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Magazine approach during a signal for food depends on Pavlovian, not instrumental, conditioning.

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Abstract

In the conditioned magazine approach paradigm, rats are exposed to a contingent relationship between a conditioned stimulus (CS) and the delivery of food (the unconditioned stimulus, US). As the rats learn the CS-US association, they make frequent anticipatory head entries into the food magazine (the conditioned response, CR) during the CS. Conventionally, this is considered to be a Pavlovian paradigm because food is contingent on the CS and not on the performance of CRs during the CS. However, because magazine entries during the CS are reliably followed by food, the increase in frequency of those responses may involve adventitious ("superstitious") instrumental conditioning. The existing evidence, from experiments using an omission schedule to eliminate the possibility of instrumental conditioning (Farwell & Ayres, 1979; Holland, 1979), is ambiguous: rats acquire magazine CRs despite the omission schedule, demonstrating that the response does not depend on instrumental conditioning, but the response rate is greatly depressed compared with that of rats trained on a yoked schedule, consistent with a contribution from instrumental conditioning under normal (non-omission) schedules. Here we describe experiments in which rats were trained on feature-positive or feature-negative type discriminations between trials that were reinforced on an omission schedule versus trials reinforced on a yoked schedule. The experiments show that the difference in responding between omission and yoked schedules is due to suppression of responding under the omission schedule rather than an elevation of responding under the yoked schedule. We conclude that magazine responses during the CS are largely or entirely Pavlovian CRs.

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In associative learning, a distinction is drawn between Pavlovian and instrumental conditioning. In the former, animals are exposed to a contingent relationship between presentations of a conditioned stimulus (CS) and an unconditioned stimulus (US); as they learn the CS-US relationship they show conditioned responses (CRs) to the CS in anticipation of the US. In instrumental conditioning, animals learn about a contingent relationship between a particular response and delivery of a US (an R-US association); the CR is reinforced by presentation of an appetitive US or by avoidance of an aversive US. Thus the distinction between Pavlovian and instrumental conditioning concerns the relationship between the CR and the US: an instrumental CR increases in strength or frequency because delivery of the US is contingent on that response, whereas Pavlovian CRs are elicited by the CS, but the CRs themselves bear no contingent relationship to the US.

While the above distinction between Pavlovian (CS-US) and instrumental (R-US) conditioning can be specified at a theoretical level, it is less easily established at a practical level, and in many conditioning preparations the nature of the CR can be ambiguous (Jenkins, 1977; Sheffield, 1965). One popular, nominally Pavlovian, paradigm that suffers from this ambiguity is magazine approach conditioning. In this paradigm, rats are exposed to a contingent relationship between the presentation of an auditory or visual CS and the delivery of a food pellet. As rats learn this CS-US relationship, they respond by making anticipatory head entries into the food magazine (the CR), and the rate of these responses during the CS is greatly elevated above the base rate observed during the pre-CS period (e.g., Boakes, 1977). The elevated rate of magazine entries during the CS is conventionally described as a Pavlovian CR because, at least from the experimenter's point of view, delivery of the US is contingent on the CS, not on the CR. However, as is sometimes acknowledged by researchers using this paradigm (e.g., Delamater, 1996; Lattal & Nakajima, 1998; Rescorla, 2000; Ricker & Bouton, 1996), the emergence of magazine approach CRs may involve a component of instrumental conditioning since collection of the food pellet is contingent on the rat entering the magazine (Gormezano & Kehoe, 1975). Indeed, even if food delivery is delayed until the end of the CS, such that responses made during the CS are never reinforced, it is nonetheless possible that within-CS responses become "superstitiously" conditioned because they are reliably followed by food at the termination of the CS. That is, even though there is no explicit contingency between food and CRs made during the CS, the CS may serve in effect as a discriminative stimulus (S^D) for reinforcement of magazine entry responses.

Our interest in questioning the associative content of magazine approach CRs has been rekindled by a recent discovery about the relationship between the rate at which rats perform magazine approach CRs during a CS and the rate at which food is delivered during the CS (Harris & Carpenter, 2011). This relationship conforms closely to a hyperbolic function, which, when inverted, can be expressed as a simple straight-line relating the inter-reinforcement interval (how long the rat must wait till the US) to the inter-response interval (how long the rat waits between magazine entries). This relationship between response rate and reinforcement rate echoes the Matching Law (Davison & McCarthy, 1988; Herrnstein, 1970), in which an animal's choice to perform a target response is set by the rate at which that response is reinforced relative to the rate of reinforcement of other available behaviors. Because the Matching Law has conventionally been demonstrated using instrumental reinforcement schedules[1], our observation of a matching-like relationship for magazine approach CRs speaks to the possibility that these responses arise, at least in part, by a process of instrumental conditioning.

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[1] It is worth noting that the majority of research demonstrating a strong matching relationship between response rate and reinforcement rate studied key-peck responses in pigeons. This paradigm is itself ambiguous with respect to the contributions of R-US versus CS-US associations (Williams & Williams, 1969).

An omission schedule is an effective way to test whether a given CR arises from an R-US association (Sheffield, 1965; Williams & Williams, 1969). In the omission schedule, each presentation of a CS is followed by the US except when the subject produces the CR. In the magazine approach paradigm, a food pellet is delivered at the end of each CS presentation, but if the rat enters the magazine during the CS the food is cancelled on that trial. The omission schedule ensures that the CRs emitted during the CS are <u>never</u> reinforced by the US, and therefore any elevation of responding during the CS cannot arise from opportunistic reinforcement of that response. Holland (1979) used this schedule in the magazine approach paradigm, and found that rats trained with an omission schedule still acquired elevated response rates during the CS (and more so for an auditory CS than a visual CS). Because these CRs could not have arisen by instrumental (R-US) conditioning, they must have been, by default, Pavlovian. However, the response rates in rats trained on the omission schedule were significantly below those of control rats trained on a yoked reinforcement schedule that matched the exact history of CS-US pairings experienced by the rats on the omission schedule (see also Farwell & Ayres, 1979). Since the omission rats and yoked rats had identical histories of CS-US pairings, the difference in their response rates must have resulted from differences in their opportunities to learn about contingent relationships between the CR and US. That is, the difference must have involved instrumental conditioning.

