the data, that the start of extinction is directly tied to the

² One method fitted an inverse cumulative Weibull function to the response rates on each trial of the extinction phase. The trial on which this function had decreased in height by 10% of its starting value was used to estimate the onset of extinction. The second method used the cumulative response record to identify the first trial on which the response rate was noticeably lower than the rate projected forward from the end of the acquisition phase.

rate of reinforcement during conditioning. I present such an analysis here using the data reported by Chan and Harris (2019). For this analysis, I have used the logarithm of the number of trials to commence extinction for each rat because a preliminary analysis showed that the distribution of trials to extinction was positively skewed and approximated a log-normal distribution (see [Figure 3A and 3B](#)). Within each experiment, the likelihood function was computed for the log-transformed data of each group to calculate the marginal likelihood of the hypothesis that the ratio of trials to extinction for the two groups was equal to the ratio of their reinforcement rates. Bayes factors, calculated as the ratio of this marginal likelihood and the likelihood of there being no difference between the two groups, revealed strong evidence in favour of the predicted effect in each experiment: $BFs = 38:1$ (for the difference between groups given 66% and 33% reinforcement), $10^9:1$ (for groups 100% and 33%), and $3 \times 10^6:1$ (for groups 100% and 20%). However, a more informative comparison is between the likelihood of the exact difference predicted here and the likelihood of some less specific PREE. Thus, the marginal likelihood of our specific hypothesis was compared to the marginal likelihood of a weakly specified hypothesis that the difference between the groups could lie anywhere between a very small PREE (the PRf group would take 1.1 times longer to extinguish) and a large PREE (the groups would differ 5-fold). In each of the three experiments, Bayes factors from these marginal likelihoods (see [Figure 3C](#)) showed that the evidence favoured the specific hypothesis over the weakly specified hypothesis: by 2.5:1 (comparing groups given 66% and 33% reinforcement), 3.5:1 (for groups given 100% versus 33% reinforcement), and 4:1 (for groups given 100% versus 20% reinforcement). Thus, each single experiment provided relatively weak evidence in support of our specific hypothesis.

However, when the evidence from all three experiments is combined, the odds are 32:1³ in favour of the hypothesis that the number of trials to extinction is directly proportional to the reinforcement rate.

----- Figure 3 about here -----

Sequential Theory and within-subjects PREE

The idea developed here is that, in the course of conditioning, the animal learns how often per trial to expect the US; after this it will show some extinction of responding on each occasion that it recognises that it has missed an expected US. This idea bears much in common with Capaldi's (1966, 1994) account of the PREE. Like most of its contemporaries, Capaldi's Sequential Theory treats the PREE as a generalisation effect controlled by the presence or absence of "after-effects" that follow reinforcement or non-reinforcement. For Capaldi, these after-effects were memories of being reinforced or of the absence of expected reinforcement. If an animal is conditioned on a consistent reinforcement schedule, each pairing of the CS and US occurs in the presence of a memory of reinforcement from the preceding trial. This memory then becomes part of the stimulus configuration that signals the US. During extinction, the memory of reinforcement is replaced by a memory of recent non-reinforcement, which produces a generalisation decrement that weakens responding. When an animal is conditioned on a partial reinforcement schedule, it experiences non-reinforced trials intermixed among reinforced trials, and some pairings of the CS and US will occur in the presence of a memory of recent non-reinforcement. This means that the memory of non-

³ This is the product of the 3 individual Bayes Factors. It is equivalent to the ratio of the joint probability of all three hypothesized effects and the joint probability of the weakly specific hypotheses for each experiment. In other words, it tests the odds of getting a 2-fold, a 3-fold, and a 5-fold effect across the three experiments versus an effect anywhere between 1.1 and 5-fold in each experiment.

reinforcement becomes part of the configuration signalling the US, such that the experience of non-reinforcement during extinction serves to promote responding and therefore delay the onset of conditioning. This is somewhat analogous to Skinner's (1938) argument that animals given instrumental conditioning on a $1:n$ ratio schedule learn about the whole sequence of n responses as a single unit that is reinforced, and therefore perform many more responses under extinction because the omission of reinforcement is only detected after n responses have been produced (Mowrer & Jones, 1945).

