Published in final edited form as:

Behav Processes. 2014 January ; 0: 38–48. doi:10.1016/j.beproc.2013.09.004.

Associative and Temporal Processes: A Dual Process Approach

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Abstract

Approaches to the study of associative learning and interval timing have traditionally diverged on methodological and theoretical levels of analysis. However, more recent attempts have been made to explain one class of phenomena in terms of the other using various single-process approaches. In this paper we suggest that an interactive dual-process approach might more accurately reflect underlying behavioral and neural processes. We will argue that timing in Pavlovian conditioning is best understood in terms of an abstract temporal code that is not a feature of the predictive stimulus (i.e., the Conditioned Stimulus, CS), per se. Rather, we assume that the time between the CS and the unconditioned stimulus (US) is encoded in the form of an abstract representation of this temporal interval produced as an output of a central multiple-oscillator interval timing system. As such, associations can then develop between the CS and this abstract temporal code in much the same way that the CS develops associations with different features of the US. To support the dual-process approach, we first show that exposure to a Pavlovian zero contingency procedure results in a failure to acquire new associations, not a failure to express learning due to some temporally defined performance mask. We also consider evidence that supports the abstract temporal coding idea in a US preexposure task, and, finally, present some evidence to encourage the dissociation between basic associative and temporal learning processes by exploring reward devaluation effects in a peak timing task.

Keywords

Sensory specific associations; zero contingency degradation; US preexposure; US devaluation; multiple oscillators

Theories of associative learning have become rather sophisticated in their treatment of simple forms of Pavlovian and instrumental learning in the last several decades. During this same time period theories of animal timing processes have also evolved in a number of interesting ways. It is a rather surprising fact that theories in these two domains have evolved largely independently of one another, though there are, of course, a large number of points of contact and, indeed, particular theories that have been proposed to explore those points of contact. In spite of this, however, by my estimation, the main flavour of these theoretical advances has been to propose ways in which either, on the one hand, timing effects can be understood in essentially associative terms, or, on the other hand, associative effects can be understood in terms of basic timing mechanisms. It is almost as though

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members of each of these distinct communities do not wish to acknowledge the existential status of the type of explanatory mechanism employed by members of the other community.

A fundamental problem, therefore, is in determining whether the sorts of conditioned behaviors that we study and take to be the product of associative or timing processes are, in fact, reflective of a common set of underlying mechanisms or dissociable ones. In other words, do timing and associative effects come from the same underlying set of mechanisms or different ones?

Let us clarify by considering a simple example. Suppose that a rat were to be trained in a Pavlovian learning task where a 30-s conditioned stimulus (CS) ended in the delivery of a food pellet unconditioned stimulus (US). Over the course of learning the rat will eventually come to respond by approaching the food magazine during the CS at levels that exceed pre-CS levels and that also exceed levels displayed in a random control group (e.g., Delamater and Holland, 2008). Moreover, when looking at responding at different moments in time over the 30-s CS period, one notices that the rate of magazine responding steadily increases as the time to the actual food delivery gets nearer. Note that this finding is commonly observed when averaging responding over blocks of trials, and we do not at this point wish to enter the debate as to whether or not responding is an all or none process. The main point here is that two clearly noticeable changes in the rat's behavior occur as a result of this training regimen – increased responding and temporally organized responding.

One common way of explaining results of this sort posits the existence of a basic associative learning process. The CS enters into an association with the US and this is responsible for producing increases in conditioned magazine approach responding. However, while this approach explains the increase in responding as reflecting a change in the associative status of the CS it requires additional assumptions if temporally organized responding is to be explained. The associative approach can readily accommodate this aspect of the data by assuming the existence of a series of “micro” stimuli or discriminable states initiated by the onset of the CS. If the CS elicits a cascade of temporally discriminable micro stimuli, and if it was assumed that there exists stimulus generalization among similar micro stimuli, then temporally organized responding can be explained quite efficiently. This tactic was probably first introduced by Pavlov in his discussion of inhibition of delay (1927, pp. 103-104) and, more recently, has been suggested in a number of different forms (e.g., Buhusi & Schmajuk, 1999; Killeen & Fetterman, 1988; Ludvig, Sutton, and Kehoe, 2012; Machado, 1997; Staddon & Higa, 1999; Vogel, Brandon, and Wagner, 2003) and has also been used to explain how cerebellar timing circuits work in the conditioned eyeblink paradigm (e.g., Grossberg & Schmajuk, 1989; Kehoe, et al, 1993; Medina, et al, 2000). Notice that this approach assumes that “timing” is regarded as something that occurs “within” the CS. There is no separate timer or timing process, per se, but, rather, temporally organized behavior reflects control by the particular CS-evoked discriminable process that is most strongly associated with the US.

In contrast, another way of characterizing the situation is to start with the assumption that the animal encodes the times at which critical events, like rewards, arrive. If the animal keeps a running record, for example, of how many times the pellet occurs and at what times, then the animal can base its “decision” to respond or not upon various computations performed on this record of the raw data. Early versions of this approach were introduced by Jenkins and his colleagues (e.g., Jenkins, Barnes, and Barrera, 1981) and by Gibbon and Balsam (1981). According to Jenkins, et al, the animal will respond when the “waiting time” to the US within the CS period is appreciably less than the waiting time to the US in the overall session. If the CS substantially reduces the waiting time to the US's arrival, then conditioned responding would emerge. The Gibbon-Balsam approach was similarly based

on a comparison, but one between the US “expectancies” inside the CS versus in the session overall (see also Miller and Schachtman, 1985). In a more recent version of this approach, Gallistel and Gibbon (2000) suggested that the comparison is between the calculated rates of US delivery within the CS and at other times. In all of these cases, conditioned responding is said to arise when an assessment of the US time of arrival, expectancy, associative strength, or rate of occurrence is more favorable than that attributed to some relevant comparison condition.