The difference in magazine response rates between rats trained on an omission schedule and those on a yoked schedule (Farwell & Ayres, 1979; Holland, 1979) is open to two distinct interpretations. One is that the yoked rats acquired instrumental magazine approach CRs, in addition to Pavlovian CRs, because the yoked schedule did not eliminate the opportunity for R-US associations. An alternative interpretation is that the explicit (negative) contingency between the CR and US in the omission schedule creates the opportunity for rats to acquire some other response (R_a) that suppress the target CR. For example, on the omission schedule, any other response that competes with, and thus reduces, magazine entry is effectively reinforced with food, and should therefore increase in frequency. Thus the available evidence is consistent with two distinct, but not mutually exclusive, accounts of the nature of magazine approach CRs. One possibility is that, when there is no omission schedule, the CRs are in part Pavlovian (as isolated by the omission schedule) and in part instrumental (as revealed by the difference in response rates between omission and yoked rats). The other possibility is that, when there is no omission schedule, the CRs are entirely based on the CS-US association, but the expression of these Pavlovian CRs is reduced by competing R_as that are reinforced when rats are trained on an omission schedule.

The present experiments were conducted to evaluate the contributions of CS-US and R-US associations to magazine approach responses in rats. Experiment 1 conditioned four CSs with different reinforcement rates (i.e., they had different mean CS-US intervals), but all four CSs were reinforced on an omission schedule. This was done to test whether, under an omission schedule, we could reproduce the hyperbolic relationship between response rate and reinforcement rate that we have previously observed among rats trained under a standard (non-omission) reinforcement schedule (Harris & Carpenter, 2011). If our previous observation was based on opportunistic R-US associations, we would not expect to see the same hyperbolic relationship when conditioning was conducted under the omission schedule. The remaining experiments were designed to tease apart the two alternative descriptions of magazine approach CRs described in the preceding paragraph. Experiment 2 used a within-subject design to assess differences in CRs to one CS reinforced on an omission schedule and a second CS reinforced on a yoked schedule. It showed that rats can learn this discrimination, responding less to the omission CS than the yoked CS, even though the two CSs had identical sequences of CS-

US pairings. To identify the source of the difference in response rates conditioned by omission versus yoked schedules of reinforcement, Experiments 3a and 3b used added-feature discriminations between an auditory CS, A, and a compound of A plus a light (LA). These were akin to feature-positive and feature-negative discriminations, except that the added feature (L) signaled the omission schedule or the yoked schedule.

Experiment 1

Experiment 1 addresses the question whether R-US associations contributed to our previously published observation that magazine approach rates are related to reinforcement rates by a hyperbolic function (Harris & Carpenter, 2011). The experiment compared response rates to four CSs that were reinforced at different rates, in the manner of our previous studies, but in this experiment all CSs were reinforced on an omission schedule. If our previous observation of the relationship between response rate and reinforcement rate was based on learning about the CS-US associations, rather than "superstitious" learning of R-US associations, then the same hyperbolic relationship should be evident here when all conditioning was conducted under the omission schedule.

Methods

Subjects

Sixteen experimentally naive male Hooded Wistar rats (Rattus norvegicus; 8 to 10 weeks of age at the start of the experiment) were obtained from the Laboratory Animal Services breeding unit at The University of Adelaide, South Australia. During the experiment, they were housed in groups of 8 in large white plastic tubs, measuring 26 x 59 x 37cm (height x length x depth), located in the animal colony maintained by the School of Psychology at the University of Sydney. They had unrestricted access to water in the home tubs. Three days prior to commencement of the experiment, they were placed on a restricted food schedule. Each day, each tub of rats received a ration of their regular dry chow equal to 5% of the total weight of all rats in the tub. The food was provided half an hour after the end of the daily training session, and all food was eaten within 3 hrs.

Apparatus

Rats were trained and tested in 16 Med Associates™ conditioning chambers measuring 28.5 x 30 x 25 cm (height x length x depth). The end walls of each chamber were made of aluminum; the sidewalls and ceiling were Plexiglas™. The floor of the chamber consisted of stainless-steel rods, 0.5 cm in diameter, spaced 1.5 cm apart. Each chamber had a recessed food magazine in the center of one end wall, with an infra-red LED and sensor located just inside the magazine to record entries by the rat. A small metal cup measuring 3.5 cm in diameter and 0.5 cm deep was fixed on the floor of each food magazine. Attached to the food magazine was a dispenser delivering 45 mg food pellets (purified rodent pellets; Bioserve, Frenchtown, NJ). Each chamber was enclosed in a sound- and light-resistant wooden shell. Throughout all sessions, fans located in the rear wall provided ventilation; the operation of these created a background noise level measuring 70dB. Experimental events were controlled and recorded automatically by computers and relays located in the same room. White noise (78dB) was presented from a speaker mounted on the wall of each conditioning chamber above and to the left of the food magazine. A steady light (30cd/m^2) was produced by an incandescent bulb mounted high on the back wall of the sound-attenuating shell. A tone (2.9 kHz) was produced from a piezo buzzer positioned on the floor of the sound-attenuating shell behind each conditioning chamber. A flashing light (2 Hz; 3.0cd/m^2) was emitted by a 3x3 array of white LEDs, located on the floor of the sound-attenuating shell in front of the conditioning chamber. The allocation of stimuli to different reinforcement conditions was counterbalanced across squads for four rats using a latin square, such that each stimulus was allocated evenly across each reinforcement rate, and stimuli from the same modality (visual or auditory) were never allocated to neighboring reinforcement rates for any rat.

Procedure

On Day 1 of the experiment, the rats commenced daily conditioning sessions 5 days per week for 28 days. (There was no prior magazine training.) Each session contained 64 trials, 16 trials of each of the four CSs. CS durations varied randomly between 1 and 15 s (mean = 8 s). Trials with each CS were randomly intermixed with the constraint that each quarter of the session included equal numbers of each CS. The CSs differed in their maximum reinforcement rates: food was scheduled on 100% of trials with one CS, on 50% of trials with a second CS, on 25% of trials with a third CS, and on 12.5% of trials with a fourth CS. The operation of the omission contingency inevitably reduced the actual reinforcement rates. For CSs with scheduled reinforcement rates less than 100%, care was taken to ensure that food was scheduled uniformly across the range of CS durations. Photo-beam interruptions by head entry into the magazine were recorded during each CS and each 20-s pre-CS period. Sessions lasted approximately 2 h.

