Beyond the information (not) given: Associative mechanisms vs representations of uncertainty in extinction in laboratory rats (Rattus norvegicus).

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Abstract

Associative learning models typically reflect statistical relationships between experienced events. Causal models can go beyond this information to specify the ways in which events are related. This meta-representational aspect of causal models allows them to reflect uncertainty about relationships between events: e.g., if a light initially leads to sucrose but subsequently the light is experienced without sucrose, this might first support formation of a *light-causes-sucrose* model and subsequently lead to uncertainty over whether the model remained accurate. Prior studies of Pavlovian conditioning in rats manipulated sucrose-magazine access during extinction to produce uncertainty about reward presence or absence. Rats were sensitive to covering of the site of reward delivery, which was interpreted as evidence for a causal-model account reflecting uncertainty. However, associative accounts – based on the direct impact of the dipper mechanism used to deliver sucrose through secondary reinforcement or contextual renewal of responding – can also explain the results. In two new experiments, manipulation of the dipper mechanism through extinction and test phases resulted in behaviour consistent with these associative accounts. However, demonstration of the importance of the sucrose dipper suggests that the reward delivery mechanism should be included in a causal model. Such a revised causal model also provides an account of the impact of manipulating the sucrose dipper. While these experiments do not conclusively decide between associative and causal models as explanations of rodent behaviour, they do illustrate the value of incremental experimental study and the importance of methodological detail in addressing questions of comparative cognition.

Keywords: Extinction, causal model, secondary reinforcement, renewal, ambiguity

Introduction

The aphorism “absence of evidence is not evidence of absence” neatly captures the idea that the absence of an event and the absence of information about that event support very different logical inferences. While this may be entirely obvious to (adult) humans, it is an open question whether non-human animals share the sensitivity to this difference. This potentially speaks to the wider issue of whether some animals’ behaviours require assuming they possess inferential capacities that exceed putatively simple associative learning mechanisms (e.g., Heyes, 2012; Penn & Povinelli, 2007). This wider issue has been controversial since at least the 19th century (for a historical overview, see Greenwood, 2016), and remains unresolved, perhaps because there have been overtones of ideological debate as opposed to a focus on incremental empirical study (e.g., Beckers et al., 2016; Heyes, 2012).

It was against this background that Waldmann et al. (2012) examined the sensitivity of rats to the difference between the absence of an event and the lack of evidence about that event via manipulations during extinction of Pavlovian conditioning. Typical Pavlovian conditioning procedures involve repeatedly presenting a relatively neutral cue (the “conditioned stimulus” or CS) in advance of a motivationally significant outcome (the “unconditioned stimulus” or US). Exposure to this relationship between the CS and US results in animals developing responses to the CS (e.g., entering the magazine where a food US was to be delivered). In turn, extinction involves presenting the CS alone, and this typically results in a reduction in responding to the CS. Waldmann et al. (2012) noted that, considered rationally, extinction potentially creates an ambiguity – initially the CS predicts the US, and so experiencing the CS without experiencing the US may reflect a change in the causal structure of the world (e.g., the CS used to cause the US to appear, but no longer does); or it may be the case that the causal structure of the world remains unchanged, but the US was missed for some reason. Furthermore, Waldmann et al. (2012) noted that the degree of ambiguity would be related to how informative the non-experience of the US would be: if the presence or absence of the US was itself ambiguous (e.g., there was no access to the place where the US would normally be delivered, and thus no way of determining if it was present or not), then simply not experiencing the US is uninformative and so there would be little reason to believe there had been a change in the causal structure of the world; in contrast, if the US was explicitly absent (e.g., there was access to the place where it had been delivered and that place was empty), then the absence of an otherwise expected US is most consistent with a change in the causal structure of the world.

Waldmann et al. (2012) reported three experiments applying exactly this manipulation: following initial training where a light CS was presented in advance of 10 s access to a sucrose US (this was delivered via raising a dipper arm into the food magazine)[1], there was an extinction phase where all rats received exposure to the light CS followed by the now-empty dipper, but critically a subset of the rats received exposure to the light CS while access to the food magazine was prevented by placing a metal cover over the magazine opening. In all three experiments, responding to the CS was higher if extinction had been delivered while access to the site of US delivery was prevented by the metal cover than if it had not been so prevented. Thus, rats clearly responded differently to the absence of the US as a function of whether or not they had access to the normal site of US delivery – the question is why.

Obviously, one possibility is that the rats did indeed distinguish between the evidence of absence (i.e., no US delivery, and access to the expected site of delivery allowing confirmation of absence), and the absence of evidence (i.e., no access to the expected site of US delivery and thus no ability to confirm if the US was, or was not, absent), and would only have changed a *light-causes-sucrose* model of the world in the former case when the absence of sucrose after seeing the light was unambiguous. This was the conclusion reached by Waldmann et al. (2012). However, Dwyer and Waldmann (2016) re-examined the evidence and noted that the details of the behavioural procedures also afforded a number of other accounts. One such account comes from renewal theory

[1] Sucrose was held in a receptacle placed underneath the food magazine. Sucrose was delivered to rats by raising a small cup – held at the end of a mechanical dipper arm – through a hole in the bottom of the food magazine. The default position of the arm was down, and rats had no access to sucrose or the cup/dipper arm except when it was raised.

which suggests that extinction is context specific, such that if there is a change of context between extinction and test, then the extinguished response can re-appear (e.g., Bouton, 2004; Delamater, 2004). Here, the magazine cover could produce a context change because extinction took place where access to the food magazine (and with it, experience of the dipper) is prevented, while testing took place with an open magazine and moving dipper[2]. Another alternative account is based on the idea of secondary reinforcement – the well-established finding that otherwise neutral cues can act as reinforcers if they have been paired with a primary reinforcer (for an overview, see Mackintosh, 1974, 1983). Here, the dipper cup/arm would potentially have become a secondary reinforcer as a result of being paired with sucrose in the training phase. In animals receiving extinction with the magazine covered, there would be no opportunity to experience the dipper without sucrose. Thus, during the test phase, the light CS would be followed by the presentation of the dipper that retained secondary reinforcing properties, and this could support responding. Conversely, without the cover during extinction, the dipper would have been experienced without sucrose and so the secondary reinforcing properties would be lost.

Critically, the causal model/uncertainty account presented by Waldmann et al. (2012) and Dwyer and Waldmann (2016) differs from both the renewal and secondary reinforcement accounts in terms of when the cover is having its effects. Considering uncertainty alone, the presence of the cover during the extinction phase should render the evidence of not experiencing the sucrose US ambiguous (it may, or may not, have been present behind the cover), and in turn, this would prevent extinction from occurring because the evidential value of no-sucrose is low. In contrast, both the secondary reinforcement and renewal accounts assume that extinction does occur, but that events during test reinvigorate responding. For secondary reinforcement, the key event is the experience of

[2] Waldmann et al. (2012) did note the possibility of a renewal theory account, but they dismissed it: Partially on the grounds that introducing a metallic cover without preventing magazine access did not produce renewal (see especially Experiment 3), and partially on the grounds that renewal theory alone did not specify what would, or would not, be a sufficient change of context to produce the effect.

the light CS followed by the dipper that had secondary reinforcement properties (in the cover condition). For renewal, the key event is the removal of the cover at test because this allows access to the moving dipper, thus increasing the difference between the extinction context (with cover, no magazine access, and no access to the moving dipper) and that of test (with no cover, magazine access, and access to the moving dipper). In turn, the larger context change would support greater renewal of the extinguished response. Thus, the accounts have a critical difference of what the cover is doing and when it is doing it: for causal model/uncertainty, the cover acts during the extinction phase itself to prevent or reduce extinction by reducing the evidential value of not receiving sucrose; for the renewal and secondary reinforcement accounts, extinction is expected to occur despite the cover, but re-experiencing the dipper at test after removal of the cover re-establishes responding.