In describing the after-effects of non-reinforcement as memories, Sequential Theory can allow them to be re-activated (retrieved) across long inter-trial intervals. Therefore, the theory can account for demonstrations of the PREE that introduced long intervals (e.g., 24 h) between non-reinforced trials and subsequent reinforced trials (Weinstock, 1954), which are otherwise difficult to explain if the after-effect is a transient reaction (Amsel, 1962; Sheffield, 1949). It also means that the memory of non-reinforcement does not only extend as far back as the most recent trial but can include a sequence of non-reinforced trials. Therefore, when an animal is trained with a partial schedule, reinforced trials occur in the presence of the memory of a run of multiple non-reinforced trials that led up to the reinforced trial. As a result, during extinction, the animal will persist in responding across repeated non-reinforced trials because it remembers being reinforced after a string of non-reinforced trials. In other words, generalisation of conditioning will only break down, and responding extinguish, when the number of non-reinforced trials during extinction exceeds the number of consecutive non-reinforced trials the animal experienced during conditioning. Moreover, because the run of non-reinforced trials in memory gets longer as the partial reinforcement schedule gets leaner, the theory can predict that the onset of extinction will be delayed by an amount

inversely proportional to the reinforcement rate per trial during conditioning (Chan & Harris, 2019).

A major challenge for Sequential Theory, as well as its contemporaries (e.g., Frustration Theory, Amsel, 1958, 1962), is to account for evidence that a PREE can be observed within-subjects. In a within-subjects design, animals are concurrently trained with a CS that is consistently reinforced and a second CS that is reinforced on a partial schedule, before responding to both CSs is extinguished. According to Sequential Theory, the fact that training trials of the consistent CS are intermixed among trials with the partial CS means that both CSs are reinforced in the presence of memories of recent non-reinforcement. Therefore, non-reinforcement during extinction will promote generalisation of responding to both CSs equally, which should eliminate any difference in the rate of extinction for the two CSs. A similar prediction is made by Frustration Theory—during the intermixed training, both CSs are reinforced in the presence of frustration elicited on non-reinforced trials of the partial CS, such that frustration becomes counter-conditioned and can promote, rather than interfere with, responding to both CSs during the extinction phase. This prediction has received some support from studies that failed to find evidence for a PREE using a within-subjects design (Amsel, Rashotte, & Mackinnon, 1966; Pearce, Redhead, & Aydin, 1997), but of course a null effect can offer at best only weak support for any theory. More crucially, the prediction has been disconfirmed by a growing number of demonstrations of a within-subjects PREE.

In the first of these demonstrations, Crawford, Steirn and Pavlik (1985), compared extinction of autoshaped key-peck responses in pigeons that had been trained with one key-light reinforced on 100% of trials and a second key-light reinforced on 50% of trials. Although they did not observe a difference in extinction of responding when the two CSs were

presented one at a time, they did observe a more persistent preference for the 50% CS than the 100% CS during choice test trials, indicative of greater resistance to extinction for the 50% CS. Rescorla (1999) reported a series of experiments, also using autoshaped key-peck responses in pigeons, that demonstrated a within-subjects PREE. More recently, we have conducted many experiments that have documented clear evidence for a PREE using a within-subjects design with rats trained in a magazine approach paradigm (Chan & Harris, 2017, 2019; Harris & Kwok, 2018; Harris, Kwok, & Gottlieb, submitted).

Those studies demonstrating a within-subjects PREE adopted procedures that may have made them particularly sensitive to detecting differences in the rate of extinction. The experiment by Crawford et al. (1985) used a choice test in which both the 50% and 100% CSs were presented simultaneously, as a method to compare directly the residual conditioning strength of the two CSs. In Rescorla's (1999) experiments, he included additional CSs that were reinforced throughout the entire experiment so that the food reinforcer continued to be delivered during the phase in which the consistent and partial CSs were extinguished. He argued that this feature increased the similarity between conditioning and extinction phases, thereby improving the generalisation of responding between those phases. Our own experiments (Chan & Harris, 2017, 2019; Harris & Kwok, 2018; Harris et al., submitted) also incorporated another CS that was reinforced throughout the experiment, again to reduce any generalisation decrement arising from the complete loss of a salient event (delivery of the US) that might otherwise lead to rapid extinction of all magazine activity and mask differences in response rate between a consistent CS and a partial CS. Our experiments also ensured that the two CSs were well matched for level of conditioned responding prior to extinction, thus avoiding the problem of comparing rates of change in responding at different locations on the response scale.