Results and Discussion

Response rates to each CS across all 28 days of the experiment are shown in the upper plot of Figure 1. The rats responded more during the CSs than during the pre-CS interval. Moreover, the rate of responding differed for the different CSs, but was in proportion to the differences in the rate of reinforcement of the CSs. To examine the relationship between response rates and reinforcement rates, we analyzed data pooled across the last 10 days of the experiment, to be consistent with our previous studies. We compared the average response rate to each of the four CSs against that during the pre-CS interval (note that, to correct for multiple comparisons, we set α at .0125). Responding to each CS was significantly higher than during the pre-CS interval: smallest $t(15) = 3.67$, $p = .002$ (for the difference between the 12.5% CS and pre-CS). An ANOVA on the response rates during the CSs revealed a significant linear trend across reinforcement rates, $F(1,15) = 25.85$, $p < .001$, confirming the systematic increase in response rate as the reinforcement rate increased.

To show the nature of the relationship between reinforcement and response rates, we have plotted the mean response rate to each CS against the actual rate at which that CS was reinforced (the effect of the omission contingency meant that the actual reinforcement rate was less than the scheduled rate). The obtained mean reinforcement rates, as the proportion of trials reinforced with a pellet (plus standard deviation), were: 0.45 (0.24), 0.27 (0.13), 0.15 (0.05), and 0.08 (0.02), for the 100%, 50%, 25%, and 12.5% CSs respectively. These reinforcement rates are plotted against the response rates in the lower left part of Figure 1. The figure includes the best-fitting hyperbolic function (the gray curve), confirming that the response rate data are well described by a hyperbolic function. The lower right part of Figure 1 plots the relationship between the inverse of response rate (response interval) against the inverse of reinforcement rate (reinforcement interval), and shows that these are well described by the straight line that is derived from the reciprocal of the x and y values of the hyperbolic function. Thus the relationship between response rate and reinforcement rate when rats are trained under an omission schedule is exactly the same as that we described previously in rats that were trained without an omission schedule (Harris & Carpenter, 2011). This demonstrates that the relationship is based on Pavlovian conditioning of magazine approach responses, and is not due to possible instrumental conditioning of those responses.

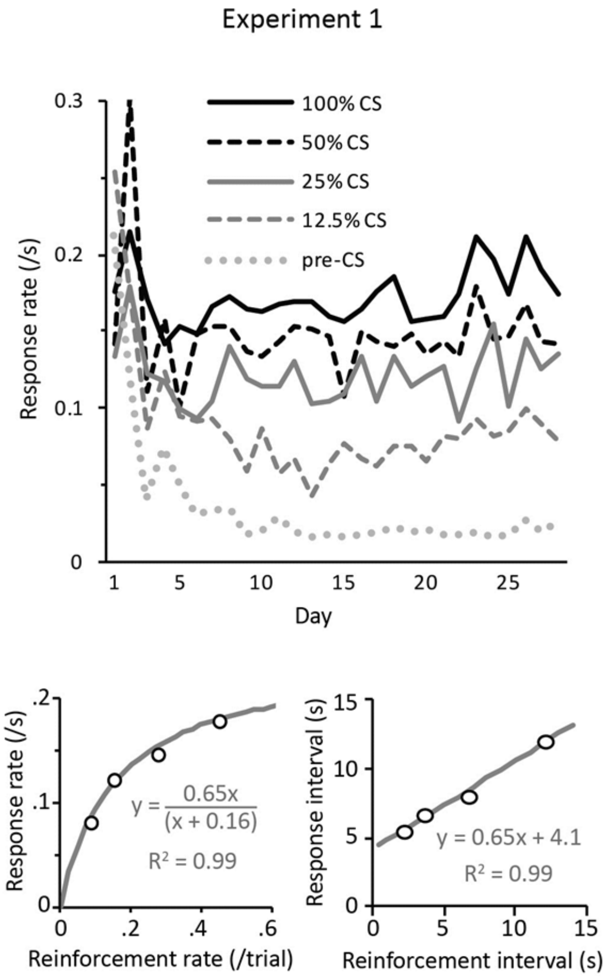

Figure 1. The top plot shows the mean response rate to each CS, and during the pre-CS interval, for each day of Experiment 1. The lower left plot shows the mean response rate to each CS, averaged over the last 10 days of the experiment, as a function of the observed reinforcement rate of the CSs (the proportion of trials reinforced with a pellet). The observed reinforcement rate was determined by the scheduled reinforcement rate and the omission contingency. We have added a plot of the best-fitting hyperbolic function (gray curve), along with the equation describing that function and the R^2 of its fit to the data. The lower right plot shows the reciprocal of the response rate (response interval) as a function of the reciprocal of the reinforcement rate (reinforcement interval), and includes the best-fitting straight line along with the equation for this line and the R^2 for its fit.

Experiment 2

The remaining three experiments compared rats' magazine responses under omission and yoked schedules to investigate the relative contributions of Pavlovian (CS-US) and instrumental (R-US) conditioning. Before running these experiments, we conducted a between-group experiment, similar to those described by Holland (1979), in which one group of rats was conditioned to a CS on an omission schedule and another group was trained on a yoked schedule. This unpublished experiment replicated the important features of Holland's results: the omission rats acquired above-baseline rates of magazine CRs, but these were well below the CR rates acquired by the yoked rats. However, we also observed a significant difference in baseline response rates between the two groups – more pre-CS responding in rats on the omission schedule than rats on the yoked schedule. The difference in baseline response rates is problematic because it complicates the comparison of response rates during the CS. One way to eliminate any confound produced by differences in baseline response rates is to use a within-subjects design because, in such a design, comparisons are made between response rates that share a common baseline. Accordingly, Experiment 2 in the present series used a within-subject design to compare rats' response rates to a CS that was conditioned on an omission schedule and a second CS that was conditioned on a yoked reinforcement schedule. As in Experiment 1, the duration of the CSs varied randomly from trial to trial.