Having established this critical difference between the causal model/uncertainty vs the renewal and secondary reinforcement accounts, Dwyer and Waldmann (2016) suggested that it could be used as the basis for empirical testing between them. Both the secondary reinforcement and renewal accounts rely (in different ways) on the operation of the empty dipper during test, but the causal model/uncertainty account does not. Thus, the secondary reinforcement and renewal accounts predict that the effect of covering the magazine during extinction should only be seen if the dipper arm was operated at test, while the causal model/uncertainty account suggests that covering should reduce/prevent extinction regardless of the dipper operation. While Dwyer and Waldmann (2016) set out experimental designs to test between various accounts based on this logic, this was done conceptually and prior to any actual experimental work. Here we report the results of two experiments applying the logic described by Dwyer and Waldmann.

From the perspective of the causal account, it is important to note that the competing theories not only postulate different representations, but also that a major difference between them concerns the role of acoustic or other cues linked to dipper movement in the extinction and/or test phases. Waldmann et al. (2012) assumed that the dipper in their experiments was not audible so that no dipper movement could be inferred in the extinction phase on the basis of an acoustic cue.

This assumption was a crucial component for the uncertainty assumption because covering the niche only creates complete uncertainty if there was no perception of a moving dipper behind the cover (a dipper that in the learning phase had signalled the upcoming appearance of food). If the dipper's movement could be inferred using an acoustic cue, this would also reduce or remove uncertainty according to a causal model account. Moreover, other things being equal, perceiving (be that via acoustic cues, or by vision/touch) the dipper in the test phase should make the presence of food more likely than not perceiving it (see General Discussion for a suggestion for an extended causal model reflecting this idea). Waldmann et al. (2012) only assumed that the dipper was not audible based on the experimenter's assessment but did not empirically test the validity of this assumption for their experimental setup. Thus, an important further goal of the present research is to examine the effects of manipulating the dipper behind the magazine cover.

Experiment 1

Table 1 shows the design of Experiment 1. This includes all groups as described in Dwyer and Waldmann (2016). Cover/No-Cover refers to the presence/absence of the cover in the extinction phase, while Dipper/No-Dipper refers to the operation/non-operation of the dipper in the extinction (middle term of the group name) or test phase (final term of the group name). The No-Cover Dipper Dipper and Cover Dipper Dipper groups correspond to the critical groups from Waldmann et al. (2012), whereby both groups were originally trained with a light CS presented in advance of 10 s access to sucrose provided by raising a dipper arm into the food magazine, then both groups received extinction with exposure to the light CS without sucrose access (but the dipper arm continued to be raised for 10 s after each CS presentation – simply without sucrose). For rats in the Cover group, extinction was performed with a metal plate over the food magazine, for those in the No-Cover group the metal plate was included but was placed so as to not prevent access to the food magazine. Finally, both groups were tested for responding to the light CS with the magazine uncovered (but with the empty dipper arm continuing to operate). These groups allow a replication confirming that the basic covering effect is reliable outside the original laboratory. Importantly, all conceptual accounts outlined in the introduction would predict higher levels of responding in the Cover Dipper Dipper than No-Cover Dipper Dipper group: for the uncertainty account, this is because covering reduced/removed the evidential value of not experiencing sucrose after the light CS in the extinction phase – and thus covering should reduce/remove the effect of extinction; for the secondary reinforcement and renewal accounts, covering would not prevent extinction occurring, but re-experiencing the moving dipper once the cover was removed at test would either form a context change allowing renewal of the extinguished response, or secondary reinforcement to be provided by the dipper that had in the cover condition never been previously experienced without sucrose.

The No-Cover No-Dipper No-Dipper and Cover No-Dipper No-Dipper groups received the same general experiences, but without operation of the empty dipper during extinction and test. This manipulation does not affect the predictions of the causal model account based on the cover producing uncertainty about the non-experience of sucrose during the extinction phase, but it critically does affect the secondary reinforcement and renewal accounts because both rely on aspects of re-experiencing the dipper at test and so in the absence of dipper operation at test these accounts no longer predict a lack of extinction when the food magazine was covered during the extinction phase.

As noted in the introduction, the possibility that the dipper movement was audible may require a modification of the causal model which would reflect the way that perception of dipper movement could be used as a diagnostic cue of the probable presence or absence of food (such a modified model will be considered in the general discussion). But regardless of the exact causal model, the possibility that auditory processing of the moving dipper behind the magazine cover may influence the covering effect is important – so an additional group (Cover Dipper No-Dipper) received extinction with the dipper operated behind the magazine cover and test with no dipper operation.

Finally, the predictions noted above all relate to the test phase as a whole, but Dwyer and Waldmann (2016) noted that the first trial of test should be materially different to the remaining trials given that the key manipulation of dipper operation (or non-operation) was only implemented after the presentation of the CS. Thus, to the degree that dipper operation during the test phase does affect responding to the CS, the effect should not be seen on the first trial because responding was measured prior to the time of dipper operation while all other test trials would follow after the dipper had, or had not been, operated. While clearly true, this may be a moot point if there was no overall effect at test of the dipper operation, thus we will return to this issue after the presentation of Experiments 1 and 2 focused on the test phase as a whole.

Table 1 – Design of Experiments 1 and 2

Experiment 1 Group	Train (3 sessions)	Extinction (3 sessions)	Test (2 sessions)
No-Cover Dipper Dipper (NC_D_D)	12 * Light (10s) -> Sucrose filled dipper raised (10s)	12 * Light (10s) -> Empty dipper raised (10s) Uncovered magazine	12 * Light (10s) -> Empty dipper raised (10s)
Cover Dipper Dipper (C_D_D)	12 * Light (10s) -> Sucrose filled dipper raised (10s)	12 * Light (10s) -> Empty dipper raised (10s) Covered magazine	12 * Light (10s) -> Empty dipper raised (10s)
No-Cover No-Dipper No-Dipper (NC_ND_ND)	12 * Light (10s) -> Sucrose filled dipper raised (10s)	12 * Light (10s) -> Ø Uncovered magazine	12 * Light (10s) -> Ø
Cover No-Dipper No-Dipper (C_ND_ND)	12 * Light (10s) -> Sucrose filled dipper raised (10s)	12 * Light (10s) -> Ø Covered magazine	12 * Light (10s) -> Ø
Cover Dipper No-Dipper (C_D_ND)	12 * Light (10s) -> Sucrose filled dipper raised (10s)	12 * Light (10s) -> Empty dipper raised (10s) Covered magazine	12 * Light (10s) -> Ø