This comparison process explains the emergence of conditioned responding, but, just as in the case of the associative approach, without further assumptions it does not explain how conditioned responding becomes temporally organized. In order to explain this feature of learned responding some authors have proposed that animals also might directly encode the interval between CS and US. Miller and his colleagues describe this in terms of their “temporal coding hypothesis,” but offer little guidance on how such temporal codes develop or arise. Similarly, Balsam and Gallistel and their colleagues (Balsam and Gallistel, 2009; Balsam, Drew, and Gallistel, 2010; Ward, Gallistel, and Balsam, 2013) suggest that organisms encode the CS-US interval and make subjective estimates of US arrival time based upon that encoding. In both cases, the temporal organization of conditioned responding is thought to reflect some comparison between the current amount of time that has elapsed since trial onset and the subjective estimate of when the US will occur. This framework, at least in spirit, is entirely consistent with earlier descriptions of interval timing in instrumentally conditioned behavior (e.g., Gibbon, Church, and Meck, 1984). Notice that with this perspective timing is not construed in terms of some associative feature of the CS, per se, as with the associative approach. Indeed, Balsam and Gallistel (2009; Balsam, Drew, & Gallistel, 2010) explicitly reject the view that associations play any key role at all in behavior. Rather, they assert that animals directly learn the intervals between events and then base their responding upon various computations performed on their representations of the interval relationships formed in the experimental situation. The rapid storage of temporal intervals, according to this approach, presumably reflects the operation of a separate timing process (i.e., a timer) that gives rise to such intervals (e.g., Gibbon, et al, 1984).

Given these quite different ways of approaching the problem of explaining why conditioned responding emerges as it does, how are we to proceed? As noted above, one approach has been to attempt to explain timing phenomena in associative terms. The other has been to attempt to explain associative phenomena in terms of various timing theories (e.g., Balsam and Gallistel, 2009; Gallistel and Gibbon, 2000; Kirkpatrick and Church, 1998; 2000). However, perhaps another way forward is to ask empirical questions that might lead to an answer that both sorts of processes (associative and timing) contribute to learned behaviors. Several integrative theories along these lines have already been proposed (e.g., Buhusi & Oprisan, 2013; Church and Broadbent, 1990; Matell & Meck, 2004; Oprisan & Buhusi, 2011), with an eye towards determining how a separable timing system might be understood in associative “connectionistic” terms. More will be said about this later.

One rather basic empirical question, it would seem, is whether timing and associative effects reflect the operation of a single underlying process or dual processes. We have begun exploring this question in several different ways, and the rest of this paper will be concerned with examining some of our findings in three key areas that all point to the validity of a dual-process approach. We will first describe the results of an experiment that we recently completed investigating what we take to be a fundamental prediction of the comparator approaches to learning described above. Then we will describe some data that we take to support the view that learning consists of associations with multiple aspects of the reward, including its time of occurrence, but show that learning involving temporal and non-temporal reward components can be dissociated. Finally, we will present some data to

support the dual-process approach, where temporal and non-temporal learning processes may interact to describe behavior in interesting ways.

Does Conditioned Responding Reflect a Comparator Process?

We start with the question of whether associative learning can always be reduced to a special instance of a timing process. If it can be shown that an associative process provides a better account of some phenomenon than other approaches, then this would help validate the notion that associative processes should, indeed, be taken seriously in a theory of behavior (cf, Gallistel & Gibbon, 2000). As Gallistel and Gibbon (2000) point out, a particularly interesting test case is the zero contingency training procedure (or “truly random control”) (Rescorla, 1967; 1968). Associative learning theories assert that training on such a task should ultimately result in no learning being displayed to the CS because its associative strength should effectively reach zero (e.g., Rescorla and Wagner, 1972). While this simplistic view is undoubtedly incomplete (e.g., see Mackintosh, 1973; Rescorla, 2000), a fundamental difference between the associative and timing approaches is that poor responding in this procedure reflects a learning deficit in the case of associative theory but a performance deficit in the case of a comparator approach (see also Gibbon & Balsam, 1981; Miller & Schachtman, 1985). If, for instance, the rates of US occurrence inside and outside the CS are comparable, then although there may be a reasonably high absolute US rate attributed to CS times this should not result in the emergence of conditioned responding for the simple reason that its comparison condition also conveys that same US rate. The CS is no better off, or conveys no “information” (Balsam and Gallistel, 2009), so responding should not occur.

Suppose that the US rate was manipulated after the conditioning treatment, but in the absence of the CS. What should be the effect, therefore, of extinguishing the context following exposure to a zero contingency procedure on subsequent test responding to that CS? The associative model expects little to no effect of this treatment. However, if responding reflects a decision to respond or not depending on the relative values of two sources of information about the US, a decision to respond should spontaneously emerge if the post-training manipulation places the CS in a more favorable position.