Methods

Subjects and Apparatus

Sixteen experimentally naive male Hooded Wistar rats (Rattus norvegicus; 8 to 10 weeks of age at the start of the experiment), were obtained from the same source and were housed in the same manner as described for Experiment 1. They were trained and tested in the same conditioning chambers, and with the same steady light and white noise stimulus, used in Experiment 1.

Procedure

On Day 1 of the experiment, the rats commenced daily conditioning sessions 5 days per week for 26 days. Each session contained 18 trials of each of the two CSs; the CS durations varied randomly between 2 and 38 s (from a uniform distribution with mean = 20 s). Trials with each CS were randomly intermixed with the constraint that each half of the session included equal numbers of both CSs (9 presentations each). One CS (light or noise, counterbalanced) was reinforced on an omission schedule. The other CS was reinforced on a schedule that was yoked to the reinforcement schedule of the Omission CS from the previous day. That is, the CS duration and outcome (reinforced or not) of all 18 trials of the Omission CS were recorded in each session, and that schedule of durations and outcomes was replayed for the Yoked CS on the following day. However the order of the Yoked trials, and how they were intermixed with Omission trials, was re-randomised between days. On Day 1 of the experiment, when there were no available data from a preceding session of trials with the Omission CS, the Yoked CS was reinforced on 50% of its trials (evenly distributed across the range of CS durations), based on our observation from the unpublished experiment that the rate of reinforcement on the omission CS was on average close to 50%. Photo-beam interruptions by head entry into the magazine were recorded during each CS and each 20-s pre-CS period. Sessions lasted approximately 90 min.

Results and Discussion

The response rates during the two CSs, and during the pre-CS interval, are shown in Figure 2. Overall, response rates in this experiment were low. Nonetheless, response rates during the Omission CS were above pre-CS baseline levels, and response rates during the Yoked CS were greater than those during the Omission CS. These observations were supported by statistical analyses. An overall ANOVA, with Greenhouse-Geisser corrections, revealed a significant main effect of CS period (during the Omission CS, Yoked CS, or pre-CS period), *F*(1.6,24) = 23.16, *p* < .001, and a significant main effect of Day, *F*(5.9,89) = 2.72, *p* = .019, as well as a significant interaction between these main effects, *F*(6.5,98) = 6.58, *p* < .001. Contrasts tested for differences between the two CSs and between each CS and the pre-CS interval. These showed that there was a significant difference between the Yoked CS and Omission CS, *F*(1,15) = 8.38, *p* = .011, and that response rates during both CSs were significant different from response rates during the pre-CS period, smaller *F*(1,15) = 25.25, both *p*'s < .001. Each of these comparisons also interacted with the linear trend across days, smallest *F*(1,15) = 9.21, largest *p* = .008.

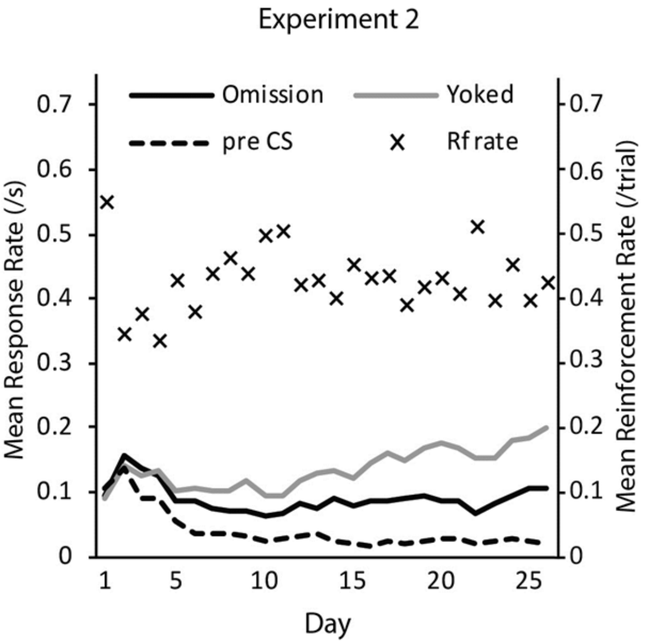

Figure 2. Mean response rates (magazine entries per second) during each of two CSs, and immediately prior to the CS, for rats in Experiment 2. One CS was conditioned on an omission schedule, the other was on a yoked reinforcement schedule. Response rates during both CSs was higher than that during the pre-CS period, however response rates during the Omission CS were lower than during the Yoked CS. Crosses show the proportion of trials each day that ended in reinforcement (Rf rate).Figure 2 also shows the proportion of trials with the Omission CS that ended in reinforcement on each daily session. This rate of reinforcement was close to 50%.

Holland (1979) reported that responding under an omission schedule was different for rats trained with an auditory CS (white noise) compared with rats trained with a visual CS (light): the rats trained with the light under an omission contingency responded at a very low rate, whereas the rats trained with the noise responded at a relatively high rate (similar to that of rats provided with reinforcement on every trial). In view of this result, we looked separately at responding for the eight rats that had the light as the Omission CS, versus the other eight rats for which the noise served as the Omission CS. There was little difference between these two sub-groups, and if anything responding during the CS was slightly greater for rats with the light as Omission CS (mean response rate over the last 5 days = .10) than for the rats with the noise as that CS (mean response rate over the last 5 days = .08). We analyzed the response data with an ANOVA that included as a between-group factor the counterbalancing of light and noise as omission versus yoked CSs. In this analysis, there was no main effect of the counterbalancing factor, $F < 1$, this factor did not interact with either CS period, $F < 1$, or session, $F(4.9,69) = 1.00$, $p = .421$, and there was no three-way interaction, $F(4.9,68) = 1.11$, $p = .365$. Therefore, we found no evidence that the responses of the rats varied depending on the allocation of the light versus noise to each CS. The reason for the discrepancy between our results and those reported by Holland may be due to differences in the location of the speaker used to deliver the white noise stimulus. In Holland's experiments, the speaker was mounted on the wall of the sound-resistant shell outside the conditioning chamber, whereas in our experiments the speaker was mounted on the wall of the conditioning chamber itself, above and to the left of the magazine. Thus our rats may have been better able to localize the source of the auditory stimulus, and as a result the noise may have elicited more orienting responses that could compete with magazine entry under the omission schedule.

