

Response Rates Are Governed More by Time Cues Than Contingency

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Abstract

Classical conditioning is normally thought to strengthen associations between stimuli, and instrumental conditioning is thought to select responses. This difference has been used to account for the usual result that instrumental conditioning produces higher response rates than classical conditioning. The present experiment suggests that the comparison of instrumental and classical tasks has overlooked temporal cues that are often confounded with response contingency, and that the time cues exert a critical influence on response rate. When the two tasks are equated for temporal cues, the response rate of rats is similar in classical and instrumental tasks.

Keywords

Classical conditioning, instrumental conditioning, contingency, response pattern, response rate, time cues

1. Introduction

Animals will often respond on classical conditioning tasks, even though responding does not directly lead to a reward — a phenomenon known as autoshaping. For example, pigeons will peck a lit key (Brown & Jenkins, 1968), monkeys will key-press (Sidman & Fletcher, 1968) and rodents will make nose pokes into a food cup (Papachristos & Gallistel, 2006), even though these behaviors are not directly reinforced with a reward. These are often the same responses used in instrumental conditioning tasks.

The distinction between classical and instrumental conditioning tasks was well established in the 1930s (Konorski & Miller, 1937; Schlosberg, 1937; Skinner, 1938).

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In classical conditioning the experimenter controlled the interval between a stimulus and a reinforcer (Pavlov, 1927); while in instrumental conditioning a response from the animal affected the time of the reinforcer delivery (Thorndike, 1898). In their influential book entitled *Conditioning and Learning*, Hilgard & Marquis (1940) began with separate chapters for ‘Classical conditioning experiments’ and ‘Instrumental conditioning experiments’. The separate treatment of these two tasks led to the development of learning theories with separate processes for classical and instrumental tasks. Today, this distinction is often taken for granted.

Based on this history, the difference between these two types of learning has often been the focus of behavior research (Rescorla & Solomon, 1967). In general, given the same response, instrumental tasks produce higher response rates than classical tasks (Domjan, 2002). This result has largely been attributed to the common sense view that instrumental tasks increase the value of actions (responses) by directly reinforcing the instrumental response, while classical tasks do not. In conditioning terminology, instrumental tasks result in a strong associative link between a stimulus and response (Hull, 1943; Thorndike, 1911), while classical tasks result in a strong associative link between a conditioned stimulus (CS) and an unconditioned stimulus (US) (Pavlov, 1927; Rescorla & Wagner, 1972).

Aside from response contingency, these two task classes differ in the informativeness of the temporal cues received by the animal. Any cues that accompany the delivery of a reward (i.e. sounds, vibrations, etc.) signal that a reward *has been delivered*. In instrumental conditioning tasks, these cues convey very little, if any, predictive information that could be used to reduce anticipatory responding. If the animal does not respond, these cues do not occur. And if these cues occur, the animal has already responded. On the other hand, in classical conditioning tasks, these cues are quite informative, since they tell the animal when food is ready to be harvested.

Below, we explore the possibility that instrumental tasks do not drive response rates up; rather, these reward-accompanying cues drive response rates down. To explore this, we used a simple 2×2 experimental design (Fig. 1) in which contingency (classical vs. instrumental) was pitted against time cues (present vs. absent). We discuss the implications in the discussion.

2. Methods

2.1. Subjects

Twenty-four male Sprague Dawley rats (Taconic Laboratories, Germantown, NY) were used in this experiment. The rats were kept in a colony room on a 12:12 light-dark cycle (lights off at 8:30 am). Dim red lights provided illumination in the colony room and testing rooms. The rats were 30 to 37 days old upon arrival and weighed between 75 and 100 g. During the first week, the rats were on a free-feeding schedule. After a week, their daily food (FormuLab 5008) was rationed to maintain their weight at 85% of the free-feeding weight. During the experimental session, the rats were fed 45-mg Dustless Precision Pellets (Bio-Serv, Rodent Grain-Base Formula, Frenchtown, NJ) as a reward. Water was available *ad libitum* in both the home cage and the testing chamber.

2.2. Apparatus

Twenty-four experiment chambers (Med Associates, dimensions $25 \times 30 \times 30$ cm) were situated in two separate experiment rooms (12 in each room). Each chamber was contained in a sound-attenuating box (Med Associates, dimensions $74 \times 38 \times 60$ cm) with a fan for ventilation. The front wall of each experiment chamber was equipped with a pellet dispenser (Med Associates, ENV-203) that delivered the reward into a food cup. A head entry into this cup interrupted a photo beam (Med Associates, ENV-254). On the opposite wall, a water bottle protruded into the chamber allowing *ad libitum* access to water during the session. A lick on the spout of the water bottle completed an electric circuit, which allowed each lick on the spout to be recorded. A white noise generator (Med Associates, ANL-926), and a house light (Med Associates, ENV-227M) were mounted on the back wall (near the water bottle). Four Gateway Pentium III/500 computers running Med-PC for Windows (version 1.15) controlled the experiments and recorded the data. The interruption of the photo beam, the completion of the lick circuit, and the noise and light onsets and terminations were recorded in time-event format with 2-ms accuracy.