Exactly this sort of result was originally reported by Lindblom and Jenkins (1981). In their study, pigeons exposed to a positive contingency treatment (between key light and grain) followed by a zero contingency treatment, showed increased responding to the key light CS when it was tested subsequently under extinction conditions. One explanation is that during the zero contingency phase responding decreased as the bird attributed a high US rate expectancy to the experimental context. If this rate expectancy was deflated more rapidly during extinction than the US rate expectancy attributed to the CS, then responding should gradually reemerge to the CS during the extinction phase – the result obtained. The problem with this interpretation is that a control group in this experiment was included that lacked the original training on the positive contingency. This group, in other words, was exposed to a zero contingency treatment and then tested under extinction conditions, and the result was no increase in responding during the extinction test (see also Durlach and Shane, 1993; Rescorla, 1989). Had the sort of comparison process described above for the recovery birds applied to these zero contingency birds, then the same emergence of responding would be expected.

Thus, it would appear that there is at least some evidence to support the conclusion that zero contingency training may, indeed, result in poor learning and not merely poor performance. However, a stronger test of this claim is necessary. Following the lead of LoLordo, Fairless, and Stanhope (1985) we have recently examined the effects of a context extinction

manipulation upon responding to a CS given zero or positive contingency training beforehand.

In this experiment we employed a conditioned magazine approach paradigm with male and female Long-Evans rats maintained at 85% of their free feeding weight. During the initial phase, half of the rats were trained with a zero CS-US contingency and half with a positive CS-US contingency. The CS was a 20 s diffuse light (8 watts, with an otherwise darkened chamber), and the US was the delivery of 2, 45 mg food pellets (Research Diet). A more complete description of the apparatus can be found in Delamater and Holland (2008). The inter-trial interval (ITI) averaged 2 min (ranging from 30 s to 210 s) and there were 12 light presentations in each session. During a light CS presentation, the pellet US was presented according to a random time 40 s schedule of delivery in both groups. However, in the zero contingency group the same rate of pellet US delivery also occurred during the ITI, whereas no ITI USs were given to the positive contingency group. This meant that the zero contingency group received more USs within the session than the positive contingency group. These training procedures continued for 18 daily sessions. At this point in the experiment, half of the rats given zero contingency training and half given positive contingency training were then given 10 context extinction sessions during which they were placed in the experimental chambers for equal times as during the conditioning phase but in the absence of any CS or US events. The remaining animals were handled daily but remained in their home cages during this time. Finally, all rats were given a series of 6 test sessions in which the light CS was tested under the same conditions as training, but without any US deliveries and with only 8 trials per session (instead of 12).

The results from the test phase of this study are presented in Figure 1 which shows mean magazine responding in pre-CS and CS periods averaged across trials within each test session. The data clearly establish that the context extinction treatment had little to no impact on conditioned responding in the groups trained initially with either a zero or positive CS-US contingency. Responding in the zero contingency group given context extinction should have been much higher during the CS than pre-CS periods, but as can be seen this group responded at slightly lower rates during the CS just like the zero contingency group not given context extinction. Furthermore, the two groups given positive contingency training initially also were minimally affected by the context extinction manipulation. In these groups, as well, context extinction could result in spontaneous increases in test responding since the background US rate expectancy would be further reduced by the extinction manipulation (at least as would be conceptualized by Gallistel & Gibbon (2000), Gibbon & Balsam (1981), and Miller & Schachtman (1985)). However, if anything, the extinction curves in the two positive contingency groups suggest that conditioned responding may have *decreased* slightly more rapidly over repeated extinction test sessions in the context extinction group (e.g., compare responding on Day 2). A Contingency (Zero, Pos) $\times$ Context Extinction (Extinction, No Extinction) $\times$ Session (1-6) ANOVA was applied to these data (converted to CS – pre CS difference scores), and the analysis revealed significant main effects of Contingency, $F(1,31) = 30.08$, and Session, $F(5, 31) = 7.86$, as well as significant Contingency $\times$ Session, $F(5,31) = 14.85$, and Context Extinction $\times$ Session, $F(5,31) = 2.74$, interactions.

These results document that positive contingency training results in more magazine responding than zero contingency training, that extinction takes place over repeated test sessions, and, most importantly, that the only effect of context extinction is to slightly *accelerate* extinction of responding to a CS given positive contingency training. In no case did we observe context extinction to spontaneously increase conditioned responding either to a stimulus given zero or to one given positive contingency training. The data provide fairly direct and unambiguous support for the view that zero contingency training results in a

learning deficit (see also LoLordo, et al, 1985). Comparator approaches to conditioned responding would need to account for consistently poor responding to a zero contingency stimulus in some fundamentally different way. In contrast, associative theories have little problem in explaining these results. In short, the answer to the question whether conditioned responding reflects a comparator process would appear to be ‘not always.’

It may be argued that various problems in our experimental design may have accounted for the lack of a context extinction effect, which, by itself, only constitutes a null result. For instance, if the context extinction manipulation used here was ineffective then it should have had little impact on conditioned responding during the test. That the extinction treatment was effective was clearly seen by examining responding during the pre-CS interval on the first day of testing. A Contingency $\times$ Extinction ANOVA performed on these data revealed significant main effects of Contingency, $F(1,28)=9.47$, and Extinction, $F(1,28)=17.29$, and a marginally significant interaction, $F(1,28)=3.82$, $p=.061$, suggesting that the extinction manipulation strongly attenuated context-evoked magazine responding and that a larger context extinction effect was evident, not surprisingly, in the zero contingency groups.