In sum, this experiment has confirmed that rats acquire magazine approach responses during a CS even when those responses are never followed by reinforcement (i.e., when the CS is reinforced on an omission schedule). However, it has also confirmed that response rates during the CS are lower following conditioning on an omission than on a yoked schedule of reinforcement.

Experiments 3a and 3b

Experiment 2 confirmed that rats acquire magazine entry responses during a CS paired with food even when those very responses lead to the omission of the food. However, it also showed that the rate of these responses is lower than that produced by the exact same pattern of CS-US pairings when food delivery is independent of responses during the CS (i.e., on a reinforcement schedule that is yoked to the omission schedule). As discussed in the Introduction, this difference in response rates between omission and yoked schedules can be explained in two distinct ways. One explanation is that response rates are elevated in the yoked schedule because that schedule provides the opportunity for "superstitious" instrumental conditioning of magazine responses when responses during the CS are followed soon after by food, whereas the omission schedule explicitly eliminates this opportunity. The other explanation is that the omission schedule provides the opportunity for instrumental conditioning of behaviors that are incompatible with magazine entry because those competing behaviors are effectively reinforced (i.e., they increase the likelihood of food). In other words, one account interprets the difference between omission and yoked schedules as the addition of instrumentally conditioned magazine responses in the yoked schedule (but not the omission schedule); the other account interprets that difference as the suppression of magazine responses in the omission schedule due to instrumental conditioning of competing responses.

Experiments 3a and 3b sought to tease apart these possible accounts, by training rats on symmetrical added-feature discriminations. The designs of the two experiments are summarized in Table 1. In both experiments, rats were trained on a discrimination between an auditory stimulus, A, versus a compound of A with a light (L). In Experiment 3a, trials with A were reinforced on an omission schedule whereas LA trials were yoked to that schedule. This was reversed in Experiment 3b: trials with LA were reinforced on an omission schedule and trials with A were yoked. To solve each discrimination, the rats must learn about the added feature L: as a signal for the yoked schedule in 3a, and as a signal for the omission schedule in 3b. The two accounts described above, of the difference between omission and yoked schedules, both predict that one of these discriminations will be more difficult than the other, but the accounts make opposite predictions about the relative difficulties.

According to the first account, rats acquire instrumentally conditioned magazine responses on the yoked schedule but not on the omission schedule. If this is correct, the discrimination in Experiment 3a should be relatively easy because L would serve as an S^D for those instrumental responses in the yoked schedule. The same account predicts that the discrimination in Experiment 3b would be more difficult because the rats must learn to make instrumental magazine responses during A but also learn to inhibit them during LA (i.e., L would have to serve as an S^Δ). According to the second account, rats acquire instrumentally conditioned competing responses in the omission schedule that interfere with magazine responses. If this is correct, the discrimination in Experiment 3b should be relatively easy because L would serve as an S^D for reinforcement of the competing responses, whereas the discrimination in Experiment 3a would be more difficult because the rats would have to acquire the competing responses during A but also learn to inhibit those responses during LA. In effect, the two experiments are comparing versions of a feature-positive and feature-negative discrimination: which discrimination is positive and which is negative depends on what is being learned about the reinforcement schedules, as described in the two accounts offered above. Since feature-negative discriminations are more difficult than feature-positive discriminations (e.g., Holland, 1991; Reberg & Leclerc, 1977; Sainsbury & Jenkins, 1967), we can observe which of the present discriminations is easier, and from this deduce the difference in content of learning on the omission and yoked schedules.

Table 1. Summary of design for Experiments 3a and 3b. A and B are auditory CSs (buzzer and white noise, counterbalanced) and L is a light.

Experiment	Discrimination training	Probe tests
3a	A-omission vs LA-yoked [and B-yoked]	LB
3b	LA-omission vs A-yoked [and B-yoked]	LB

As shown in Table 1, in both experiments, rats were additionally trained with a second auditory CS, B, that was reinforced on a yoked schedule. We included B so that, after extended training on the discrimination between A and AL, we could conduct transfer tests to assess the impact of L on responding to B. For this reason, towards the end of each experiment, the daily training sessions included probe trials with the compound LB. If L acquires the ability to control responding in the A versus AL discrimination, either as an S^D for instrumental magazine responses or as an S^D for competing instrumental responses, this influence should also be observed on trials with LB, either increasing or decreasing magazine responding compared to trials with B alone.

Methods

Subjects and Apparatus

Each experiment tested 16 experimentally naive male Hooded Wistar rats (Rattus norvegicus; 8 to 10 weeks of age at the start of the experiment), that were obtained from the same source and were housed in the same manner as described for Experiment 1. The rats were trained and tested in the same conditioning chambers used in Experiment 1, and with the same steady light and white noise stimuli described for that experiment. They were additionally trained with a second auditory stimulus, a clicker, delivered from a separate module (Med Associates, product ENV 135M) located on the wall of the conditioning chamber above and to the right of the magazine. The white noise and clicker were allocated as stimulus A and stimulus B in counterbalanced fashion.

Procedure

From Day 1 of the experiments, rats commenced daily conditioning sessions, 5 days per week for 35 days. For the first 21 days, each session contained 60 trials, 20 trials of each of A, B, and LA. For the next 14 days, each session included two probe trials with the compound LB, one 5 s long, the other 15 s long (the order of these two trials alternated between days and was counterbalanced across rats). To facilitate acquisition, CS durations were shorter than those used in the previous experiments: presentations of A, B, and LA varied randomly between 1 and 19 s (mean = 10 s). Trials with A, B, and LA were randomly intermixed with the constraint that each quarter of the session included equal numbers of all trial types (5 presentations each). LB probe trials were always presented as Trials 21 and 41 of the session.

In Experiment 3a, each presentation of A was reinforced on an omission schedule. Each presentation of B, and of the compound LA, was reinforced on a schedule that was yoked to the reinforcement schedule of A from the previous day, in the manner described for the Yoked CS in Experiment 2. In Experiment 3b, each presentation of the compound LA was reinforced on an omission schedule, and each presentation of A and B was yoked to the schedule of LA from the previous day. On Day 1 of both experiments, the yoked CSs were reinforced on 50% of trials (evenly distributed across the range of CS durations).