To the extent that these various measures were important in revealing a within-subjects PREE, one might conclude that the effect is at least weaker than the PREE observed between-subjects. However, one finding from the study by Chan and Harris (Chan & Harris, 2019) suggests that this is not the case. In addition to the between-group experiments described earlier, Chan and Harris also ran a within-subjects experiment in which one group was conditioned with a CS reinforced on 100% of trials and a CS reinforced on 33% of trials. Not only did the rats respond more to the 33% CS during extinction, but when Chan and Harris measured the rate of extinction for the two CSs, they found that the rats took almost exactly 3 times as many trials to commence extinction of responding to the 33% CS than the 100% CS. In other words, the magnitude of the PREE in this within-subjects design was the same as that using a between-subjects design. A comparable result has been obtained in another recent experiment in our lab demonstrating a within-subjects PREE (Experiment 1, Harris et al., submitted). In that experiment, rats were conditioned with a 100% CS and a 50% CS that were matched for total reinforcement rate, and subsequently showed slower extinction of responding to the 50% CS. Using modified Weibull functions fitted to the extinction data to extract an estimate of the onset of extinction, these data show that it took just over twice as many trials for responding to extinguish by 10% for the 50% CS than for the 100% CS (23.9 trials versus 11 trials). Therefore, the strength of the PREE observed within subjects has the same relationship to reinforcement rate as the PREE observed between subjects.

Trials and episodic memory

Does the evidence for a within-subjects PREE refute the idea that it is due to differences in generalisation of responding from conditioning to extinction, as proposed by accounts such as Sequential Theory and Frustration Theory? It is hard to see how those

theories, as originally stated, can explain the presence of a within-subjects PREE. Nonetheless, the theories can be elaborated to account for the CS-specific differences in rate of extinction described above. This requires the assumption that the after-effects of non-reinforcement are not just about the absence of the US itself but incorporate the CS as well. For Sequential Theory, the animal would not simply carry a memory of non-reinforcement from one trial to the next, but would remember which particular CS had not been reinforced on the previous trial. When the animal next encounters that CS, it retrieves a memory of the earlier non-reinforced trial of that CS, and if the current trial is reinforced then the memory itself becomes associated with the US. Therefore, after training with both a partially reinforced CS and a consistently reinforced CS, the animal will have memories of non-reinforced trials of the partial CS that are themselves associated with US, but will have no equivalent memory of the consistent CS. As a result, during subsequent extinction of both CSs, memories of non-reinforcement that are associated with the US will only be retrieved during presentations of the partial CS, and responding will be maintained for this CS but not the consistent CS. A similar case can be made for Frustration Theory⁴.

The extension described here to enable Sequential Theory to explain the within-subjects PREE makes particular use of the idea that animals have specific memories of non-reinforced trials with a particular CS. But the nature of such memories implies something special. They constitute a memory for a prior event that was defined by the presence of one

⁴ In this case, the animal is not simply frustrated after failing to receive an expected US, it is frustrated with the specific CS that signalled the US on that trial. Therefore, frustration with the partial CS will itself become associated with reinforcement during conditioning, which will help to maintain responding during extinction of that CS. Responding to the consistent CS will not be preserved because the animal's frustration with that CS, that develops across extinction trials, has not been counter-conditioned with reinforcement. However, I focus in this review on Sequential Theory because it can more successfully accommodate evidence that the PREE survives even with very long (24 h) inter-trial intervals during conditioning, and it can predict that the number of non-reinforced trials per reinforced trial will directly determine how much extinction is delayed following partial reinforcement.

object (the CS) but also by the absence of another (the US). To form or retrieve a memory that specifies what did not occur requires recognition of an event as a single temporally-bounded episode—to say that something did not occur requires specifying *when* it did not occur. Either the animal has a sequence of separate memories of each moment during the trial when the US did not occur, or more plausibly it has a memory of the trial as a single episode that did not include the US—what is, in effect, an episodic memory.