Another potential interpretive problem is that the tests were conducted in the conditioning contexts rather than in a different, more neutral context. One might argue that differences in the associative values to the contexts in the different groups contaminated an assessment of control by the CS. Although we cannot completely reject this concern, it is worth noting that the comparator theories we put to a test assume that test responding should have been dramatically affected by the context extinction manipulation, especially in the zero contingency group, under our test conditions. Our failure to find any hint of such an effect should not be interpreted as merely a null result. The overall pattern of results from the four groups we ran came out as predicted by an associative approach, but not by the comparator theory approaches. The fact that our positive contingency groups responded more than the zero contingency groups clearly demonstrates that our procedures were sensitive at detecting differences caused by the different training conditions. We think the absence of an effect of context extinction on CS responding in these circumstances reflects the fact that zero contingency training results in an associative, not a performance, deficit.

Learning About Multiple Attributes of Reward

The data just described would appear to vindicate the associative level of explanation for at least some classes of data, and present a fundamental challenge to one of the most basic assumptions of comparator theories. However, a different approach we have taken to the timing-associative learning problem is to begin by exploring the possibility that “associative learning” might actually consist of a rather rich set of specific associations formed between the CS and each of several distinct components of the US. Konorski (1967) and Wagner and Brandon (1989) asserted, for instance, that in Pavlovian learning the CS forms separate associations with the sensory and emotive elements of the US. We have elaborated this approach elsewhere (e.g., Delamater and Oakeshott, 2007; Delamater, 2012a; 2012b), but for the present purposes we would like to discuss the possibility that learning about non-temporal US features and learning about its time of occurrence may entail different, but sometimes interacting, underlying systems.

One way we have approached this possibility is by asking the simple question of whether learning about such distinct features of the US might emerge at different points during the acquisition process. Our analysis has focused on learning about highly specific sensory features of the US as well as learning about the temporal location of the US. In fear conditioning, Davis and his colleagues have reported that rats quite rapidly learn about the temporal locus of a shock US (Davis, Schlesinger, and Sorenson, 1989). Similar questions

have not been explored in appetitive tasks, and, more importantly, to our knowledge there has not been any research directly assessing the relative speeds at which learning about sensory-specific properties of the US and temporally specific properties of the US might proceed. Delamater and Holland (2008) found that when conditioned magazine approach responding to a CS in a group given normal delay conditioning first diverged from responding in a random contingency control group, such responding was not temporally organized (i.e., it occurred equally across the CS). However, although the result is consistent with the view that some non-temporal aspect of learning emerges prior to a temporal aspect, such a measure (magazine responding) does not permit conclusions regarding the sensory specific nature of that learning.

We have employed a Pavlovian-to-instrumental transfer (PIT) paradigm to explore questions regarding the sensory-specific nature of the underlying learning. In this task, it has been shown repeatedly in our lab and many others that a separately trained Pavlovian cue will selectively elevate instrumental responding more when the test response was previously reinforced by the same (as opposed to a different) reward as that signaled by the cue (e.g., Kruse et al, 1983). Further, we (Delamater and Holland, 2008) have demonstrated that if during Pavlovian training the US is consistently presented at CS offset (as in a delay conditioning procedure), then the largest selective PIT effect is seen towards the end of the CS compared to earlier during its presentation. Thus, the selective PIT task can be used simultaneously to assess learning about sensory specific US qualities as well as its temporal locus.

Delamater and Oakeshott (2007) reported that learning about the sensory specific features of reward might emerge sooner in conditioning than learning about its time of occurrence. This conclusion may have been somewhat premature and the emerging picture from our lab is more complex. In particular, it appears as though learning about both temporal and sensory specific qualities of reward occurs quite early in training; however, their contributions to performance change as a function of the amount of Pavlovian training.

The basic plan of these experiments was to first train two different instrumental responses with different reinforcing outcomes. The manipulanda (two levers or one lever and one chain) were located to the right and left of the food magazine, and the responses were reinforced on separate variable interval (VI) schedules of reinforcement by different reinforcers (two 45 mg food pellets, 0.1 ml of a 20% sucrose solution). The two responses were trained in separate sessions during this phase. Subsequently, the rats were given Pavlovian training with two CS-US pairs. In one set of rats, the CSs (white noise, light) were presented for 120 s, and the appropriate US (pellets or sucrose) was presented 20 s after CS onset. Both CSs were presented four times in each conditioning session and trials occurred in an irregular sequence with an inter-trial interval of 5 min. Different sub-groups of rats received either two or four Pavlovian training sessions, such that one sub-group received a total of 8 pairings of each CS with its corresponding US while the second sub-group received a total of 16 pairings. The two groups' training sessions were staggered so that both completed their training on the same day. Finally, both sub-groups were given two PIT tests (with each test session being preceded by a single day of instrumental retraining). In each PIT test, animals were given a choice of both instrumental responses under extinction conditions, and the CSs were presented for a total of 4 times each in an irregular sequence. The test sessions began with a 6 min period of no stimuli to lower instrumental responding (in an effort to render the responses more sensitive to the elevating effects of the CSs). Then, 2-min periods of no CS were alternated with 2-min CS periods until both CSs were tested 4 times each. The primary data consist of instrumental responding on the two alternatives in pre-CS and CS periods. Because these two sub-groups were part of a larger experiment designed to examine the effects of extinction on sensory-specific PIT (data not reported

here), there was a 10-day period that elapsed between Pavlovian training and the onset of PIT testing. These two sub-groups of rats were simply weighed and handled during this period (and served as non-extinguished control groups in that other experiment).