Due to equipment failure, no data were recorded for four rats (#9 to #12) on Day 17 of Experiment 3a. In order to include the remaining data from these rats in our statistical analyses, we used the average response rates from Days 16 and 18 as filler data on Day 17 for those 4 rats. Equipment problems also afflicted data from one rat in Experiment 3b: the infra-red sensor in one conditioning chamber occasionally malfunctioned and recorded large numbers of responses even when there was nothing inside the magazine. Because this occurred on a total of 6 days, we decided to remove from the analyses all data from this rat (#9), thus reducing the number of rats to 15. Nonetheless, the unaffected data from this rat showed that it learned the discrimination between A and LA, as did most of the other 15 rats.

Results

Experiment 3a.

The results of Experiment 3a are presented in the left plot of Figure 3. The rats rapidly acquired higher response rates during each CS (A, B, and LA) than during the pre-CS interval. Most importantly, however, they did not appear to learn to discriminate between trials with A, reinforced on the omission schedule, and trials with LA, reinforced on the yoked schedule. There is some suggestion that the rats did learn to respond more during B than during A and LA, but probe trials with the compound LB did not elicit response rates any different from those to B alone. An overall ANOVA, with Greenhouse-Geisser correction, revealed a significant main effect of response interval (A, B, LA, and pre-CS), $F(1.4,22) = 13.36$, $p = .001$, and main effect of Day, $F(5.6,184) = 6.73$, $p < .001$, and a significant interaction, $F(7.2,108) = 2.83$, $p = .009$. This was followed by comparisons between response rates during the different CSs and pre-CS period, which showed that response rates during each of the three CSs were significantly greater than during the pre-CS interval, smallest $F(1,15) = 20.56$, all *p*s $< .001$. However, there was no overall difference between A and LA, $F(1,15) < 1$, nor between A and B, $F(1,15) = 1.58$, $p = .227$. To test whether the rats had learned to discriminate between yoked and omission trials by the end of training, which might be missed by the omnibus analysis, we analyzed response rates over the final 5 days of the experiment. The difference between response rates during A and LA fell short of an appropriately corrected level of significance, *t*(15) = 2.13, *p* = .049, and we note that this difference, such as it was, was in the wrong direction for the discrimination (i.e., responding during A was greater than that during LA). Over the last 5 days, the difference between A and B was not significant, *t*(15) = 1.36, *p* = .194. An analysis over the last 14 days, when LB probe trials were included in each session, showed that there was no difference between responses during B and those during LB, *t*(15) < 1.

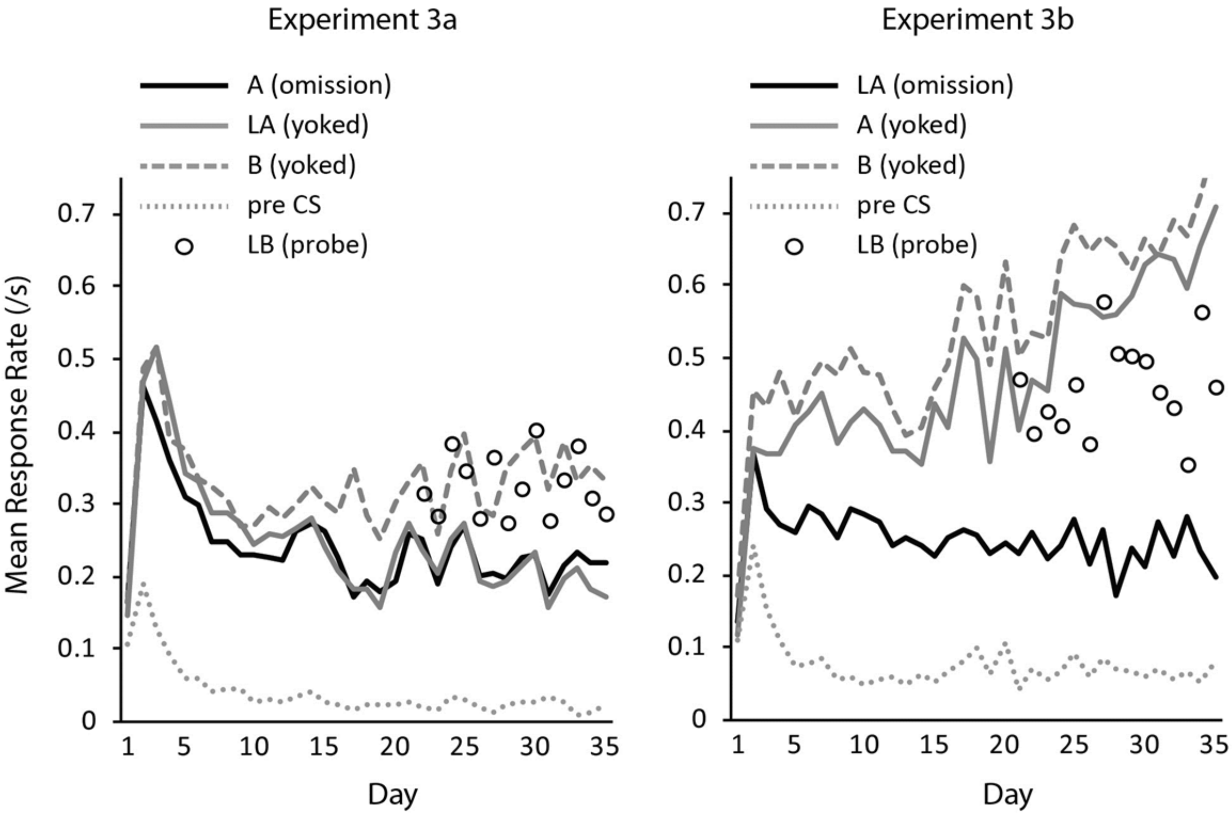

Figure 3. Mean response rate per day for rats in Experiments 3a and 3b. Rats in Experiment 3a (left) were trained on a discrimination between an auditory CS, A, reinforced on an omission schedule, and a compound (LA, composed of A and a light) that was reinforced on a schedule yoked to A's reinforcement sequence. The rats in Experiment 3b (right) were also trained on a discrimination between A and LA, but LA trials were reinforced on the omission schedule whereas A's reinforcement was yoked to LA's reinforcement sequence. In both experiments, the rats were also trained with a second auditory CS, B, that was yoked to the reinforcement schedule of the omission CS/compound. From Day 21 on, each daily session also included 2 probe trials with a compound of L and B.