Experiment 2 Group	Train (5 sessions)	Extinction (5 sessions)	Test (2 sessions)
No-Cover Dipper Dipper (NC_D_D)	12 * Light (10s) -> Sucrose filled dipper raised (10s)	12 * Light (10s) -> Empty dipper raised (10s) Uncovered magazine	12 * Light (10s) -> Empty dipper raised (10s)
Cover Dipper Dipper (C_D_D)	12 * Light (10s) -> Sucrose filled dipper raised (10s)	12 * Light (10s) -> Empty dipper raised (10s) Covered magazine	12 * Light (10s) -> Empty dipper raised (10s)
No-Cover No-Dipper No-Dipper (NC_ND_ND)	12 * Light (10s) -> Sucrose filled dipper raised (10s)	12 * Light (10s) -> Ø Uncovered magazine	12 * Light (10s) -> Ø
Cover No-Dipper No-Dipper (C_ND_ND)	12 * Light (10s) -> Sucrose filled dipper raised (10s)	12 * Light (10s) -> Ø Covered magazine	12 * Light (10s) -> Ø
Cover Dipper No-Dipper (C_D_ND)	12 * Light (10s) -> Sucrose filled dipper raised (10s)	12 * Light (10s) -> Empty dipper raised (10s) Covered magazine	12 * Light (10s) -> Ø
Cover No-Dipper Dipper (C_ND_D)	12 * Light (10s) -> Sucrose filled dipper raised (10s)	12 * Light (10s) -> Ø Covered magazine	12 * Light (10s) -> Empty dipper raised (10s)

Note – In the group names: Cover/No-Cover refers to the presence/absence of a metal plate covering the opening to the food magazine (this manipulation only applied during the Extinction Phase). Dipper/No-Dipper refers to the operation of the dipper arm used to deliver sucrose (the first appearance in the group name referring to the Extinction phase; the second to the Test phase). The default position of the arm was down and outside the food magazine, when operated it was raised into the magazine for 10s allowing rats access to the cup on its end (the cup contained sucrose during the training phase and nothing subsequently). Abbreviated group names are given for the figures.

Methods

Animals

Group sizes were determined by reference to the previous experimental investigation of this issue by Waldmann et al. (2012) where groups ranged from 8-11 animals. A total of 48 experimentally naive Lister Hooded male rats, approximately 110 days old, supplied by Harlan, United Kingdom, were used. This allowed for planned group sizes of 9-10. All procedures reported here were conducted in accordance with the Animals Scientific Procedures Act (1986) requirements and the specific authority noted under Home Office project license PPL 30-3243 held by D. Dwyer. The rats were housed in fours, with sawdust bedding, wooden chewsticks, and cardboard play tubes. The holding room was maintained under a 12 h/12 h light/dark cycle, with temperature maintained between 19 and 21 degrees centigrade, and relative humidity between 45 and 65%. The rats had free access to water throughout. All experimental manipulations took place during the light phase of the cycle. Their mean free feeding weight before the start of the experiment was 359 g (range: 305-440g) and they were maintained at between 90% and 95% of these weights by giving them restricted access to food at the end of each day.

Apparatus

Eight identical conditioning boxes measuring 30×24×21 cm (H×W×D; Med Associates, Georgia, VT) were used. Each box was placed in a sound-attenuating shell that incorporated a ventilation fan, which maintained the background noise at 68 dB(A). The boxes had aluminum side walls and clear acrylic front back and top. The floor was constructed from 19 steel rods (4.8 mm diameter, 16 mm apart) and was situated above a stainless-steel tray. Background illumination was provided by a houselight placed at the top of the right aluminum wall (turned on only during the experimental sessions). The rewarding sucrose solution (20% w/w in water) was delivered to a recessed food well (aperture: 5.3×5.3 cm) mounted 2 cm above floor level in the center of the right aluminum wall. Sucrose delivery was performed using a 0.05 ml cup attached to the end of a dipper arm. When the dipper arm was raised the cup protruded into the food magazine and its content was accessible to the rats, when lowered the cup was inaccessible. The default position of the dipper arm was down. The food magazine was equipped with infrared detectors that allowed the entry to the magazine to be automatically recorded. Both the number of entries and duration of entry time were recorded. A steel plate (6.5×9.0 cm) could be secured by magnets either over the magazine aperture (the “cover” condition) or directly above the aperture (the “no-cover” condition). The placement of the plate in the box when not being used to block magazine access was based on Waldmann et al. (2012) who found no material effect of different ways of implementing the no cover condition. When the plate was placed over the aperture rats were unable to access or see into the food magazine (including not being able to see whether the dipper arm was moving or not), but the sound of the electric motor driving the dipper arm could be discerned whether the cover was in place or not[3]. The flashing light CS was provided by two diffuse jewel lights mounted 9 cm to the left or right, and 6 cm above, the food magazine. The lights were flashed in alternation (0.2 s on/off) for the 10 s duration of each CS.

Procedure

After acclimatizing to the feeding schedule for six days, all rats received two sessions of magazine training (one per day) to familiarize them with the apparatus and dipper. Each session consisted of 20 × 10 s presentations of the sucrose filled dipper (mean ITI 60 s, range 40-80 s). As was noted above, the default position of the dipper was down and inaccessible from the food magazine, thus sucrose delivery was performed by raising the dipper arm so the sucrose-filled cup

[3] Although Waldmann et al. (2012) used similar Med Associates equipment, they reported that the movement of the dipper behind the cover plate produced “no noticeable vibrations for the human ear”. It was not possible to conclusively determine the source of this difference, but it may be due to the presence of a white noise generator providing a constant background noise in the original lab (personal communication Aaron Blaisdell, December 2023).

was accessible for 10 s. For magazine training sessions, the metal cover plate was mounted directly above the magazine aperture.

The three training sessions (one per day) each comprised 12 × 10 s presentations of the flashing light CS, with the offset of the CS followed immediately by 10 s presentation of the sucrose filled dipper. CSs were presented with a mean ITI of 240 s (range 165-315). Again, the metal cover plate was mounted directly above the magazine aperture during this phase for all animals. The number (and duration) of magazine entries was measured for 30 s prior to the CS as well as during the CS, with the key response measure being the number of magazine entries during the 10 s CS, minus 1/3 of the number of pre-CS magazine entries (to put the pre-CS and CS on the same scale). Animals were assigned to groups at the end of training in order to match response rates across groups, with four animals failing to show acquisition of responding to the CS (i.e., negative CS – PreCS scores) and thus they were excluded from the analysis. Final numbers assigned to the experimental groups were: No-Cover Dipper Dipper (N = 9), Cover Dipper Dipper (N = 9), No-Cover No-Dipper No-Dipper (N = 8), Cover No-Dipper No-Dipper (N = 9), and Cover Dipper No-Dipper (N = 9).