A second set of groups was similarly trained and tested; however, during the Pavlovian training phase they received a more standard delay conditioning procedure. In particular, the CS durations were 60 s and the relevant US always occurred at CS offset. The inter-trial interval for these rats also averaged 5 min. Rats trained in this manner either received a total of 4 or 8 pairings of each CS with its appropriate US before entering the PIT test phase. Please note that rats trained with early or late USs received different numbers of pairings (8 or 16 for “Early US” groups, and 4 or 8 in “Late US” groups). However, earlier work in our lab suggested that these numbers of pairings would result in equivalently low and moderate amounts of learning, respectively, in the different training conditions.

The results from the two PIT tests were combined (because there were no reliable differences across tests and more stability in the data was achieved in this way) and are presented in Figure 2. The figure shows responding in 5 successive bins (24 or 12 s) during the pre-CS and CS periods. The two sub-groups trained with the delay conditioning procedure (Late US) are presented in the bottom two graphs and the two sub-groups trained with USs occurring early in the CS periods (Early US) are on the top. Further, data from the sub-groups given relatively few Pavlovian training trials appear on the left, while data from the groups given greater numbers of Pavlovian training trials prior to PIT testing appear on the right. Responding is distinguished by whether the particular response had previously been reinforced with the same or different US as that signaled by the CS on a given test trial. If the CSs had become associated with highly specific sensory features of the US then we would expect the CS to activate “same” responses more than “diff” responses compared to the pre-CS interval. Further, if the CSs acquired information regarding the time at which the USs occurred, then we would expect for behavior to be temporally organized. The data from the two delay conditioning sub-groups (bottom) were originally presented by Delamater and Oakeshott (2007) and are re-presented and analyzed here.

As is clear from the data, there was no preference between the two instrumental responses during the pre-CS periods in any of the conditions. However, the animals preferred the “same” response to the “diff” response in the presence of the CSs. This illustrates that the rats had learned to associate each CS with the specific sensory qualities of the US with which it was paired. However, notice that this effect shows no temporal specificity when the PIT test occurred after a more limited amount of Pavlovian training (4 training trials with late USs or 8 trials with early USs). With more extended training (8 trials with late USs and 16 trials with early USs), each of the selective PIT effects became more highly temporally organized. The specific transfer effect grew over the interval when Pavlovian training occurred with late USs, but it was largest early and diminished over the interval when such training occurred with early USs.

Although the specific PIT effects seen in groups given more limited training do not show any temporal specificity, notice that their behavior, overall, is temporally organized. In particular, responding during the CSs slightly decreased over time within the CS in the group trained with early USs, but it increased over time in the group trained with late USs. This somewhat complex pattern of results suggests that after limited training the rats’ behavior is controlled by both sensory and temporal learning processes in an additive manner, but with more training their behavior is controlled by these processes more interactively.

The CS data from the two groups given limited training were analyzed using a Response (Same/Different) $\times$ Interval (1-5) $\times$ Group (US early/late) ANOVA. This analysis confirmed the above impressions with a significant main effect of Response, $F(1,46)=4.10$, $p<.05$, and a significant Interval $\times$ Group interaction, $F(4,184)=5.72$, $p<.05$. Importantly, there were no other significant effects. The Interval $\times$ Group interaction was assessed by examining the slopes of the best fitting lines that comprised the average responding across the 5 CS intervals for each group. If responding, overall, decreased across time in the group given limited training with early USs, and increased across time in the group given training with late USs, then the slopes of these best fitting lines should differ as a function of training and they should be negative and positive, respectively. The mean slopes for Groups Early US and Late US, respectively, were -0.157 and 0.181 . This difference was significant, $F(1,47)=15.08$, $p<.05$, and the 95% confidence intervals did not encompass zero (-0.268 to -0.047 for Group Early US, and 0.068 to 0.295 for Group Late US) indicating that the two slopes reliably differed from zero.

The data from the two sub-groups given more extended Pavlovian training were similarly analyzed, and this analysis revealed significant main effects of Response, $F(1,46)=15.46$, $p<.05$, and Interval, $F(4,184)=2.75$, $p<.05$, as well as significant Interval $\times$ Group, $F(4,184)=10.51$, $p<.05$, and Response $\times$ Interval $\times$ Group, $F(4,184)=3.62$, $p<.05$, interactions. These data demonstrate that the largest selective PIT effects were seen early in the CS for Group Early US, but late in the CS for Group Late US.

The findings from this study point to an interesting way that learning about specific sensory and temporal features of the US relate to performance, and how this changes across Pavlovian training. While the rats' instrumental performance was temporally organized after limited Pavlovian training, specific PIT effects were not. However, after more extended Pavlovian training specific PIT effects became more temporally confined to the period in which the USs were anticipated. What accounts for this change in the manner in which specific sensory and temporal information is used in controlling performance in this task? One possibility is that during Pavlovian acquisition the CS associates, rather independently, with specific sensory features of the US as well as with a representation of its time of occurrence. However, with additional Pavlovian training, the representation of the US that becomes associatively connected to the CS itself becomes more integrated. Apparently, the specific sensory and temporal qualities of the US in some fashion get bound together to form a more unitary US representation with more extended training.