The appeal to discrete episodic memories of non-reinforced trials is consistent with evidence that extinction is bounded by time and place (extinguished responses can spontaneously recover over time and can be renewed if the CS is presented in a different context, Bouton, Westbrook, Corcoran, & Maren, 2006). It also provides a basis from which to address a further challenge: to account for the observations made by Chan and Harris (2019) that the onset of extinction is delayed by an amount exactly proportional to the number of non-reinforced trials per reinforced trial during conditioning. To show such specific sensitivity to partial reinforcement, animals must do more than simply remember on each reinforced trial with the partial CS that previous trials with that CS had been non-reinforced. They would have to accumulate some knowledge about the number of previous non-reinforced trials. That is, the animal would have to remember that the last n consecutive trials with that CS had not been reinforced and to associate that specific information with the occurrence of reinforcement on the current trial. This is at the heart of Sequential Theory and requires animals have memories not only for discrete episodes but also for the order in which those episodes occurred.

Within-subjects demonstrations of the PREE raise another pertinent question: Can animals keep track of the length of runs of non-reinforced trials for one CS when those trials

are intermixed with reinforced trials of another CS? All the experiments reported by Chan and Harris (2019) were conducted under such conditions—rats were trained with a partially reinforced CS while given concurrent training with one (in the between-subjects designs) or two (in the within-subjects design) other CSs that were consistently reinforced. It would require a surprising feat of working memory for rats to keep track of the exact number of consecutive non-reinforced trials of the partial CS under these conditions. This would be necessary if rats had to keep track of all runs of non-reinforced trials with the partial CS. But could they get away with less? If rats can only remember a sequence of trials with a CS if it was uninterrupted by trials with any other CS, would they still be able to show the systematic relationship between reinforcement rate and extinction identified by Chan and Harris?

To address the question just raised, I have analysed the trial sequences in the experiments by Chan and Harris (2019) to measure the runs of non-reinforced trials of the partial CS that are followed by a reinforced trial of that CS. The analysis compares the lengths of uninterrupted runs as they occurred in the experiment with the length of those runs ignoring interruptions from other CSs. Examples of these comparisons are shown in [Figure 4](#). As expected, there are fewer long uninterrupted runs of non-reinforced trials followed by a reinforced trial than total runs including sequences that be interrupted. However, it is also clear that the rats did experience a substantial number (more than 10) of uninterrupted runs that matched the expected run length based on the reinforcement rate. For example, the most frequent non-reinforced run length of the 20% CS is expected to be 4 (ignoring interruptions), but the most frequently occurring run length was 1 or 2. Nonetheless, those rats still received 15 occurrences (across 20 sessions) of uninterrupted runs of 4 non-reinforced trials followed by a reinforced trial. Therefore, if extinction is affected by the maximum run length experienced during training, rather than the average run length, then

the rats in Chan and Harris's experiments could still have learned to expect reinforcement after a run of n non-reinforced trials, where $n = 1/\text{reinforcement rate}$.

----- Figure 4 about here -----

Associations or information?

According to Sequential Theory, when an animal is trained with partial reinforcement, it forms memories of sequences of non-reinforced trials, and these memories become associated with subsequent reinforcement. In effect, the animal learns how many trials occur per reinforcement. On the face of it, this description is equivalent to the idea that animals learn about the rate or probability of reinforcement per trial (which is the reciprocal of the number of trials per reinforcement). However, there is an important distinction between these descriptions that brings us back to the fundamental difference, described at the beginning of this review, between associative models of conditioning and information-based models. Sequential Theory offers an associative account of the PREE—animals learn to associate memories of non-reinforced trials, or sequences of such trials, with subsequent reinforcement, and this association is responsible for maintaining responding under extinction. The alternative description is that animals acquire information about the rate of reinforcement per trial (or number of trials per reinforcement) and use this information to generate expectancies of when the US will occur. This account is, in effect, a trial-based version of RET.