2.3. Task

Twenty-four rats were randomly partitioned into one of four groups. The experiment was a 2×2 design (Fig. 1) in which response contingency (classical vs. instrumental) was pitted against time cues (present vs. absent). We used either fixed time (classical) or fixed interval (instrumental) tasks, both 60 s long. In two of the four groups (Instrumental Click and Classical Click), an auditory 'click' was given at the time food was available to be harvested (i.e. 60 s following the previous food delivery). There was no intertrial-interval. In slightly more detail:

Instrumental: A single food pellet was delivered contingent on the first head entry into the food cup at or after 60 s following the previous food delivery (Fig. 1a).

Instrumental Click: A single food pellet was delivered contingent on the first head entry at or after 60 s following the previous food delivery. Additionally, an auditory 'click' occurred at 60 s following the previous food delivery, signaling the time after which a response would be rewarded (Fig. 1b).

Classical: A single food pellet was delivered every 60 s (Fig. 1c).

Classical Click: A single food pellet was delivered every 60 s. Additionally, an auditory 'click' occurred simultaneously with reward delivery (Fig. 1d).

There were three phases, each to test a different hypothesis. The first phase occurred as described above. This was to test the main hypothesis that the Instrumental Click rats have lower response rates than the Instrumental rats (results shown in Figs 2c, 3, and 4). In the second phase, the probability of a reward was 0.75 for each trial, although for the Click rats, a click was given on every trial regardless of reward delivery. This phase was to make sure the Click rats used the click as a time cue (results shown in Fig. 5b). The third phase was extinction with a twist. We delivered the reward with a probability of 0.75 on each trial, but diverted the food into a receptacle outside the experimental chambers. This was to test the hypothesis that the rats that did not receive a click (Instrumental and Classical) could, in principle, use feeder cues as time cues (results are shown in Fig. 6).

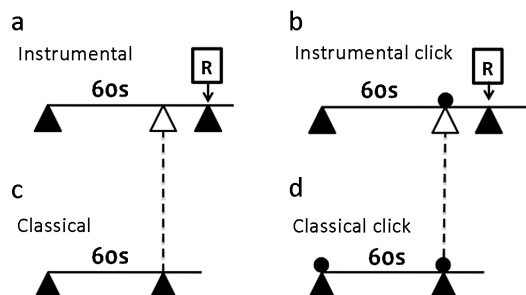


Figure 1. The 2×2 experimental design used in this experiment. Panels a, b, c, and d show the Instrumental, Instrumental Click, Classical, and Classical Click tasks respectively. The filled triangles represent food deliveries. Open triangles represent the time at which food is available on instrumental tasks. The filled circles represent an auditory click. The R enclosed in a box represents a response by the rat.

Further, we reanalyzed the data presented in MacInnis, Marshall, Freestone & Church (2010), in which rats were trained in the Instrumental and Instrumental Click groups with lever presses, rather than head-entries. The main purpose of that study was to test the hypothesis that precise time cues, at the time of food availability, would have differential and *independent* effects on response rate (how quickly the rats respond) and response pattern (how the rats distribute their responses in time). That these two critical pieces of behavior are independent is an important assumption of Modular theory (Guilhardi, Yi & Church, 2007), but can only be detected under certain conditions. MacInnis et al. (2010) tested the rats in one of those conditions.

For our present purposes, we show a previously unreported result in this data set (Fig. 7b). We included this data set here because it incorporated a phase in which the time cues in the task switched (Instrumental rats became Instrumental Click rats, and vice versa). This allowed us to test the hypothesis that the effects of the click are reversible; in particular, to test the hypothesis that removing the click increases response rates. The results are shown in Fig. 7.

3. Results

The hypothesis is simple: the Classical, Classical Click, and Instrumental Click groups should be statistically indistinguishable because the tasks all contain the same temporal information (a cue at the time of food availability). Moreover, they should all have lower response rates than the Instrumental (without click) rats. The Classical group is a particularly important control because it is the theoretical baseline from which 'statistically indistinguishable' is measured.

3.1. Analysis

To test the hypothesis, we compared the response rate gradients (Fig. 2c), and response pattern (Fig. 3) during steady-state behavior. We performed these comparisons in two ways. First, we fit the following function to the response gradients:

$$R = r + A\Phi(\mu, \mu\gamma) \quad (1)$$

where Φ is the cumulative normal distribution function (see Guilhardi et al., 2007, for theoretical justification for equation (1)). The parameters r and A are measures of response rate (low operant rate and high asymptotic rate, respectively). In contrast, μ and γ are measures of timing (μ is the mean of the cumulative normal distribution, γ is the familiar coefficient of variation, abbreviated cv). Each individual gradient was fit using least squares curve fitting in Matlab.