Balsam and his colleagues (e.g., Drew, et al, 2005) have recently argued that when learning first develops, CRs emerge at or near the US time. This finding inspired the claim that what animals learn in Pavlovian conditioning is the temporal interval between CS and US, and it serves as the basis of the claim that conditioning mainly reflects a computational process where temporal encoding lies at the heart of the process. This conclusion regarding the accuracy of CR timing was challenged by Delamater and Holland (2008) who observed that the temporal distribution of magazine CRs across the CS is flat when conditioning first differs between paired and random control groups. It was also challenged by the findings of Vogel, Brandon, and Wagner (2003) that in eyeblink conditioning with rabbits the CR first appears early in the CS-US interval and then migrates closer in time to the actual US time. It is noteworthy that there exist many procedural differences in the experiments just cited that could account for their different patterns of results. Nevertheless, we think that strong claims concerning the primacy of timing processes should be tempered in view of such results. Further, the results presented here speak against the most basic claim that what the animals learn is best described as the time of the US's arrival. In the context of the present results, this view appears too simplistic. The present study directly contrasted learning about sensory-specific and temporally-specific US qualities, and the results showed that how such

learning influences performance depends upon the amount of training (cf Gottlieb, 2008; Gottlieb and Rescorla, 2010). It seems appropriate to think of these two aspects of learning as initially involving different independent systems, non-reducible to one another, but with the two systems interacting following more extensive Pavlovian training. To make these points stronger, of course, it will be necessary to find manipulations that affect these different aspects of learning in different ways, but, nevertheless, the present results point to interesting ways in which learning about sensory-specific features of the US and learning about the US's time of occurrence may influence performance in different ways across training. One reason why we are drawn to a different conclusion about timing and associative processes than Balsam and his colleagues is that PIT studies reveal aspects of learning (e.g., sensory-specific aspects) quite different from what can be seen in conditioned responding alone.

A Dual System Approach: Evidence from US Preexposure and US Devaluation Studies

If one assumes that timing and associative learning entail two separate learning systems (as opposed to a single system in which one process is reduced to the other), then it should follow that different manipulations would have differential effects on these two learning processes. We have begun looking at this question in several ways, but we will discuss results from two rather different kinds of experiments. In one of these situations the strategy is to manipulate the timing process and determine if this might interact with the associative process in interesting ways. In the second experimental situation, the strategy is to manipulate the associative process and determine if this might interact in interesting ways with the timing process.

Delamater (2011) described the results from a US preexposure experiment in which the time between US presentations was varied during the preexposure phase. It is a well-known fact about Pavlovian conditioning that an unsignalled US preexposure treatment attenuates learning when CS-US pairings are subsequently given in the same context in which the US was preexposed (e.g., Randich & LoLordo, 1979). However, we are not aware of any Pavlovian experiments in which the time between USs during the preexposure phase has been explored. Trapold, Carlson, and Myers (1965) found that this factor was important in an instrumental learning situation. In the Delamater (2011) experiment, three groups of rats initially received magazine training with pellets in 10-min sessions. Pellets were delivered according to a fixed time 30 s schedule (FT) for one group or a variable time 30 s schedule (VT) for a second group. A third group received one day with the FT and one day with the VT schedules. The US preexposure phase continued for 20 more sessions (during which session length was increased to 20 min). However, the control group during this phase was placed in the experimental chambers without any further pellet deliveries. During the subsequent conditioning phase, all three groups of rats received light-pellet pairings in which a 30-s light CS ended in pellet delivery. Control rats acquired magazine approach responding to the light faster than the two groups given US preexposures, but rats preexposed on an FT schedule were less impaired than rats preexposed on the VT schedule.

These results can readily be understood if it is accepted that associative and timing processes both contribute to performance. First, the results present problems for timing approaches that only consider the rate of US delivery in the presence and absence of the CS in controlling responding (e.g., Gallistel & Gibbon, 2000). If rats learn during the preexposure phase that pellets are delivered at a rate of once every 30 s on average, then such learning would impair them learning to respond to a CS that also signals the same rate of pellet deliveries. However, according to this view it should not matter whether pellets were delivered on an FT or VT schedule. Both would convey the same rate.

In contrast, for a similar reason, a purely associative approach would face difficulties. For instance, according to the Rescorla-Wagner model (1972) the experimental context should associate with pellet delivery during the preexposure phase and this would be expected to block conditioning to the light CS during the training phase. Furthermore, this blocking effect should not differ between the FT and VT groups since the same number of context-pellet pairings would have occurred in both of these groups. However, if one allows that time cues in the FT group could overshadow the context, then somewhat less blocking might be expected in the FT group compared to the VT group. Delamater (2011) showed that this was unlikely, though, because pre-CS responding, a measure of context conditioning, was actually higher in Group FT than VT during the first training session. Thus, the data cannot so easily be understood from an associative perspective alone.

A dual-process associative – timing approach may account for these findings. During the preexposure phase rats in the FT 30 condition could learn to represent the 30-s US-US interval. We know from earlier work that animals represent the timing of events by constructing an abstract amodal representation of duration. For instance, Meck & Church (1982) showed that rats generalized various duration discriminations learned in one stimulus modality to others with relatively little response decrement. In the present circumstance, if learning a 30-s US-US interval generalized to a 30-s CS-US interval, FT preexposed rats would do much better than VT preexposed rats. However, if this were the only process at work, then the FT group should have performed better than even the control group. On the other hand, if the preexposed rats were subject to a normal context blocking effect as well, then this associative process would result in diminished learning. In other words, the two processes together could readily explain this pattern of results.