Distinguishing on empirical ground between these two accounts is difficult because they make such similar predictions for extinction. For example, both predict that the onset of extinction will be delayed by an amount that is precisely proportional to the ratio of non-reinforced trials to reinforced trials, as was reported by Chan and Harris. However, the two

accounts can be shown to differ when it comes to explaining how animals show a within-subjects PREE. For both accounts, the within-subjects PREE requires that the animals can discriminate between the CS configuration that is partially reinforced and the CS configuration that is consistently reinforced (otherwise they could not show any difference in the rate of extinction between the two configurations). Crucially, this discrimination is symmetrical for the information-based account but is inherently asymmetrical for the associative (Sequential Theory) account. This is because, for Sequential Theory, the PREE depends on learning about non-reinforced trials specifically. To show a within-subjects PREE, what the animal learns about non-reinforced trials with the partially-reinforced configuration must not generalise to the consistently-reinforced configuration. Therefore, if we have two configurations, A and B, that are asymmetrical in their similarity such that there is more generalisation from A to B than from B to A, then Sequential Theory predicts that it will be harder for animals to show a within-subjects PREE if A is partially reinforced and B is consistently reinforced than if B is partially reinforced and A is consistently reinforced. This is not true for the information-based account. There, the PREE depends equally on what the animal learns about the rate of reinforcement of both configurations—there is nothing special about partial reinforcement versus consistent reinforcement in how they determine the rate of subsequent extinction. As such, it will not matter which configuration is associated with partial reinforcement and which with consistent reinforcement, the evidence for a PREE will be affected equally by generalisation in either direction.

We have recently constructed a design that tests for evidence of a within-subjects PREE when there is asymmetrical generalisation between the two CS configurations. Rats were trained with two configurations: A (a light or a noise) and AX (the compound of the light and noise). In studies of simple excitatory conditioning and extinction, generalisation from A

to AX is greater than generalisation from AX to A (e.g., Bouton, Doyle-Burr, & Vurbic, 2012; Brandon, Vogel, & Wagner, 2000). This asymmetry is also evident when comparing between simple A vs AX discriminations: animals are quicker to master a discrimination in which AX is always reinforced and A is never reinforced (AX+ vs A-) than the reverse discrimination (A+ vs AX-, Holland, 1991; Reberg & Leclerc, 1977; Sainsbury & Jenkins, 1967). The second discrimination is harder because responding to A generalises strongly to trials with AX (because all of A is present on AX trials), whereas responding to AX generalises relatively weakly to A (because only 50% of AX is present on trials with A) making the first discrimination easier. We have extended this logic to a discrimination between a partially-reinforced configuration and a consistently reinforced configuration. One group of rats was trained on a partial reinforcement schedule with A and a consistent reinforcement schedule with AX (A+/- vs AX+); a second group was trained on a partial schedule with AX and a consistent schedule with A (AX+/- vs A+). Sequential Theory predicts there will be better evidence for a PREE in the second group than in the first group because, for the first group, learning about partial reinforcement of AX will generalise weakly to A, whereas for the second group learning about partial reinforcement of A will generalise strongly to AX. The results confirmed this prediction. When, after training, responding to A and AX was extinguished, the second group showed significantly slower extinction of responding to AX than to A, whereas the first group showed no difference in the rate of extinction to the two configurations. Moreover, extinction for both A and AX appeared to be delayed in the first group, as if there was a PREE for both configurations. This too is predicted by Sequential Theory, since learning about partial reinforcement of A would generalise to AX. These results are consistent with the associative framework adopted by Sequential Theory because that framework can predict asymmetrical generalisation of associative strength between a compound stimulus and its individual

elements. In contrast, it is far from obvious how the results can be explained by an information-based theory, even one that adopts trials as the unit of reinforcement rate.