The second way in which we compared groups was with transition analysis. The well-known response rate gradient (Fig. 2c) is the result of averaging of single trial step functions (Schneider, 1969). Each trial begins with the absence of responses (similar to a post-reinforcement pause), and then the rat transitions to a high response rate until the end of the trial (Fig. 2a and b). This transition point has been explored extensively (see Balci et al., 2009b; Church, Meck & Gibbon, 1994; Schneider, 1969; Taylor, Horvitz & Balsam, 2007). We calculated the transition point using a well-known method (Church et al., 1994), although our presentation follows Gallistel, Fairhurst & Balsam (2004). These two methods are equivalent, in this case, and both are special cases of the OLS-CUSUM test (Ploberger & Kramer, 1992). The transition time is the time of the response at which the interresponse times

in the cycle become shorter. The method is most easily calculated by cumulating the interresponse times, and finding the maximum deviation between this and the straight line that connects the origin to the last point (see Gallistel et al., 2004, Fig. 5). Mathematically, this can be written as

$$W_n = \sum_{i=0}^n (t_i - \bar{t}) \quad (2)$$

where n is the response number ($1, 2, \dots, N$) and t_i is the i th interresponse time ($t_0 = 0$ so that t_1 is the time of the first response). W_n is a cumulative function with a minimum, and the location of this minimum, $c = \operatorname{argmin}_n [W_n]$, gives the location of the transition point, t_c . Using these equations, Matlab can compute thousands of transition points in only hundreds of milliseconds.

The mean transition point and its coefficient of variation are measures of timing (similar to μ and γ in equation (1)). The response rate before and after the transition point are measures of response rate (similar to r and A in equation (1)).

These two analyses (equations (1) and (2)) provide similar information about the data. The fits to the response gradient provide high-level information gained from fitting curves to averaged data, and the transition analysis comes from single trials. This is useful redundancy; the results are not due to the particular analysis chosen. For more measures, see Table 1 for a relatively comprehensive list based on Guilhardi & Church (2004).

All descriptive statistics are displayed as mean \pm c.i. One rat was a clear outlier in the data set (both across groups and within its group), and was removed from the analysis (see the small dots in Fig. 4b, c). The outlier criterion was $q_3 + 1.5(q_3 - q_1)$, a standard method for outlier rejection (q_1 and q_3 are the first and third quartiles, respectively). In the following results section, we first report the statistics from the transition analysis (equation (2)), and then report the statistics from the parameter fits (equation (1)). For the accompanying figures (Figs 3 and 4), the top plot (panel a) shows a measure obtained from the transition analysis (equation (2)), and panels b and c show measures obtained from the parameter fits (equation (1)).

4. General Results

Visual results are shown in Fig. 2a and b. A raster plot of data from a single, randomly chosen, Classical rat (Fig. 2a) and a single, randomly chosen, Instrumental rat (Fig. 2b) is shown. The data show individual cycles 1000 through 1250 for each rat. The mean number of cycles used in all analyses was 2928 ± 5.09 per rat. Figure 2c shows the crucial result. The mean response gradient for the Instrumental Click group lies almost on top of the Classical group, while the Instrumental group is much higher (for visual clarity, error bars are not shown).

Table 1.

Measures of response rate and response pattern for each group, and simple inferential statistics; the choice of timing measures to display was taken from a comprehensive list of timing measures (Gulhardi & Church, 2004)

	Instrumental	Instrumental click	Classical	Classical click	F-score	p
Measures of response rate						
Rate prior to transition (RPM)	10.54 (1.46)	5.16 (0.96)	5.82 (1.12)	5.93 (0.76)	$F_{(3,20)} = 4.99$	0.01
Rate following transition (RPM)	84.67 (9.32)	48.84 (12.94)	43.86 (5.88)	56.61 (4.79)	$F_{(3,20)} = 4.26$	0.02
Overall mean rate (RPM)	28.22 (1.74)	11.97 (3.27)	11.69 (2.00)	15.11 (1.79)	$F_{(3,20)} = 11.61$	<0.01
Measures of response pattern						
Curvature index	0.42 (0.04)	0.45 (0.07)	0.44 (0.03)	0.44 (0.02)	$F_{(3,20)} = 0.11$	0.96
Ogive center	48.70 (0.87)	44.47 (5.60)	49.21 (0.46)	48.17 (0.90)	$F_{(3,20)} = 0.56$	0.68
Ogive scale	5.47 (0.50)	5.11 (0.48)	5.07 (0.37)	6.10 (0.46)	$F_{(3,20)} = 1.09$	0.36
Transition point (s)	40.81 (0.86)	41.85 (2.59)	42.26 (0.71)	40.50 (0.65)	$F_{(3,20)} = 0.33$	0.80
Quarter life (s)	38.71 (2.18)	40.59 (2.85)	40.06 (1.21)	38.93 (0.72)	$F_{(3,20)} = 0.01$	0.88
Time of median response (s)	46.65 (1.13)	45.64 (3.07)	46.30 (0.82)	45.02 (0.80)	$F_{(3,20)} = 0.08$	0.91
Temporal discrimination ratio	0.81 (0.04)	0.80 (0.05)	0.81 (0.03)	0.81 (0.03)	$F_{(3,20)} = 0.03$	0.99