The three extinction phase sessions (one per day) also comprised 12 × 10 s presentations of the flashing light CS (with the same ITIs as in training), but without presentation of sucrose reward. For the “Cover” conditions (Cover Dipper Dipper, Cover No-Dipper No-Dipper, Cover Dipper No-Dipper), the extinction sessions were performed with the metal cover plate mounted over the magazine aperture; for the “No-Cover” conditions (No-Cover Dipper Dipper, No-Cover No-Dipper No-Dipper) they were performed with the metal plate mounted directly above the magazine aperture. That is, the metal cover plate was present in all conditions, but in the “Cover” conditions it prevented access to the magazine, and in the “No-Cover” conditions it did not. In addition, for the “Dipper” conditions (No-Cover Dipper Dipper, Cover Dipper Dipper, Cover Dipper No-Dipper), the dipper arm was operated as in the training phase (i.e., raised into the magazine for 10 s at the offset of the CS), but the cup did not contain sucrose. For the "No-Dipper" conditions (Cover No-Dipper No-Dipper, No-Cover No-Dipper No-Dipper) the dipper arm was not operated.

The two test phase sessions (one per day) also comprised 12 × 10 s presentations of the flashing light CS (with the same ITIs as in training) without presentation of sucrose reward, and with the metal cover plate mounted directly above the magazine aperture for all animals. As with extinction, for the "Dipper" conditions (No-Cover Dipper Dipper, Cover Dipper Dipper), the dipper arm was operated as in the training phase (i.e., raised into the magazine for 10 s at the offset of the CS), but the cup did not contain sucrose. For the "No-Dipper" conditions (Cover No-Dipper No-Dipper, No-Cover No-Dipper No-Dipper, Cover Dipper No-Dipper) the dipper arm was not operated.

Data handling & analysis

As was noted above, the primary measure of performance was the number of magazine entries during the CS less the rate of Pre-CS magazine entries (with animals showing negative scores on this measure at the end of training excluded from the analysis). This response number measure is standardly used in our laboratory, although it differs from the response duration measure reported by Waldmann et al. (2012), and thus response durations were also recorded and analysed. The two measures gave broadly similar results and only the places where there were material differences will be noted subsequently. The primary analysis was performed on data aggregated across trials within a session.

Data from the final training session was examined using one-way between-subjects ANOVA with a factor of group, while extinction phase data was examined with mixed ANOVA with a within-subject factor of extinction session and a between-subjects factor of group (only including the No-Cover groups as the cover prevented magazine entry and so magazine entry rates were by definition zero in all Cover groups during extinction). Test phase data was examined with mixed ANOVA with a within-subject factor of test session and a between-subjects factor of group. Initial analyses were performed using IBM SPSS Version 27, with supplementary Bayesian analysis performed using JASP

Version 0.14, using the default settings for implementing Bayesian ANOVA as described by Rouder et al. (2012) and post hoc testing as described by van den Burgh et al. (2020). Bayes analyses are reported as Bayes factors relating the ratio of probability for the observed data under a model based on the null hypothesis compared with a model based on some specified alternative (BF01). BF01 values greater than 1 indicate increasing evidence for the null over the alternative and were interpreted according to the following conventions suggested by Jeffreys (1961): a Bayes factor between 1 and 3 gives weak or anecdotal support to the null, a factor between 3 and 10 represents some supporting evidence, while a factor more than 10 indicates strong evidence for the null.

Transparency and Openness Statement

Data for Experiments 1 and 2 is available at the OSF (osf.io/va8fc). Analyses were performed as described above using the packages noted and so no analysis code is available. Experimental materials are not available to readers, other than MED-PC programs which can be requested from the corresponding author. While the general experimental designs were described previously (see Dwyer & Waldmann, 2016) the experiments were not preregistered and nor were the analysis plans. We confirm that we have reported how we determined our sample size, all data exclusions, all manipulations, and all measures in the study.

Results

Table 2 shows the mean magazine response rates at the end of training, and ANOVA revealed no statistically significant effect of group [$F(4, 39) = 0.14$, $p = .963$, $\eta^2_p = .015$, BF01 = 8.91]. Table 2 also shows extinction phase response rates, which clearly decline across sessions until negligible levels of magazine entry during the CS were seen in the final extinction session. Although the levels of responding appear higher in group No-Cover Dipper Dipper than No-Cover No-Dipper No-Dipper, ANOVA revealed only a significant main effect of extinction session [$F(2, 30) = 25.30$, p <

.001, η^2_p = .628], and no significant main effect of group [F(1, 15) = 3.48, *p* = .082, η^2_p = .188], or interaction between the two factors [F(2, 30) = 1.47, *p* = .246, η^2_p = .089].

The test session data are shown in Figure 1, and notwithstanding the numerical difference between test 1 and test 2 for group Cover Dipper No-Dipper, ANOVA revealed only a significant main effect of group [F(4, 39) = 6.77, *p* < .001, η^2_p = .410], and no significant main effect of test session [F(1, 39) = 2.17, *p* = .149, η^2_p = .053], or interaction between the two factors [F(4, 39) = 1.56, *p* = .203, η^2_p = .138][4]. Considering the main effect of group, pairwise comparisons revealed that group Cover Dipper Dipper displayed greater test phase responding than group No-Cover Dipper Dipper [F(1, 39) = 18.59, *p* < .001]. This replicates the key result reported by Waldmann et al. (2012), namely that covering the magazine during extinction resulted in greater levels of test-phase responding than if the magazine had not been covered (at least when the sucrose dipper was operated throughout all phases of the experiment). In contrast, there was no significant difference between groups Cover No-Dipper No-Dipper and No-Cover No-Dipper No-Dipper [F(1, 39) < 0.01, *p* = .924, BF01 = 3.01], and a contrast analysis revealed that the difference between the cover and no-cover groups was greater when the dipper was operated than when it was not [t(39) = 2.43, *p* = 0.02]. That is, the effect of covering the magazine during extinction was greater when the dipper was operated during the extinction and test phases than when it was not operated (and there was no evidence that covering the magazine during extinction impacted test phase responding in the absence of operation of the empty dipper in the extinction and test phases).

The performance of group Cover Dipper No-Dipper is difficult to interpret as ANOVA does not reveal a significant interaction between group and test session, yet there is a numerical difference in responding between test sessions in this condition (larger than that seen in any other group), and its overall response levels appear intermediate between those of group Cover Dipper

[4] An analysis based on the duration of responses also revealed only a main effect of group with no interaction with test, but in the duration data there was no suggestion of test phase responding in group Cover Dipper No-Dipper during test 1.

Dipper [$F(1, 39) = 5.21$, $p = .024$], and that of all other groups [largest $F(1, 39) = 3.86$, $p = .057$, for the comparison to group No-Cover Dipper Dipper]. Regardless, the results of Experiment 1 suggest that covering the magazine fails to impact on the effectiveness of extinction if the dipper used to deliver the sucrose reward was no longer operated after the training phase. However, the somewhat ambiguous results from group Cover Dipper No-Dipper make it unclear whether the critical period for continued dipper operation was during the extinction or test phases (or both). Thus, further consideration of the implications of these results will only be made after the report of Experiment 2.

Table 2 – Experiment 1 training and extinction data

Group	Train 3	Ext 1	Ext 2	Ext 3
No-Cover Dipper Dipper (NC_D_D)	2.63 (0.40)	1.31 (0.29)	0.22 (0.13)	0.08 (0.12)
Cover Dipper Dipper (C_D_D)	2.67 (0.34)			
No-Cover No-Dipper No-Dipper (NC_ND_ND)	2.97 (0.44)	0.66 (0.21)	-0.02 (0.13)	-0.06 (0.08)
Cover No-Dipper No-Dipper (C_ND_ND)	2.61 (0.31)			
Cover Dipper No-Dipper (C_D_ND)	2.67 (0.35)			

Note – Table shows mean (with SEM) number of magazine entries (as CS – Pre-CS rates) per trial for the final training session, and each of the three extinction sessions. No magazine entries were possible for the groups with the magazine covered during the extinction phase.