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Experiment 3b.

The results of Experiment 3b are presented in the right plot of Figure 3. Once again the rats rapidly acquired higher response rates during each CS (A, B, and LA) than during the pre-CS interval. Further, in contrast to Experiment 3a, the rats did appear to discriminate between the omission trials (with LA) and the yoked trials (with A alone). They also appeared to learn to respond more during B than A, and response rates during probe trials with LB were lower than those during B alone. An overall ANOVA with Greenhouse-Geisser correction revealed a significant main effect of response interval (A, B, LA, and pre-CS), *F*(1.9,26) = 18.27, *p* < .001, and main effect of Day, *F*(4.5,64) = 4.73, *p* = .001, as well as a significant interaction, *F*(3.7,52) = 5.71, *p* = .001. This was followed by comparisons between response rates during the different CSs and pre-CS period, which showed that response rates during each of the three CSs (A, B, and AL) were significantly greater than during the pre-CS interval, smallest *F*(1,14) = 29.18, all *p*s < .001. There was also a significant difference between LA and A, *F*(1,14) = 8.59, *p* = .011, as well as between LA and B, *F*(1,14) = 10.99, *p* = .005. Finally, a comparison between responses during B and LB probes, pooled across the last 14 days, showed that response rates during LB were significantly lower than during B, *t*(14) = 2.44, *p* = .029.

Comparison across Experiments 3a and 3b.

We conducted a further analysis to compare discrimination performance for omission versus yoked trials between rats in Experiment 3a and those in 3b. The analysis took the form of a 2x(2)x(35) ANOVA with Experiment (3a vs 3b) as a between-group factor, and Schedule (Omission vs Yoked) and Days as within-subject factors. There were significant main effects of Schedule, *F*(1,29) = 9.47, *p* = .005, and Days, *F*(7.5,217) = 4.34, *p* < .001, as well as a significant interaction between these, *F*(2.9,83) = 3.80, *p* = .014. The main effect of Experiment was not significant, *F*(1,29) = 3.67, *p* = .065, but there were significant interactions between Experiment and Days, *F*(7.5,217)= 5.37, *p* < .001, between Experiment and Schedule, *F*(1,29) = 8.29, *p* = .007, and a significant three-way interaction between Experiment, Schedule and Days, *F*(2.9,83) = 6.31, *p* = .001. These last two interactions confirm that the rats in Experiment 3b were significantly better than rats in Experiment 3a at discriminating between the omission and yoked schedules. Separate ANOVAs compared rats in Experiments 3a and 3b for their responding to each schedule. There was a significant difference between experiments in the response rates to the Yoked schedule, *F*(1,29) = 6.12, *p* = .019 for response rates averaged over all 35 days, and *F*(4.9,142) = 7.45, *p* < .001 for the interaction between Experiment and Days. There was no difference between the experiments in responding to the Omission schedule, *F*(1,29) < 1 for response rates over all 35 days, and *F*(8,231) = 1.43, *p* = .184 for the interaction between Experiment and Days. Finally, an across experiment ANOVA comparing response rates to B versus LB showed there was a significant interaction between Experiment (3a versus 3b) and Trial type (B versus LB), *F*(1,29) = 5.26, *p* = .029.

Discussion

Experiments 3a and 3b have shown that rats can learn an added-feature discrimination between trials on an omission schedule and trials on a yoked schedule if the omission trials are signaled by the added feature (LA-omission vs A-yoked; Experiment 3b), but not if the yoked trials are signaled by the added feature (LA-yoked vs A-omission; Experiment 3a). The control over responding exerted by the added feature, L, in Experiment 3b was confirmed by a transfer test which showed that L also reduced responding to another yoked CS, B. The absence of any control by L in Experiment 3a was confirmed by transfer tests showing that L did not affect responding when compounded with the yoked CS B. The results show that rats learn to suppress magazine responses when a CS is reinforced on an omission schedule, rather than learning to increase those responses when a CS is reinforced on a yoked schedule.

General Discussion

The experiments described here used an omission schedule to examine the potential contribution of instrumental conditioning to the acquisition of magazine approach responses during a CS for food. Experiment 1 showed that the nature of the relationship between reinforcement rate and response rate that we previously identified in this paradigm is not dependent on possible instrumental conditioning of magazine approach responses. The same hyperbolic function was obtained when all CS-US conditioning took place under an omission schedule which eliminates any possibility of instrumental conditioning of magazine responses during the CS. Therefore, even though evidence for a hyperbolic relationship between reinforcement and response rates has historically come from instrumental reinforcement schedules (Davison & McCarthy, 1988; Herrnstein, 1970), we have shown here that it applies to Pavlovian CRs. The conventional interpretation of the hyperbolic relationship in terms of a simple choice rule (Luce, 1977) would imply that the Pavlovian CRs measured here are subject to the same selection processes (as, for example, argued by Gallistel & Gibbon, 2000). Alternatively, one can view this relation as a form of behavioral normalization process, in which the probability that a target CR will be produced is given by the strength of the CS-US association divided by the sum of strengths of all influences on the animal's behavior. A third possibility is that the associative strength between the CS and US is itself a hyperbolic function of reinforcement rate. Indeed, as we have previously demonstrated (Harris & Carpenter, 2011), this relationship can be formally derived from a simple error-correction learning rule, such as that used in the Rescorla-Wagner model (Rescorla & Wagner, 1972).

Using a within-subjects design, Experiment 2 confirmed previous evidence (Holland, 1979) showing that rats do acquire magazine responses during a CS paired with food even when an omission contingency is in operation that prevents any opportunity for reinforcement of those responses during the CS. Therefore, Pavlovian conditioning of the CS-US association must be sufficient to produce magazine approach CRs during the CS (above pre-CS baseline levels). However, that experiment also confirmed previous findings that the omission schedule reduces magazine response rates, below those produced by a yoked schedule of reinforcement. We have considered two explanations for this difference. One is that the yoked schedule allows for instrumental conditioning of magazine responses that add to the Pavlovian CRs isolated in the omission schedule. In other words, under normal conditions of reinforcement, when no omission schedule is in operation, magazine approach CRs are a combination of Pavlovian and instrumental conditioning. The other explanation for the difference between CRs produced by omission and yoked schedules is that the CRs acquired under normal (non-omission) schedules are entirely Pavlovian, but the expression of these CRs is reduced when rats are trained under the omission schedule. In particular, the explicit negative contingency between magazine responses and food in the omission schedule means that any behavior that interferes with (is incompatible with) magazine entry will be effectively reinforced.