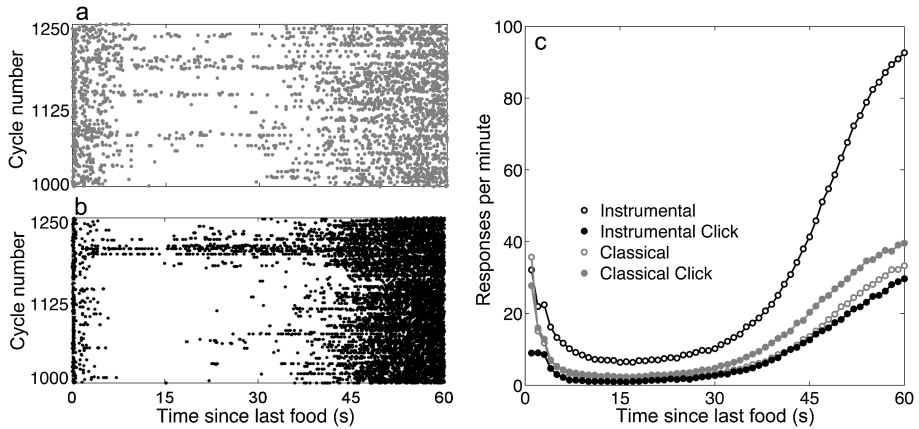


Figure 2. Response rate as a function of time since the last food (s). The two panels on the left (a, b) show raster plots of individual cycles from one Classical rat (panel a), and one Instrumental rat (panel b). Panel c on the right shows mean response rate as a function of time for the Instrumental, Instrumental click, Classical, and Classical Click rats (open black circles, filled black circles, open gray circles, and filled gray circles, respectively). One intuitive way to think about this response gradient is that it is similar to a (scaled) probability of a response in each one-second time bin since the previous food delivery.

The most straightforward test is a comparison among the overall mean response rates. There were significant differences among the groups in the mean response rate ($F_{(3,20)} = 11.37$, $p \leq 0.001$), and a significant contingency by click interaction ($F_{(1,20)} = 18.44$, $p \leq 0.001$). A simple-effects post hoc test showed that the Instrumental (without click) task resulted in a significantly higher response rate than the other three groups ($F_{(1,20)} \geq 16.39$, $p \leq 0.001$), but the response rates of the other three groups were not significantly different from each other ($F_{(1,20)} \leq 1.11$, $p \geq 0.25$).

4.1. Response Pattern

Response pattern refers to measures that quantify the timing of the responses (i.e., things that shift along the time-axis). Our primary measures of response pattern are μ and γ from equation (1), and the mean and cv of the transition times (t_c ; equation (2)). Other measures are shown in Table 1. The response pattern results are displayed in Fig. 3. Figure 3a shows the transition point (t_c) distributions computed in 1-s bins. There were no differences in the mean transition point ($F_{(3,20)} = 0.33$, $p = 0.802$), or coefficient of variation of these transition points ($F_{(3,20)} = 0.05$, $p = 0.986$) among the groups. There was no effect of click, contingency, or click by contingency interaction for either the mean or the coefficient of variation of these transition points. Tukey's HSD showed that no group significantly differed from any other ($p \geq 0.82$).

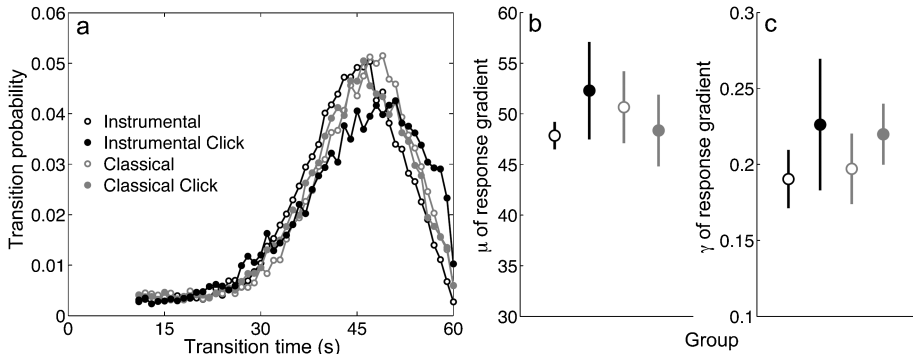


Figure 3. Measures of timing. Panel a shows the transition time probability distributions (distributions of t_c , see equation (2)) for the Instrumental, Instrumental Click, Classical, and Classical Click groups (open black circles, filled black circles, open gray circles, and filled gray circles, respectively). The right two panels show the two fitted timing parameters μ and γ for each of the groups (see equation (1)). Error bars indicate the 95% confidence interval. There are no significant differences in any of the timing measures.

There were no significant differences among the groups for the fitted timing parameters computed from equation (1). Figure 3b shows μ across groups ($F_{(3,22)} = 1.34$, $p = 0.2901$), and Fig. 3c shows γ ($F_{(3,22)} = 1.61$, $p = 0.22$). There was no effect of click, contingency, or click by contingency interaction for either the μ or the γ parameters of the gradient fits. Tukey's HSD showed that no group significantly differed from any other ($p \geq 0.29$).

4.2. Response Rate

Response rate refers to measures that quantify how quickly the rat responds (i.e. things that shift along the y-axis in Fig. 1c). There were significant differences among the groups on the two rate measures obtained from equation (2) (response rates before and after the transition time). For the low rates before the transition time, there was an overall main effect of group ($F_{(3,22)} = 12.087$, $p < 0.0001$), a significant effect of click ($F_{(3,22)} = 17.37$, $p = 0.001$), a significant contingency by click interaction ($F_{(3,22)} = 15.481$, $p = 0.001$), but the effect of contingency only trended toward significance ($F_{(3,22)} = 17.378$, $p = 0.082$). Tukey's HSD showed all groups significantly differed from the Instrumental group ($p \leq 0.003$), but the other three groups did not significantly differ from each other ($p \geq 0.397$). The same results held, and were stronger, for the high response rates after the transition time. Figure 4a shows the distributions of these high response rates for each group. There was an overall main effect of group on the response rate after the transition ($F_{(3,22)} = 18.529$, $p \leq 0.0001$), a significant effect of click ($F_{(3,22)} = 8.249$, $p = 0.010$), and a significant contingency by click interaction ($F_{(3,22)} = 29.602$, $p \leq 0.0001$). There was also an effect of contingency ($F_{(3,22)} = 15.903$, $p = 0.001$). As before, the effects were driven by a much higher