Conclusions

The concept of the trial has long been used as a tool for designing and describing experiments and for associative models of conditioning that attempt to describe how animals learn to associate one event, such as the occurrence of a CS, with another event, such as delivery of a US. However, descriptions of learning that are entirely based on trials fail to capture important details about the effects of time within and between trials. The legitimacy of the trial has also been questioned on other empirical and conceptual grounds in recent years. Notwithstanding these criticisms, I have reviewed evidence that the trial is more than just a nominal time interval, identified for the convenience of the experimenter and modeller, that fails to capture meaningful information about what an animal learns as it continuously samples from its environment. The trial itself is an important and meaningful construct in descriptions of conditioning.

The evidence for the importance of trials is clearest when considering how animals learn about non-reinforcement during extinction or under schedules of partial reinforcement. Non-reinforcement is problematic in any framework that describes learning as a perpetual process embedded within the animal's continuous experience because the absence of the US is not an "event" that ever occurs. This problem is compounded by evidence that extinction of responding proceeds trial by trial, regardless of the length of each trial. This shows that the learning process responsible for extinction does not operate continuously within each trial but operates on the trial *as a whole*. Since, in most conditioning experiments, each trial represents a single opportunity for reinforcement, it stands to reason that each trial also

represents a single occurrence of non-reinforcement. This should change if reinforcement can occur more than once per trial, or if the animal learns that only some trials are reinforced. This prediction is confirmed by demonstrations of the PREE. When reinforcement occurs only every n^{th} trial under a partial reinforcement schedule, extinction no longer occurs on every trial but is delayed by n trials. Following Capaldi (1966, 1994), I have argued that, during partial reinforcement, the animal has a memory of the preceding non-reinforced trial, or sequence of non-reinforced trials, which becomes associated with the US on the next reinforced trial. These memories contain information about what was present (the CS) but also about what was absent (the US). It is, I believe, for this reason that the animal represents and remembers the entire event or trial as a single temporally-bounded episode—because it allows the animal to remember that the US did not occur without having to remember each and every moment that the US could have occurred but didn't.

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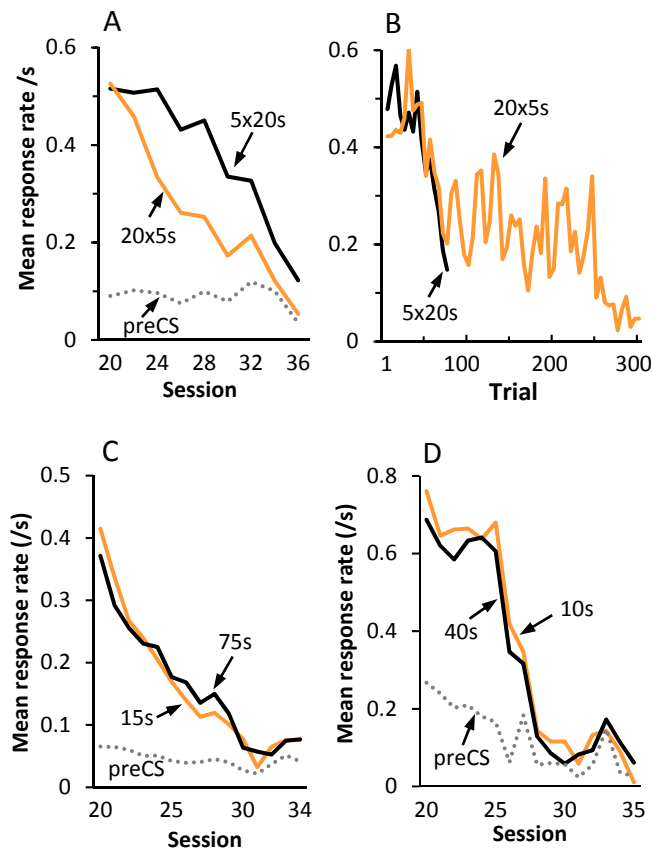


Figure 1. Response rates during extinction in three experiments described by Harris & Andrew (2017). **A** shows response rates averaged over each session of Experiment 1. One CS was presented 5 times per session for a mean duration of 20 s; a second CS was presented 20 times for a mean duration of 5 s (thus the cumulative duration of both CSs equalled 100 s). **B** shows response rates from the same experiment but averaged over 5 consecutive trials for each CS. **C** shows response rates per session of Experiment 2 in which two CSs had the same number of extinction trials per session but differed five-fold in the mean length of those trials (15 s vs 75 s). **D** shows response rates per session of Experiment 4 in which two CSs had been reinforced at a random time during each presentation of the CS, and were then extinguished with the same number of trials but a mean duration of either 10 s or 40 s. Each session of the 10-s CS included one 40-s trial, and response rates shown here were measured from that trial, so that response rates to that CS could be compared with responding to the full length of the 40-s CS.