We have conducted another experiment recently that picks up on this dual-process theme by adopting the second strategy noted above. In particular, we asked whether a manipulation designed to affect the responding supported by an association between the CS and the sensory qualities of reward would have any impact on responding supported by learning about reward timing. On the assumption that these two aspects of learning involve different underlying systems we would expect that the manipulation would be selective to sensory-specific learning. The manipulation we chose was a US devaluation task applied after training on a Pavlovian version of the “peak” procedure (Roberts, 1981).

During Pavlovian training two 20 s CSs (1500 Hz tone, and diffuse flashing light) were each paired with different USs (pellets, liquid sucrose) presented at CS offset on 6 of 8 conditioning trials (for each CS). The remaining trials were non-reinforced probe trials where the CSs were presented for 60 s without reward. The average inter-trial interval was 5 min and training continued for 40 daily sessions, until good temporal control was evident on non-reinforced probe trials. Following Pavlovian training, one of the USs was devalued. This occurred over 5 devaluation cycles where the devalued US was presented, as in magazine training, non-contingently (VT 60 s) in a 20 min session on day 1 of each cycle and the non-devalued US was presented on day 2 of each cycle. At the end of the session on day 1 on each cycle, the rats were given an injection of LiCl (.3M, 1% body weight), but no injections were given following the session on day 2 of each cycle. By the end of this training the rats stopped consuming the devalued US but still fully consumed the non-devalued US. Finally, the rats were given two test sessions in which each CS was presented 6 times under extinction conditions at the probe duration of 60 s with a variable 5 min ITI as before.

Figure 3 shows the data from these test sessions broken down by whether the CS had previously been paired with a US that had been devalued or not. The top panel shows the mean % time the animals spent in the food magazine in 12 successive 5-s intervals during

the CS presentation, whereas the bottom panel shows these same data expressed as a ratio of baseline responding (i.e., $a/(a+b)$ where “a” refers to test responding and “b” refers to responding averaged over the entire CS on days 36-40 of training). The data clearly illustrate that responding was overall higher in the presence of the CS whose associated US was still valuable at the time of test. The effect of the US devaluation treatment was to lower the overall level of responding across the CS interval without substantially affecting the peak distribution of responding. The data were analyzed with a Stimulus (CS dev/nondev) $\times$ Interval (1-12) ANOVA on the mean ratio data. This analysis revealed significant main effects of Stimulus, $F(1,15)=9.19$, $p<.05$, and Interval, $F(11,165)=7.66$, $p<.05$, but no interaction between the two, and supports the idea that the manipulation lowered overall responding without affecting the temporal distribution of responding to the CS whose associated US had been devalued.

The results agree with those reported by Ohyama, Gibbon, Deich, and Balsam (1999) who found that as the overall motivation to respond declined over repeated extinction sessions the temporal distribution of responding was unaffected (see also Ward, et al, 2009). However, the results do not agree with findings reported by Galtres and Kirkpatrick (2009) who showed that various US devaluation treatments lowered overall responding in an instrumental peak timing task while at the same time shifted peak responding to the right. While further work will be required to explain the different patterns of results in these studies it is worth pointing out that the tasks differ in a number of ways including the Pavlovian versus instrumental nature of the tasks as well as the fact that two stimulus-outcome pairs were trained in the present study compared with a single stimulus-outcome pair in the Galtres and Kirkpatrick (2009) study. Moreover, there was more extensive reward devaluation training conducted in the present study compared to the Galtres and Kirkpatrick (2009) study, and in the present study an assessment was made between devalued and non-devalued conditions at the same time whereas in the Galtres and Kirkpatrick study the relevant comparison was made at different times (prior to and following reward devaluation). Any of these procedural differences may be important.

The main issue addressed in the present study was to determine if timing and sensory-specific learning processes might interact in the present circumstance. The data clearly indicate that they contribute to performance in an additive way. This additivity would make sense from the perspective that the animals come to associate the CS with the specific sensory aspects of the US and some representation of its timing independently of one another. A manipulation designed to affect control by the sensory-specific association leaves temporal control unaffected. However, if, as Balsam and Gallistel (2009) suggest, learning consists not of associations but of the storage of when events occur in time, it is not so obvious that the present results should arise. If, for instance, rats learn to anticipate a pellet 20 s into a visual CS and liquid sucrose 20 s into an auditory CS, then the maximum difference between these two anticipations should occur at the 20 s point. If one of those outcomes had been devalued, then the strongest reinforcer devaluation effect might be expected to occur at around that time. But we observed that the magnitude of the devaluation effect was constant across time within the CS.

Summary and Conclusions

The purpose of this paper has been to explore fruitful ways of considering how timing and associative processes may jointly play a role in controlling learned behavior. We started by acknowledging that two rich approaches have emerged in the study of basic Pavlovian and instrumental learning; they can be loosely characterized as the associative tradition, on the one hand, and the interval timing tradition, on the other. While the study of basic associative and timing phenomena have largely evolved in independent ways, it is clear that many

points of intersection exist between the two domains. Efforts have been made to develop adequate ways of construing timing effects in associative learning, and such efforts have led to attempts by theorists within each camp to describe timing and associative learning phenomena in their own reductionistic terms (e.g., see Balsam & Gallistel, 2009; Kirkpatrick & Church, 1998; Pavlov, 1927). The main theme in this paper is that this approach may not be the proper way forward.