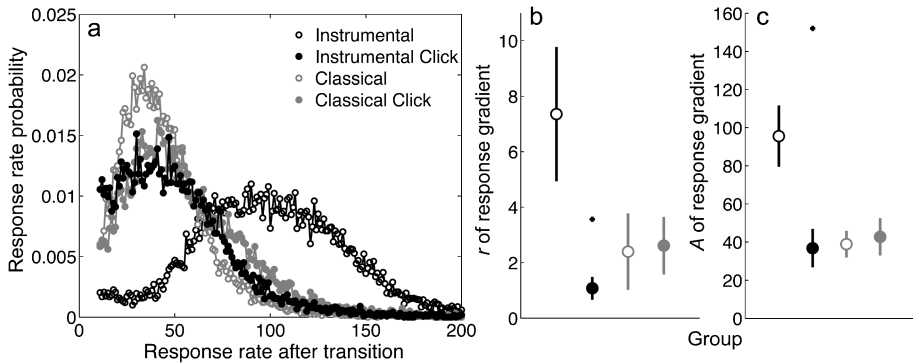


Figure 4. Measures of rate. Panel a shows the probability distributions of the response rate following the point of transition (the average response rate after t_c , see equation (2)) for the Instrumental, Instrumental Click, Classical, and Classical Click rats (open black circles, filled black circles, open gray circles, and filled gray circles, respectively). The right two panels show the two fitted rate parameters r and A for each of the groups (see equation (1)). The small black dot in panels b and c show the outlier. Error bars indicate the 95% confidence interval. The Instrumental rats are significantly different from the other three groups in all measures, but the other three groups do not differ from each other.

rate in the Instrumental group than any other group ($p \leq 0.0001$), but the other three groups did not significantly differ from each other ($p \geq 0.277$).

There were also significant differences among the groups when comparing the two rate parameters computed from equation (1) (r and A). Figure 4b shows r ($F_{(3,20)} = 11.82$, $p = 0.0001$), and Fig. 4c shows A ($F_{(3,20)} = 23.98$, $p < 0.0001$). For both parameters, there was a significant effect of click ($F_{(3,22)} \geq 14.288$, $p = 0.001$), contingency ($F_{(3,22)} \geq 4.532$, $p \leq 0.047$), and a contingency by click interaction ($F_{(3,22)} \geq 14.288$, $p \leq 0.001$). In addition, Tukey's HSD showed all groups as significantly different from the Instrumental group ($p \leq 0.002$), but the other three groups did not differ significantly from each other ($p \geq 0.559$).

4.3. Contingency or Cue?

The ideal statistical result would *reject* the null hypothesis that the Instrumental Click and Instrumental groups were the same (as we have done), but *support* the null hypothesis that the Instrumental Click and Classical groups were the same (i.e. that they came from the same underlying population). Traditional null-hypothesis significance testing cannot support a null hypothesis. However, we can treat the null hypothesis and the alternative hypothesis as nested models, and use model selection methods to determine the relative likelihood of the null model over the alternative (Burnham & Anderson, 2002, 2004; Gallistel, 2009).

In Table 2, we show the pairwise AIC values (see below for definition and detailed explanation). Each element in the table displays the relative likelihood that the two groups (given by the row and column) come from the same underlying

normal distribution. Negative numbers favor the alternative hypothesis (that the groups are different), while positive numbers favor the null hypothesis. The numbers represent the log evidence ratio; the number 4.41 indicates the null hypothesis is 82.3 times more likely to have generated the data than the alternative hypothesis.

The Akaike Information Criterion (AIC ; Akaike, 1974; Burnham & Anderson, 2002) is a goodness of fit measure that allows us to compare any arbitrary hypothesis (even the null) in favor of another. The sample-size adjusted AIC for a hypothesis is

$$AIC_i = -2 \ln \mathcal{L} + 2k + \frac{2k(k+1)}{n-k-1} \quad (3a)$$

where n is the number of samples considered, and k is the number of parameters in the model. \mathcal{L} is the likelihood that the response rate parameter for each subject (A in equation (1)) came from the underlying distribution assumed in model i . For example, we can construct a model that assumes the response rates (parameter A) for the Instrumental and Instrumental Click rats come from the same underlying normal distribution (the null model; $AIC_0 = 113.67$). We can also construct a model that assumes they come from different underlying normal distributions (the alternative model; $AIC_1 = 104.35$). The smaller AIC is the preferred model. The second two terms in equation (3a) penalize model i for its complexity (its finite sample size and number of parameters). Akaike weights can be constructed which indicate how well one model does in proportion to all the others tested:

$$w_i = \frac{\exp(-\frac{1}{2} \Delta_i)}{\sum_j \exp(-\frac{1}{2} \Delta_j)} \quad (3b)$$

with

$$\Delta_i = AIC_i - \min(AIC)$$

And finally, the ratio of the weights of any two models gives how much more likely one model is to have generated the data than the other. For our example above, it is $\frac{w_1}{w_0} = 105.30$ times more likely that the two groups came from different underlying distributions. In this case, we showed a similar result using the F -test above, but now we are able to say how much more likely the alternative hypotheses is. It is common to report the log of the evidence ratio ($\log(105.30) = 4.66$). We do this in Table 2. For convention, Model₀ is the null hypothesis, and Model₁ is the alternative. This means that negative values favor the alternative model, while positive values favor the null model.