Figure 1 – Experiment 1 test data

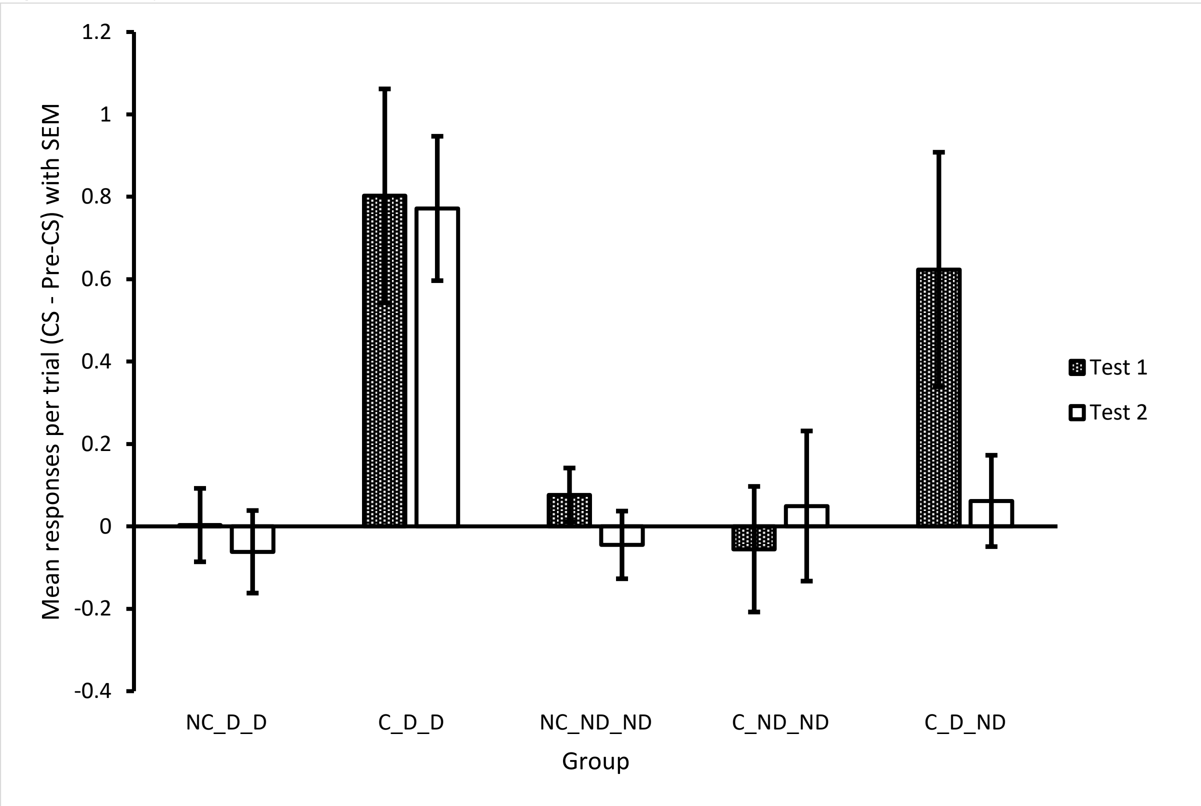

Figure 1 – Shows mean (with SEM) number of magazine entry responses (as CS – Pre-CS rates) per trial as a function of group (see Table 1 for details of abbreviated group names) and testing session.

Experiment 2

As was noted in the introduction to Experiment 1, the possibility that the operation of the sucrose dipper could be detected by the rats when the magazine was covered is not ideal given the intention of the covering manipulation was to make the presence/absence of the reward uncertain. Moreover, the performance of group Cover Dipper No-Dipper in Experiment 1 was somewhat ambiguous and raised the question of whether the dipper operation was critical during the extinction or test phases (or both). Thus, this group was again included in Experiment 2. In addition, a group was added where the dipper was not operated behind the magazine cover in extinction but was operated during the test phase (group Cover No-Dipper Dipper). Finally, given the potential importance of the effects of dipper manipulation in the interpretation of the effects of magazine covering, Experiment 2 also replicated the remaining key groups from Experiment 1 (namely No-Cover Dipper Dipper, Cover Dipper Dipper, No-Cover No-Dipper No-Dipper, and Cover No-Dipper No-Dipper).

Methods

Animals & Apparatus

The equipment, and general husbandry conditions for the animals, were as in Experiment 1. 48 Lister Hooded male rats, approximately 90 days old, supplied by Harlan, United Kingdom, were used. Thus, initial group sizes were comparable to Experiment 1. The rats had previously been used in a flavour preference study using different equipment and involving access to flavoured maltodextrin solutions. Their mean free feeding weight before the start of the experiment was 318 g (range: 283-346 g) and they were maintained at between 90% and 95% of these weights by giving them restricted access to food at the end of each day.

Procedure

The general experimental procedures were as described for Experiment 1 in terms of the details of the CS and US stimuli, number and distribution of trials within sessions, and manipulations of magazine covering and dipper operation with the following exceptions: only four days acclimation to the feeding schedule were given prior to magazine training (because rats had prior experience of the feeding schedule due to their previous use); the training phase consisted of five sessions (acquisition was slower than in Experiment 1 so training was extended to allow animals to reach similar levels of baseline performance); the extinction phase consisted of five sessions (perhaps because of the longer training phase, extinction was also slower than in Experiment 1 and so was extended to ensure responding had been reduced to floor levels).

As with Experiment 1, all animals were trained with the metal cover plate mounted directly above the magazine aperture during this phase, and animals were assigned to groups at the end of training in order to match response rates across groups, with six animals failing to show acquisition of responding to the CS (i.e., negative CS – PreCS scores) excluded from the analysis. Thus, all groups had an effective size of seven rats.

During the extinction phase, the CS was presented without sucrose reward. For the "Cover" conditions (Cover Dipper Dipper, Cover No-Dipper No-Dipper, Cover Dipper No-Dipper, Cover No-Dipper Dipper), the metal cover plate was mounted over the magazine aperture, and for the "No-Cover" conditions (No-Cover Dipper Dipper, No-Cover No-Dipper No-Dipper), the metal plate was mounted directly above the magazine aperture. In addition, for the "Dipper" conditions (No-Cover Dipper Dipper, Cover Dipper Dipper, Cover Dipper No-Dipper), the dipper arm was operated as in the training phase but the cup did not contain sucrose, while for the "No-Dipper" conditions (Cover No-Dipper No-Dipper, Cover No-Dipper Dipper, No-Cover No-Dipper No-Dipper), the dipper arm was not operated.