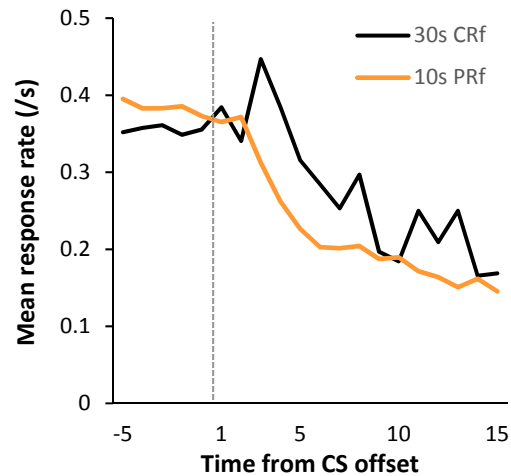


Figure 2. Response rates across trials with a long consistently reinforced CS (30 s CRf) and a short partially reinforced CS (10 s PRf), in Experiment 1 of Harris & Kwok (2018). The plot shows mean response rates per second for the last 5 s of the CS presentations, as well as across a 15-s interval after offset of the CS (marked by the dashed gray vertical line). The data shown here were only from trials that were not reinforced with a food pellet (1 out of 8 trials per session for the CRf CS, and 17 out of 24 trials per session for the PRf CS). Response rates during the last 5 s of the CS did not differ significantly between the two CSs ($t(15) = 0.86$, $p = .403$), but the rats responded significantly more after presentations of the CRf CS than after presentations of the PRf CS ($t(15) = 2.39$, $p = .031$).