We conducted two sets of AIC analyses. The first tested two groups at a time. For each comparison we asked how likely is it that the two groups came from the same underlying distribution (the null hypothesis). These results are displayed in Table 2. Each number in the table is the log evidence ratio in favor of the null hypothesis.

Table 2.

The Akaike Information Criterion (AIC) results for the groups compared among each other. Each element in this table gives the log evidence ratio (Equation 3) that the A parameter (see Equation 1) of the two groups comes from the same underlying distribution. Positive numbers favor the null hypothesis; negative numbers favor the alternative hypothesis. A value of 4.41, for example, indicates that it is 82.27 times more likely that the A parameter for the two groups came from the same underlying distribution. The Instrumental rats are different from the other three groups (the top row is negative), but the other three groups likely come from the same underlying distribution (all other values are positive)

	Instrumental	Instrumental click	Classical	Classical click
Instrumental	–	–4.66	–7.29	–4.79
Instrumental click		–	4.41	4.25
Classical			–	3.69
Classical click				–

The second set of AIC analyses asked, what is the best way to reduce the four groups to two? We chose a reduction to two groups because of our 2×2 design. The common sense view would group the Instrumental rats together, and the Classical rats together, and then separate the Instrumental rats from the Classical rats. However, the best model for our dataset grouped the three cue groups (Classical, Classical Click, and Instrumental Click) together, and put the Instrumental rats in their own group. The F -test above alluded to this result, but now it is explicitly stated. This model was favored 4628:1 (8.44:1 on log scale) over the *second* best model, which still grouped the Instrumental Click and Classical rats together (and separated them from the Instrumental and Classical Click rats).

4.4. Are the Click Groups Using the Click?

To determine the degree to which the rats in the two Click groups used the click, we looked at the 25% of cycles in which food was not delivered (Phase 2; Fig. 5). The Instrumental and Classical rats show the familiar peak result (Roberts, 1981). The Instrumental Click and Classical Click rats, however, show a sharp peak when the click occurs, followed by a sharp decline, and then anticipatory responding. To quantify this, we measured the mean response rate shortly after 60 s (70–80 s), and expressed this as a proportion of the maximum response rate (which occurred around 60 s). This measures the degree to which the response rate dropped following the time at which food is expected (60 s). A two-way ANOVA showed a significant main effect of group ($F_{(3,22)} = 57.86$, $p < 0.0001$), and a significant effect of contingency ($F_{(3,22)} = 6.289$, $p = 0.021$), and click ($F_{(3,22)} = 161.77$, $p < 0.0001$). The interaction of the two factors trended towards significance ($F_{(3,22)} = 3.65$, $p = 0.071$). Tukey's HSD showed that the Instrumental group had the highest response rate ($p \leq 0.022$), the Classical group had the next high-

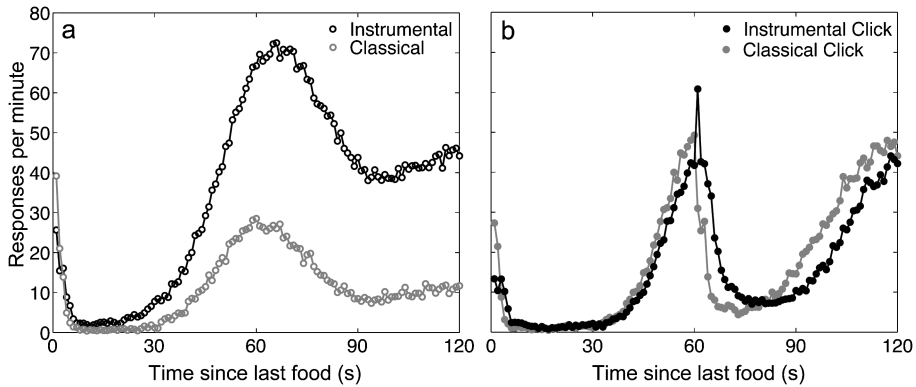


Figure 5. Response rate as a function of time since the last food during partial reinforcement training. Panel a (left) shows the response gradients for the Instrumental and Classical groups (open black circles and open gray circles, respectively). Panel b (right) shows the response gradients for the Instrumental Click and Classical Click groups (filled black circles and filled gray circles, respectively). The Click rats (both Instrumental and Classical) use the click as a time cue on peak trials.

est response rate ($p \leq 0.022$), and the two click groups, which did not differ from each other ($p = 0.976$), had the lowest response rates.