Experiments 3a and 3b aimed to select between these alternative accounts of how magazine approach CRs are acquired, by training rats on discriminations between an auditory CS, A, and a compound of A and a light (LA). Trials with A and LA differed in that one type of trial was reinforced on an omission schedule and the other on a yoked schedule. In Experiment 3a, A was reinforced on the omission schedule and LA was yoked; in Experiment 3b, LA was on the omission schedule and A was yoked. To solve these discriminations, the rats must learn what is signaled by the added feature, L. If rats acquire instrumentally conditioned magazine responses in the yoked schedule, but not in the omission schedule, then they should have been able to learn to discriminate between A and LA in Experiment 3a because L served as an S^D for the instrumental magazine CRs, but they should have had greater difficulty learning to discriminate between A and LA in Experiment 3b. The reverse predictions are made by the alternative hypothesis about the difference in what is learned under omission and yoked schedules. If rats acquire Pavlovian magazine CRs under the yoked schedule, and acquire competing instrumental CRs under the omission schedule, they should learn to discriminate between A and LA in Experiment 3b, because L is will serve as an S^D for the competing responses, but have greater difficulty learning to discriminate between A and LA in Experiment 3a.

The results of Experiments 3a and 3b were conclusive: the rats learned to discriminate between A and LA in Experiment 3b but not in Experiment 3a. That is, they learned about the added feature, L, when it signaled the omission schedule, but not when it signaled the yoked schedule. This confirms the hypothesis that the difference in response rates established by omission and yoked schedules is due to the suppression of magazine responses by the omission schedule, most likely via reinforcement of competing responses. It also disconfirms the alternative hypothesis that, under the yoked schedule, magazine responses are instrumentally conditioned, and that these add to the Pavlovian CRs that are isolated by the omission schedule.

There may be another, less interesting explanation for the difference between Experiments 3a and 3b in terms of the way that the light controlled responding. If the light *per se* had a tendency to suppress magazine entry responses, for instance as a result of interference from orienting responses to the light, then this impact of the light would interact differently with discrimination performance in each experiment. In Experiment 3a, suppression of responding by the light would subtract from responding on the yoked schedule, and thus the light would impair discrimination performance; in Experiment 3b, suppression of responding by the light would add to suppression of responding on the omission schedule, and thus the light would enhance discrimination performance. However, there is evidence in the present experiments that directly disconfirms the suggestion that the light *per se* suppressed responding. First, any such impact of the light should have been evident in Experiment 2, where we would expect to have seen better discrimination between the omission and yoked schedules for rats trained with the light on the omission schedule and the noise on the yoked schedule, and a comparatively poor discrimination for rats trained with the noise on the omission schedule and the light on the yoked schedule. However, we did not observe any such difference in Experiment 2, and indeed there was a small (but not significant) difference in the opposite direction. There was also no evidence that the light helped to suppress responding on the omission schedule in an unpublished between-subjects experiment we had conducted earlier, in which one group of rats was trained with a single CS, light or noise, on an omission schedule and a second group were trained with a single CS, light or noise, on a yoked schedule.

The second piece of evidence against the suggestion that the light *per se* suppressed responding is that response rates to the omission schedule were very similar across Experiments 3a and 3b, regardless of whether that schedule was signaled by LA (in Experiment 3b) or by A alone (Experiment 3a). If the light were to assist with the discrimination in Experiment 3b by suppressing responding, we would expect to see less responding to LA in Experiment 3b than to A in Experiment 3a. This was not the case. We note that our favored interpretation of the present findings could also make the same unconfirmed prediction – any competing response that was reinforced under the omission schedule might have been acquired more readily to the light in Experiment 3b than to stimulus A in Experiment 3a because the light signaled the omission schedule on 100% of trials in 3b, whereas A signaled the omission schedule on only 50% of its trials in Experiment 3a.

Finally, our reasoning, up to this point, has rested on the assumption that the omission and yoked reinforcement schedules produce equivalent conditioning of the CS-US (Pavlovian) association because the history of the CS-US pairings were matched. However, as Church (1964) pointed out, there may nonetheless be systematic differences in reinforcement between experimental and yoked conditions due to random fluctuation in US effectiveness (if these random fluctuations are independent for the two conditions). For example, in the present paradigm we might consider there to be some noise in the processes governing retrieval of the CS-US association on each trial. For the omission CS, random fluctuation in CS-US associative strength will directly impact on the probability of the rat making a magazine response. Therefore, trials on which the US is omitted (because the rat responds) will be trials on which the retrieved CS-US strength will be high, and trials on which the US was delivered will be ones on which the retrieved CS-US strength was low. Because this correlation between retrieved CS-US strength and reinforcement will not exist for the yoked CS, the yoked CS will on average have higher associative strength than the omission CS on non-reinforced trials, but lower associative strength on reinforced trials. If learning on each trial is related to the discrepancy between retrieved associative strength and the outcome, then on non-reinforced trials there will be a larger negative error for the omission CS than the yoked CS, but on reinforced trials there will be a larger positive error for the omission CS than the yoked CS. If the rate of learning is equal on reinforced and non-reinforced trials (if the rate parameter is the same for the presence and absence of the US), then these differences will cancel each other out, and associative strength will, as assumed, be matched for the omission and yoked CSs. However, if the rates of learning about reinforcement and non-reinforcement differ, then the associative strengths of the omission and yoked CSs will also differ. If the learning rate for reinforcement is higher than for non-reinforcement, as is conventionally assumed (Rescorla & Wagner, 1972; Wagner, 1981), then the above analysis predicts higher associative strength for the omission CS than the yoked CS. Conversely, if the learning rate is higher for non-reinforcement than for reinforcement, then the above analysis predicts higher associative strength for the yoked CS than for the omission CS. Thus, this analysis can only explain higher responding to the yoked CS if it assumes a higher learning rate for non-reinforcement than reinforcement.

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