During test, the CS was again presented without sucrose reward, and with the metal cover plate mounted directly above the magazine aperture for all animals. As with extinction, for the "Dipper" conditions (No-Cover Dipper Dipper, Cover Dipper Dipper, Cover No-Dipper Dipper), the dipper arm was operated as in the training phase, but the cup did not contain sucrose, while for the "No-Dipper" conditions (Cover No-Dipper No-Dipper, No-Cover No-Dipper No-Dipper, Cover Dipper No-Dipper), the dipper arm was not operated. Data handling and analysis was performed as in Experiment 1 except that the CS – PreCS response rate calculation was performed using the 10 s period prior to each CS to set the PreCS response rate.

Results & Discussion

Table 3 shows the mean magazine response rates at the end of training, and ANOVA revealed no statistically significant effect of group [F(5, 36) = 0.12, p = .988, η^2_p = .016, BF01 = 10.03]. Table 3 also shows extinction phase response rates, which clearly declined across sessions until negligible levels of magazine entry during the CS were seen in the final extinction session. Although the levels of responding again appeared higher in group No-Cover Dipper Dipper than No-Cover No-Dipper No-Dipper at the start of extinction, ANOVA revealed only a significant main effect of extinction session [F(4, 48) = 23.15, p < .001, η^2_p = .659], and no significant main effect of group [F(1, 12) = 1.03, p = .330, η^2_p = .079] or interaction between the two factors [F(4, 48) = 0.99, p = .425, η^2_p = .076].

The test session data are shown in Figure 2, and ANOVA revealed only a significant main effect of group [F(5, 36) = 9.21, p < .001, η^2_p = .561], and no significant main effect of test session [F(1, 36) < 0.01, p = .996, η^2_p < .001], or interaction between the two factors [F(5, 36) = 1.65, p = .172, η^2_p = .137]. Considering the main effect of group, pairwise comparisons revealed that group Cover Dipper Dipper displayed greater test phase responding than group No-Cover Dipper Dipper [F(1, 36) = 18.47, p < .001] replicating the results of Experiment 1 and Waldmann et al. (2012). In contrast, there was no significant difference between groups Cover No-Dipper No-Dipper and No-Cover No-Dipper No-Dipper [F(1, 36) = 0.69, p = .412, BF01 = 1.31], and a contrast analysis revealed that the difference between the cover and no-cover groups was greater when the dipper was operated than when it was not [t(36) = 2.45, p = 0.019], again replicating the results of Experiment 1.

Moreover, group Cover No-Dipper Dipper responded at similar levels to that of group Cover Dipper Dipper [$F(1, 36) < 0.01$, $p = .985$, BF01 = 2.83], and far higher than any other group [smallest $F(1, 36) = 12.93$, $p = .001$, for the comparison to group Cover Dipper No-Dipper]. Finally, unlike in Experiment 1, there was little suggestion of higher test phase responding in group Cover Dipper No-Dipper compared to groups where extinction would be expected to be successful [largest $F(1, 36) = 1.10$, $p = .300$, BF01 = 1.75] for the comparison to group No-Cover No-Dipper No-Dipper]. The relative performance of groups Cover No-Dipper Dipper and Cover Dipper No-Dipper suggest that it is the operation of the dipper during the test phase, rather than during the extinction phase, that is critical in observing the higher test phase responses after magazine covering during extinction.

Table 3 – Experiment 2 training and extinction data

Group	Train 5	Ext 1	Ext 2	Ext 3	Ext 4	Ext 5
No-Cover Dipper Dipper (NC_D_D)	2.49 (0.97)	1.84 (0.30)	0.97 (0.29)	0.39 (0.24)	0.36 (0.26)	0.09 (0.16)
Cover Dipper Dipper (C_D_D)	2.46 (0.44)					
No-Cover No-Dipper No-Dipper (NC_ND_ND)	2.95 (0.47)	1.40 (0.36)	0.62 (0.26)	0.32 (0.14)	-0.22 (0.33)	0.15 (0.10)
Cover No-Dipper No-Dipper (C_ND_ND)	2.63 (0.31)					
Cover Dipper No-Dipper (C_D_ND)	2.61 (0.32)					
Cover No-Dipper Dipper (C_ND_D)	2.55 (0.28)					

Note – Table shows number of magazine entries (as number during the 10s CS – number during the 10s Pre-CS period) per trial for the final training session, and each of the five extinction sessions. No magazine entries were possible for the groups with the magazine covered during the extinction phase.

Figure 2 – Experiment 2 test data

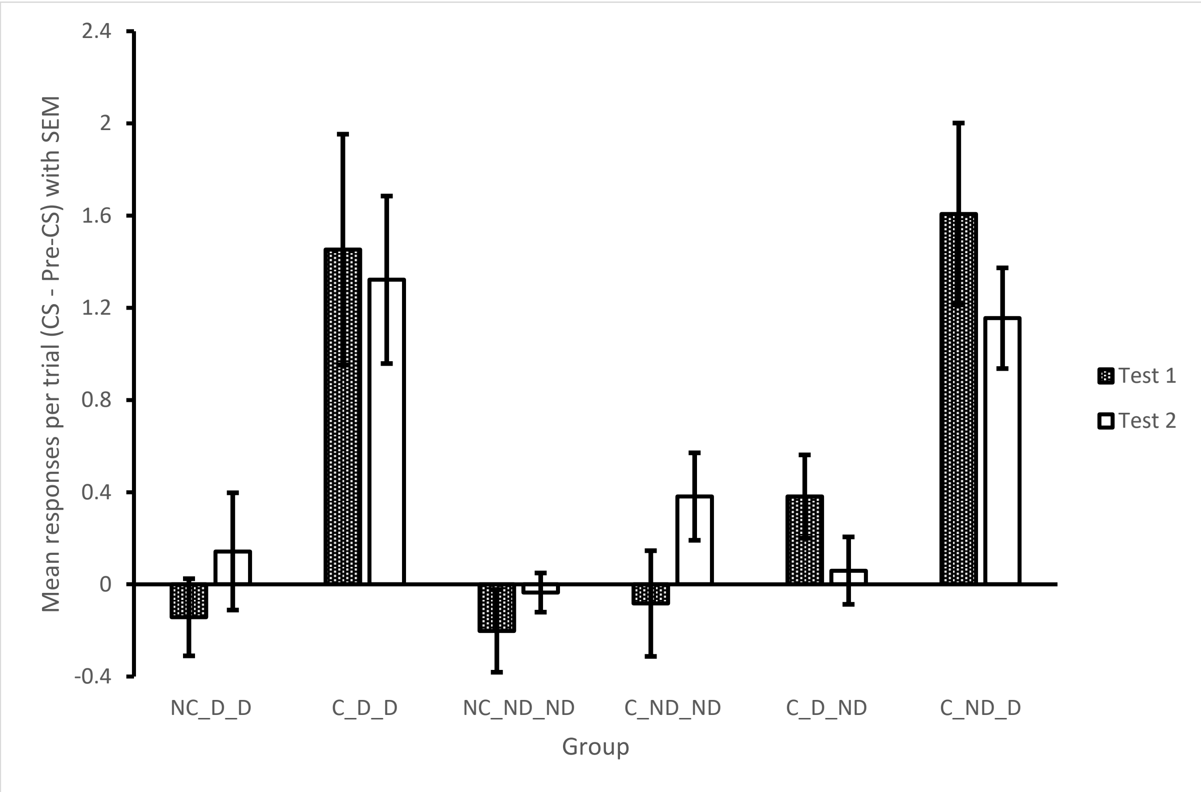

Figure 2 – Shows mean (with SEM) number of magazine entry responses (as CS – Pre-CS rates) per trial as a function of group (see Table 1 for details of abbreviated group names) and testing session.