4.5. Are There Food Delivery Cues?

In Fig. 5, we showed that the Click groups used the click as a time cue. And throughout this article we have argued that the feeder has accompanying cues, but we have not yet shown it. Figure 6 shows the peak cycles during extinction. At zero seconds, the feeder delivered a food pellet to a receptacle outside of the experimental chamber. At 60 s, neither food nor its accompanying cues were delivered (although the Click rats still received a click). In all groups, there was a spike in response rate (and subsequent decline) at zero seconds, when the feeder cues (but not food) were presented. All groups showed a significant decrease in response rate following the initial reaction to the feeder cues ($t_{(\geq 4)} \geq 4.32$, $p \leq 0.008$).

There was another response spike at 60 s in the Click groups, as expected. The Click rats responded significantly more after the click at 60 s than baseline ($t_{(\geq 4)} \geq 5.26$, $p \leq 0.006$). A two-way ANOVA on the mean rate after the expected time of food (60–65 s) showed a significant main effect of group ($F_{(3,22)} = 20.19$, $p < 0.0001$), a significant effect of click ($F_{(3,22)} = 16.29$, $p \leq 0.001$), a significant effect of contingency ($F_{(3,22)} = 38.57$, $p < 0.0001$), and a significant interaction ($F_{(3,22)} = 10.77$, $p \leq 0.004$). Tukey's HSD showed that these effects were completely driven by the high rate in the Instrumental Click group, which differed significantly from the other three groups ($p \leq 0.0001$). No other group differed from each other ($p \geq 0.182$).

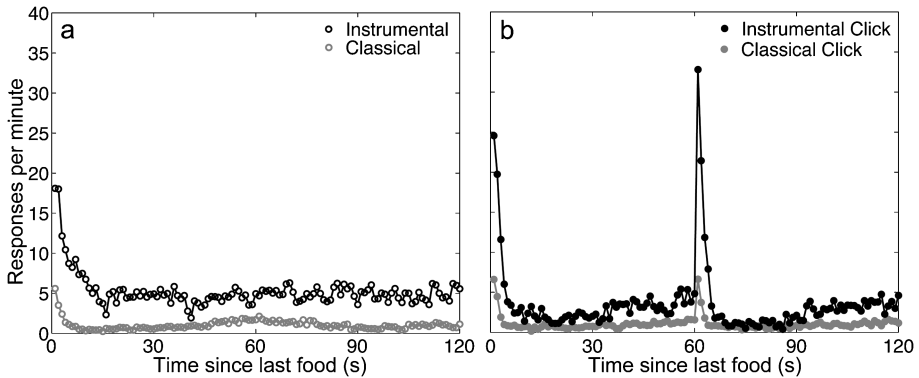


Figure 6. Response rate as a function of time since the last food cue, during extinction. Panel (a) (left) shows the response gradients for the Instrumental and Classical groups (open black circles and open gray circles, respectively). Panel (b) (right) shows that the response gradients for the Instrumental Click and Classical Click groups (filled black circles and filled gray circles, respectively). The initial increase in responding (panel a) shows the rats that did not receive a click still use the feeder cues as time cues. The Instrumental Click rats (panel b) hint at an effect of contingency.

4.6. Adding and Removing a Cue

Finally, we reanalyzed MacInnis et al. (2010) to ensure that the decreased response rate in the Instrumental Click group is reversible. MacInnis et al. used an instrumental lever press task in which a click either was (group 1) or was not (group 2) presented at the time of reward availability (60 s). In Phase 2, these two groups of rats swapped tasks. Aside from the response (a lever press), this is identical to our Instrumental and Instrumental Click groups, except using a within-subject design. Figure 7 shows the result. The rats significantly decreased their terminal response rate when a click was added at the time of reward availability ($t_{(5)} = 3.35$, $p < 0.05$), and significantly increased their response rate when the click was removed ($t_{(5)} = -6.24$, $p < 0.05$).

5. Discussion

The goal of this article is to show that, for determining response rate, time cues trump response contingency. We demonstrated this in four steps. First, we showed that the response rates for the Instrumental Click rats were statistically indistinguishable from the Classical rats (Figs 2–4, Tables 1, 2). Second, we showed that the Click rats were using the click to guide responding (Fig. 5). Third, we showed that, in addition to delivering rewards, the feeders also delivered cues (Fig. 6). Finally, we showed that the effects of the click were reversible (Fig. 7). In an unreported experiment, we tried, and failed, to mask the cues that accompany the reward delivery.

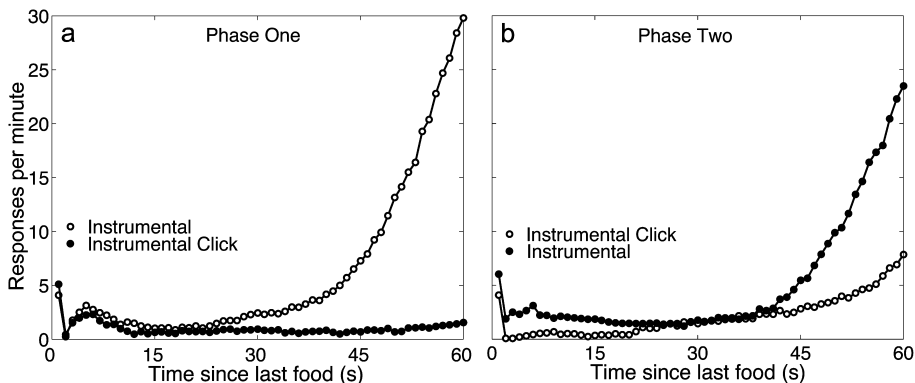


Figure 7. Response rate as a function of time using the unreported data from MacInnis et al. (2010). Panel a (left) shows the response gradients from Phase 1 for Instrumental (open circles), and Instrumental Click (filled circles) groups. Panel b (right) shows the response rate gradients from Phase 2, when the tasks were swapped in a within-subjects design. For both panels, the open circles are the rats that transitioned from the Instrumental task to Instrumental Click task. Filled circles show the rats that transitioned from the Instrumental Click task to the Instrumental task. These data show that the effect of the click can be reversed.