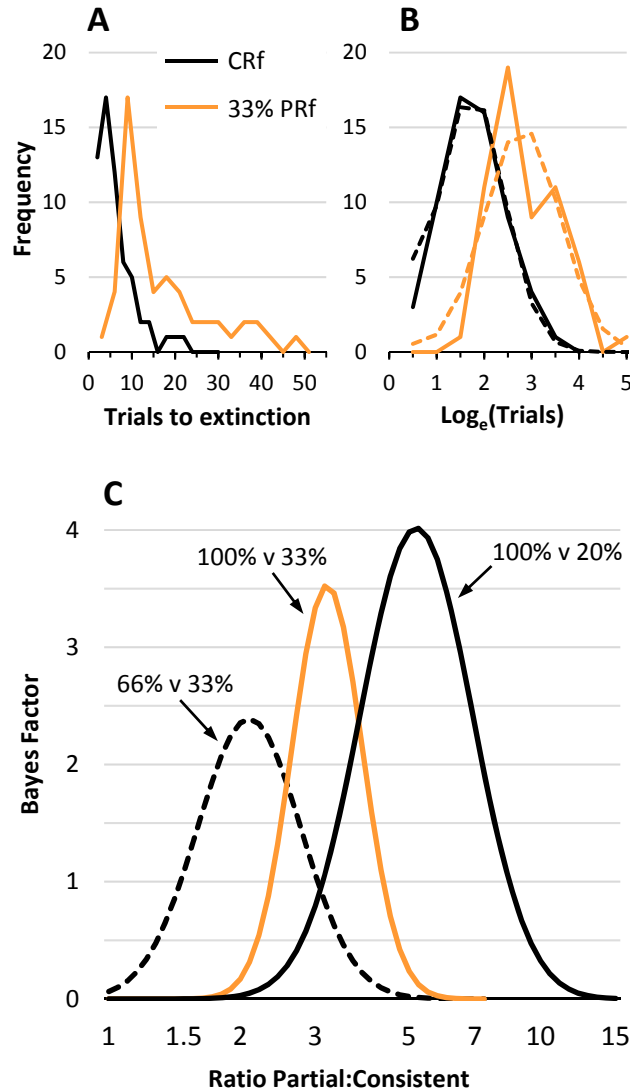


Figure 3. **A:** The frequency distribution of trials to commence extinction for all rats ($n = 60$) trained with a consistently reinforced CS (CRf) and all rats ($n = 57$) trained with a 33% partially reinforced CS (PRf) in the experiments described in Chan and Harris (2019). **B:** The same frequency distribution for the natural log of trials to extinction. A normal distribution (dashed line) is superimposed over each plot. **C:** Bayes factors representing the evidence in favour of differences in trials to extinction, expressed as a ratio, for the two groups in three experiments by Chan and Harris (2019). For the experiment that compared a group trained with 33% reinforcement and a group trained with 66% reinforcement (black dashed line), the Bayes factor peaks very close to the point on the X-axis where the ratio is 2:1. For the experiment comparing a group trained with 33% reinforcement and a group given 100% reinforcement (orange/grey line), the Bayes factor peaks at a ratio close to 3:1. For the experiment comparing groups given 20% reinforcement versus 100% reinforcement (black unbroken line), the Bayes factor peaks close to a ratio of 5:1. Thus, in each experiment, the evidence most strongly favoured a ratio for trials to extinction that matched the ratio of trials per reinforcement during conditioning.

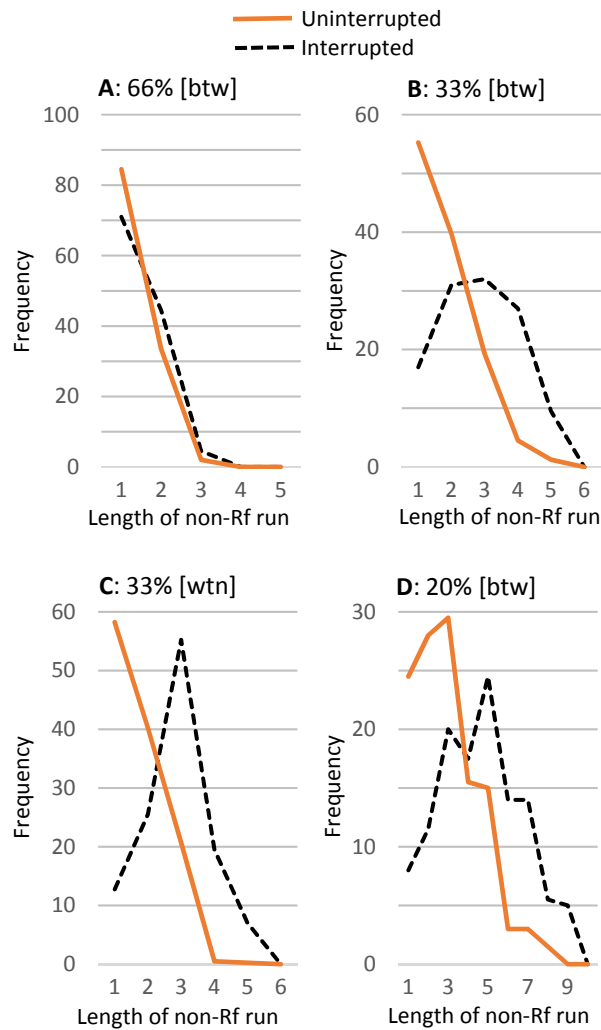


Figure 4. The frequency of runs of non-reinforced trials prior to each reinforced trial of the partially reinforced CS in each of the experiments by Chan & Harris (in press). The dashed black lines show runs of non-reinforced trials ignoring interruptions by trials with a different CS. The solid orange (gray) lines show runs of non-reinforced trials that were uninterrupted by trials with a different CS. The CS was reinforced on 66%, 33%, or 20% of trials. Runs of consecutive trials could be interrupted by one other CS, in experiments using a between-subjects (btw) design, or by two CSs, in experiments using a within-subjects (wtn) design.