Additional Analysis Experiments 1 & 2

The primary analysis of the current experiments was based on responses aggregated across all trials during test. This maximises power by removing trial by trial variability which is typical in animal conditioning experiments, and indeed was the approach used by Waldmann et al. (2012). However, as noted by Dwyer and Waldmann (2016), there is a potentially important distinction between the first trial of test and the remainder: namely that on the first trial, responding to the CS is assessed prior to the animals having a chance to experience whatever outcome may or may not follow that CS; while all other trials take place after animals have experienced the programmed consequence of the CS. This is particularly important in light of the idea that experience of the empty dipper might play a role at test (e.g., as a renewal cue or as a secondary reinforcer). That is, to the extent that the effects of magazine covering during extinction depend on the experience of the empty dipper during test, then its effects could only be seen after the first trial.

Although the experiments reported here were not powered with the aim of examining responding as a function of trial, the fact that both of Experiments 1 and 2 include the same manipulation as in Waldmann et al. (2012) – namely the comparison of groups where the magazine was covered or not during extinction while the empty dipper was operated during both extinction and test – allows for a potentially more powerful re-analysis based on the combined groups. Thus, the data from Test 1 in the groups replicating those from the original experiments were re-examined using a mixed ANOVA with a within-subject factor of test Trial (Trial 1 vs Average of Trials 2-12), and between-subjects factors of Group (No-Cover Dipper Dipper vs Cover Dipper Dipper) and Experiment (Experiment 1 vs Experiment 2).

Figure 3 shows this combined data and suggests that the difference between the Cover and No-Cover conditions was indeed most apparent after the first trial. Consistent with this observation, ANOVA revealed a significant Group by Trial interaction [$F(1, 28) = 11.13$, $p = .002$, $\eta^2_p = .284$], and follow up tests found that there was no significant difference between the Cover and No-Cover conditions on the first test trial [$F(1, 28) < 0.01$, $p = .985$, BF01 = 3.72], but that there was one for the remaining trials [$F(1, 28) = 21.70$, $p < .001$]. The remainder of the ANOVA revealed a significant main effect of Trial [$F(1, 28) = 13.37$, $p = .001$, $\eta^2_p = .323$], that the main effect of Group did not reach standard levels of significance [$F(1, 28) = 3.97$, $p = .056$, $\eta^2_p = .124$, and that there was no significant main effect of Experiment [$F(1, 28) = 0.97$, $p = .332$, $\eta^2_p = .034$], or any significant interaction involving this factor [Group by Experiment $F(1, 28) = 1.63$, $p = .212$, $\eta^2_p = .055$; Trial by Experiment $F(1, 28) = 0.18$, $p = .676$, $\eta^2_p = .006$; Trial by Group by Experiment [$F(1, 28) = 0.01$, $p = .913$, $\eta^2_p < .001$].

Thus, although based on a post-hoc analysis, it appears that the critical difference between the Cover and No-Cover conditions is only apparent after animals had the chance to experience the operation of the empty dipper in the test phase of the experiment.

Figure 3 – Combined Experiments 1 & 2 data

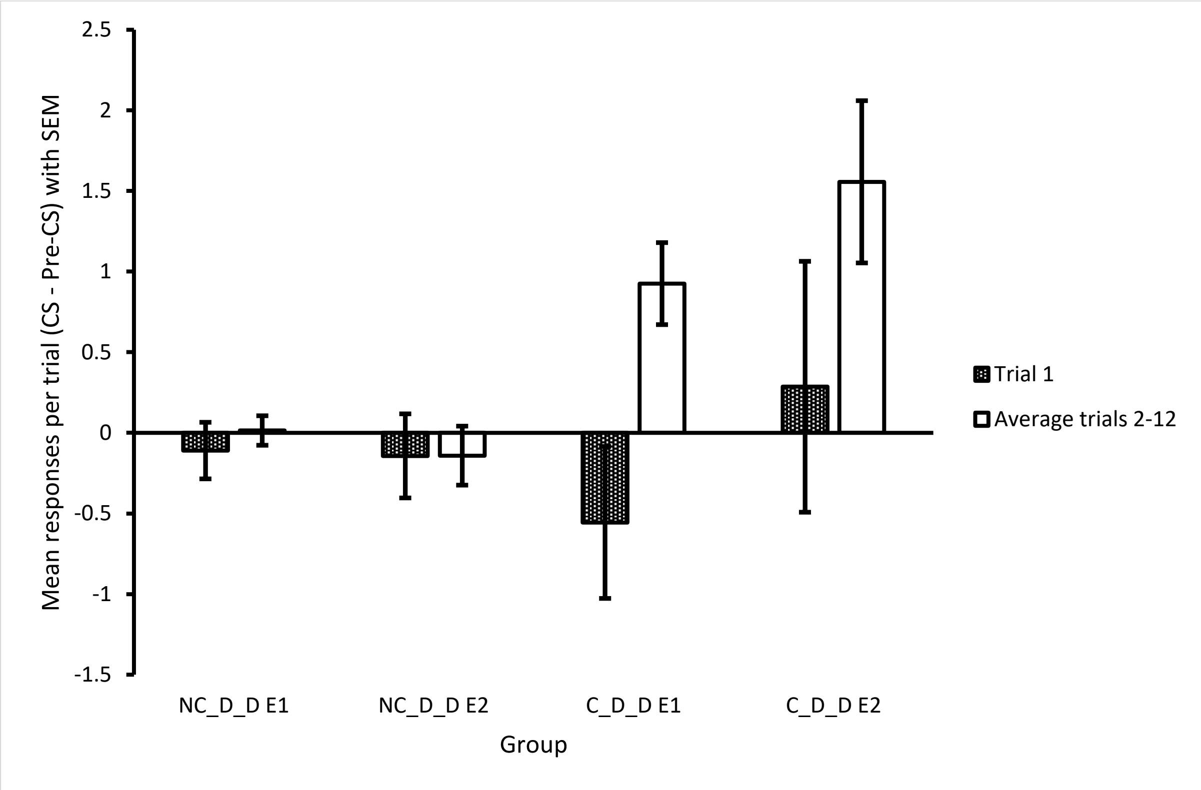

Figure 3 – Shows mean (with SEM) number of magazine entry responses (as CS – Pre-CS rates) per trial for the groups replicating the original Waldmann et al. (2012) conditions from Experiments 1 and 2 with responses separated between the first test trial (i.e., before the dipper would be presented during the test phase) and the remaining trials from test session 1.

General Discussion

The experiments reported here were inspired by Waldmann et al. (2012) reporting that test phase responding to a light CS (previously paired with access to a sucrose-filled dipper) was greater after extinction if that extinction was performed where a metal cover prevented access to the food magazine. The current experiments replicate that basic effect, but additional groups demonstrate that the impact of covering the magazine during extinction was itself dependent on the continued operation of the now-empty dipper during the test phase. The original experiments were motivated by the possibility that rats might be sensitive to the difference between the absence of events and that lack of evidence about them, while the additional manipulations reported here were motivated by alternative accounts derived from associative learning theory. We will initially consider the overall pattern of results separately from each theoretical perspective.