The delivery of the reward is often overlooked as a stimulus (Freestone & Church, 2009), and the fact that the delivery method is almost always accompanied by cues is rarely mentioned. Our feeders, for example, often regarded as ‘silent feeders’ still delivered time cues along with a reward (Fig. 6). We believe this simple oversight has given too much credibility to the Instrumental vs. Classical distinction, and not enough credit to time cues.

The traditional view — one taken for granted in much of today’s literature — is that response rate is a window into associative strength. For instrumental tasks, reinforcement leads to a direct associative link from stimuli to actions (responses). In classical tasks, the associative link is among stimuli, and sometimes, appropriate actions follow (conditioned responding). From this, it is plausible to assume that instrumental tasks produce higher response rates for the same action than classical tasks. The small amount of evidence for this in our experiment comes from Fig. 6. During extinction, when a click occurs, the instrumental rats respond noticeably more than the classical rats (although it is not significant).

On the other hand, the onsets and terminations of all stimuli serve as time cues that convey information about the temporal relationships between events. A time cue is informative to the degree that it reduces uncertainty about when (or if) an upcoming event will occur (in our case, the delivery of a pellet of food). Uncertainty is a measurable quantity. In the sensory-cue combination literature, uncertainty is the variability (σ^2) with which rats can represent intervals, and its inverse is reliability ($1/\sigma^2$). This reciprocal relationship ensures that time cues with less uncertainty are more reliable (Trommershauser, Landy & Kording, 2011). In information

theory, uncertainty is defined as the entropy of the distribution of estimated intervals (i.e. food times), which also heavily depends on σ^2 (Balsam & Gallistel, 2009). Shorter time intervals (i.e. time cues that signal shorter intervals) are timed with more absolute precision, and are therefore more reliable (see Gallistel, 2011). If the reliability of the cue governs response rate, the four groups in our experiment could be reduced to two: those without reliable time cues (Instrumental rats), and those with reliable time cues (Classical, Classical Click, Instrumental Click). This is the exact pattern of results we observed (i.e. our AIC results grouped the rats this way).

Another important alternative to entertain is overshadowing. The term overshadowing can refer to an experimental design, a result, or an explanation of that result (and sometimes the term refers to all three at once). The overshadowing procedure includes a comparison of a compound stimulus with its elements. The overshadowing result is that prior compound training reduces subsequent response rates to each individual stimulus, relative to controls that never received compound training. The overshadowing explanation provides the reason that the procedure produced the results. For example, one stimulus often elicits more responding than the other, and potential psychological explanation is that one cue is more salient (Mackintosh, 1976). A potential algorithmic explanation is that the stimuli compete for associative strength, and the more salient cue wins.

Although it was not a traditional overshadowing task design, the overshadowing result provides a description of our data. Rats that received an extra stimulus at the time of food availability (Instrumental Click) responded less than the rats that only had one of the stimuli (Instrumental). However, this description of the data does not provide an explanatory mechanism for the behavior. The traditional associative framework views overshadowing as the result of an association that cannot reach full strength (because it competes with another cue). If time is considered to be a cue, the rat should learn less about the time interval. We found no evidence of this; there were no differences among any of our timing measures. In fact, others have shown intact timing in a task specifically designed to test how overshadowing affects timing (Jennings, Bonardi & Kirkpatrick, 2007).

Our results are consistent with a growing body of work hinting that animals use time cues based on their reliability (Fairhurst, Gallistel & Gibbon, 2003; Guilhardi, Keen, MacInnis & Church, 2005; MacInnis et al., 2010). In many classical conditioning paradigms, the (often) overlooked time cues that accompany food delivery are, in principle, the most reliable time cues that can be provided. They signal to the rat the exact time at which food is available to be harvested. The explanation for our data is that response rates rise with unreliable time cues, and fall with reliable ones.

Of course, many other factors cause response rates to rise or fall. A major contributor is the value of the reward. Higher reward rates, more reward, or higher probabilities of reward all lead to higher response rates (Herrnstein, 1970; Weatherly, McSweeney & Swindell, 2004; Roberts, 1981, respectively). We controlled for

these and many other factors with our task design. Contingency, too, can lead to higher response rates (see Ferster & Skinner, 1957). But when directly pitted against each other, as we have done, response rate is governed more by time cues than contingency.

6. Conclusion

We designed an experiment to determine the degree to which response rates were governed by response contingency and time cues. We found that time cues are a far better predictor of response rate, but that contingency still played a role, albeit subdued (see especially the Instrumental Click spike at 60 s in Fig. 6). We explained these findings by suggesting that the reliability of the time cues determines response rate. We also noted that reliability could be measured with the tools already in the timing researcher's toolkit.

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