An associative learning perspective

The "headline" result from Waldmann et al. (2012), and replicated here, was that rats which received extinction exposure to a CS alone responded more during test if that extinction had been performed when access to the place where the sucrose US had been presented during original training was prevented by covering with a metal plate. In these broad terms, associative theory offers relatively little by way of obvious explanation. However, particular details of how the sucrose US was presented (and then not presented during extinction and test) do afford several potential associative explanations of the covering effect. The sucrose US was delivered by raising a small cup at the end of a dipper arm into the base of a food magazine, and – somewhat unusually – non-delivery of the sucrose US was performed by operating the dipper arm as it had been in training, but with the cup empty. As described in the introduction, renewal theory suggests that the operation of the empty dipper arm at test would enhance any renewal effect because it would maximise the difference in context between extinction (cover over the magazine, no access to the magazine or to the moving dipper) and test (no cover over the magazine, access to the magazine and the moving dipper). Alternatively, the fact that the dipper was experienced with sucrose in training should establish the dipper as a potential secondary reinforcer. In the absence of a magazine cover, extinction would remove this potential (not only is the CS no longer followed by sucrose, but the dipper is now experienced without sucrose), but covering the magazine during extinction would mean that the dipper is never experienced without sucrose and should retain its secondary reinforcement properties, thus allowing it to re-establish responding in the test phase when presented after the CS. In short, both associative accounts suggest that the apparently minor detail of operating the empty dipper arm during test was critical for covering the magazine during extinction to produce enhanced responding at test – and exactly this result was observed in Experiments 1 and 2[5]. Moreover, the fact that the first trial of test (where responding to the CS was examined prior to the operation of the dipper) did not show enhanced responding after covering, but subsequent trials do, is also consistent with the importance of dipper operation during the test phase as predicted by the associative accounts.

In contrast, the account of the basic effect proffered by Waldmann et al. (2012) was that rats were sensitive to the fact that covering the magazine during extinction created uncertainty over whether or not the sucrose US was present, and in turn this uncertainty would reduce the evidential value of experiencing the CS without its previously-paired US, which would prevent or reduce extinction. That is, the uncertainty account previously proposed by Waldmann et al. (2012) refers only to the act of covering itself, and is predicated on the idea that the uncertainty produced by

[5] Firstly, it should be noted that dipper operation is essential to the secondary reinforcement account, but renewal theory allows any context change to support renewal – and so the covering itself could in-principle be sufficient to support some re-emergence of responding during test. The fact that we did not observe any effect of covering without continued dipper operation could be interpreted as favouring the secondary reinforcement account, or as evidence that the cover alone was insufficient context change to support renewal.
Secondly, both the secondary reinforcement and renewal accounts are mainly focused on the impact of dipper operation at test and are less well developed about the possible impact of acoustic cues to dipper operation during the extinction phase. This potential complication is largely moot given the observation in Experiment 2 that operating or not operating the dipper behind the cover in the extinction phase had no obvious impact.

covering acts at the time of extinction and thus manipulations during the test phase should be without effect.

An uncertainty/cognitive perspective

The uncertainty account proposed by Waldmann et al. (2012) was based on the assumption that there was no further cue suggesting the presence or absence of sucrose in the extinction or test phases. In particular, it was assumed that the dipper movement, which could be such a cue, was inaudible. However, the results of the present experiments suggest that dipper movement is a potential cue that could reduce uncertainty. To represent such a situation, the causal model needs to be augmented by including dipper movement as a diagnostic cue of potential sucrose presentation. So, while the original suggestion was that rats may form a *light-causes-sucrose* model of the world, it is clearly possible to suggest that the rats may have formed a more complex model such as *light-causes-sucrose-via-a-dipper.* Because this more detailed model includes the operation of the dipper, it also affords an explanation of why there was no responding during test if the empty dipper was not operated: for example, this detailed model implies that sucrose would only be delivered if the dipper was working, and so in the absence of dipper operation, there is no reason to expect sucrose (and with that, no reason to enter the magazine)[6]. That is, the absence of dipper operation at test would directly undermine the model *light-causes-sucrose-via-a-dipper*, and so the question of whether that model had been maintained across extinction because the presence/absence of the sucrose was uncertain due to magazine covering would be moot. Thus, while the current results are inconsistent with the exact cognitive account described by Waldmann et al. (2012), they remain entirely consistent with the more general idea that rats might learn by

[6] This also makes the further prediction that any removal of the dipper operation should reduce or remove responding. Examination of the extinction phase suggests some numerical trends towards such an effect, but not a large enough one to reach standard levels of statistical significance.

forming causal models of the world and making inferences about the world based on evidence relative to those models – including potential sensitivity to uncertainty about that evidence.

Thus, the current results are not inconsistent with the wider idea that animal learning may be best understood as an example of causal reasoning or other “level 2” beyond associative accounts (to use the terminology introduced by Dwyer & Waldmann, 2016). Nor is the idea of considering more complex causal models purely ad-hoc, as people’s causal models typically omit causally irrelevant events and often also omit the details of mechanisms mediating between initial causes and ultimate effects (Keil, 2003; Rozenblit & Keil, 2002). In this light, manipulations of the operation or non-operation of the dipper could act as a prompt to examine the adequacy of a model without that mediating step, and aid the development of a more detailed causal understanding. Similarly, prior knowledge will play a role in identifying and characterising plausible causal relationships (e.g., Griffiths & Tenenbaum, 2009), and the dipper manipulation could add to that prior knowledge and suggest that a causal relationship between a light and sucrose would be implausible without intervening steps.

Final comments

As was discussed by Dwyer and Waldmann (2016), deciding between level 1/associative or level 2/cognitive accounts of animal behaviour can be exceptionally difficult. This is our (current) best attempt in the context of magazine covering in extinction of Pavlovian conditioning, and the fact that we find it possible to make a case for the results being consistent with either Level 1 or Level 2 accounts suggests that this attempt was not conclusive (as has been said of many other prior studies – as was noted in the introduction). Nevertheless, there is a degree of reciprocity in this theoretical development: the original limited causal model account motivated the experiments of Waldmann et al. (2012); the results of those experiments inspired the development of the associative accounts and with them the design of the additional manipulations examined here; the results of these new experiment required a refinement of the more detailed causal model account sketched out above. From the perspective of a causal account, future studies would be desirable that more clearly afford the inference that the experimental setup created uncertainty.

While this series of experiments may not have provided a conclusive answer to the question of whether level 1/associative or level 2/cognitive theories offer the best account of rats' learning abilities in general, they have refined the detail of both associative and cognitive accounts. The current experiments also highlight the way in which details of the implementation of an experimental design that might appear inconsequential can actually have critically important effects. This is entirely in line with the suggestion that progress in this general area might be best served by focussing on incremental empirical study (e.g., Beckers et al., 2016; Heyes, 2012). In short, the current results provide novel data on the issue of whether rats are sensitive to uncertainty and place material constraints on any possible account of how preventing access to the physical location where events occur influences rats' behaviour. We leave any interpretation of the current results regarding the more general question of whether animal cognition can be understood purely in associative terms or requires more advanced cognitive capacities to the reader.

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