Instead, it has been argued that there are reasonably good empirical reasons for thinking that associative phenomena cannot be reduced to special instances of timing processes, and that it may be better to consider a dual process approach where basic timing and associative processes both contribute in interesting ways to performance. In particular, we have suggested that comparator models will face fundamental problems in describing failures to perform in zero contingency situations. In addition, following Konorski (1967) and Wagner and Brandon (1989) we have suggested that simple Pavlovian learning might profitably be understood as reflecting the learning of associations between the CS and multiple aspects of the US (see also Delamater, 2012a; 2012b). If the time at which the US occurs may itself be encoded in the form of an abstract amodal representation of the CS-US interval (see Meck & Church, 1982), then it is possible that the CS could associate with this abstract temporal representation just like it enters into associations with different US features. Further, we have presented data to support this dual process approach by showing that information regarding the sensory and temporal features of reward determines performance in additive or interactive ways as a function of the amount of training. In addition, we illustrate how classic associative learning phenomena, such as the US preexposure and US devaluation effects, reflect the separate contributions of timing and associative processes. What remains is some discussion of precisely how these dual processes might be imagined to coexist in a single theoretical system.

What follows is a sketch of one possible approach. First, we assume that in Pavlovian conditioning the CS representation can enter into separate and dissociable associations with multiple features of the US (e.g., with its specific sensory and emotive features), and that learning about these multiple US features entails separate learning modules (e.g., see Balleine & Killcross, 2006; Corbit & Balleine, 2005; 2011). Delamater (2012b) has described how a multi-layered connectionist system can provide an explanation for complex Pavlovian learning about the specific sensory qualities of the US. We view such a network as characteristic of the module that learns about sensory specific US features. Here, we assume that another learning module is one in which CSs can enter into associations with an abstract temporal representation of the CS-US interval. We further assume that this temporal representation arises as an output of a central timing system that occurs at the moment of US presentation. In essence, once a CS is presented we assume this engages a multiple oscillator timing process (see also Buhusi & Oprisan, 2013; Church & Broadbent, 1990; Matell & Meck, 2004; Oprisan & Buhusi, 2011), and the elapsed time once the US is presented is itself a neural representation that can become an associative target of the CS. In other words, rather than seeing time as a discriminable microstimulus evoked by the CS (cf., Buhusi & Schmajuk, 1999; Grossberg & Schmajuk, 1989; Kehoe, et al, 1993; Ludvig, Sutton, and Kehoe, 2012; Machado, 1997; Pavlov, 1927; Vogel, Brandon, and Wagner, 2003) or some function of memory decay (Staddon & Higa, 1999) or behavioral states (Killeen & Fetterman, 1988), we assume that non-temporal aspects of the CS are capable of entering into an association with some internal multiple oscillator representation that reflects the time between the CS and US.

Figure 4 illustrates these basic ideas. The notion that a CS can associate with multiple target features of the US is depicted in panel A. These target features include the sensory qualities of the US (US_S), its emotive qualities (US_E), and its time of occurrence (US_T). The single

link between the CS and each of these target aspects of the US is meant to imply that learning about each of these characteristics could involve separate modules. As Delamater (2012b) showed, it is profitable to think that the CS-USs module may actually involve multiple layers (i.e., input – hidden – output) within the network. The same may also apply to learning in these other modules, but those specific network architectures remain unspecified. A further issue of empirical interest concerns specifying how learning across the various modules might interact with one another. Earlier in this paper, we presented some data to suggest that learning about sensory and temporal qualities of reward may vary as a function of the amount of training, and this, presumably, reflects an interaction between the modules that represent these distinct qualities. Elsewhere, Williams and LoLordo (Williams, Frame, & LoLordo, 1992; Williams & LoLordo, 1995; LoLordo, Williams, & McPhee, 2001) showed that CSs fail to block or overshadow temporal learning but that temporal learning can interfere with learning about CSs, and this supports the general view that there may be important asymmetries in how a temporal learning module might interact with others. Clearly, further work will be required to specify the nature of the interactions that may take place between the systems that learn about different US features.

A schematic representation of the basic elements of a multiple oscillator model of timing is depicted in panel B of Figure 4. Church and Broadbent (1990) introduced a multiple oscillator connectionist theory of interval timing, and Matell and Meck (2004) and Buhusi and Oprisan (2013; Oprisan & Buhusi, 2011) later demonstrated how a biologically plausible multiple oscillator timing system (the striatal beat frequency theory) could be applied to a variety of interval timing data. The key idea behind these approaches is that different neural processes (i.e., oscillators) are activated with different periodicities, but that the presentation of some salient event will reset their starting points. With these assumptions, different temporal intervals can be represented by the status of the different oscillators at any given moment in time since different constellations of activation patterns across these oscillators occur over time. This can be seen by examining any particular vertical slice through the different waveforms shown in Figure 4B. Notice that each vertical slice consists of a distinct activation pattern across the different oscillators shown. These different activation patterns can be used to represent different temporal intervals.

Depicted in Figure 4C is one way in which the associative and multiple oscillator approaches to timing might be integrated. This dual process model assumes that a representation of the CS can enter into separable associations with the sensory and emotive features of the US as well as with an abstract temporal representation that reflects the CS-US interval as an output of the multiple oscillator timing system. Figure 4C is meant to be an elaboration of the CS-US_T association shown in Figure 4A. A collection of oscillatory units (neurons or sets of neurons) is shown to converge on another collection of units whose particular constellation of activation patterns change with time, since these are driven by the different activation patterns displayed in the oscillatory units themselves. On any given conditioning trial the CS onset will reset these oscillatory processes, and, as a result, any given interval in time *t* sec after CS onset will be coded as the same unique pattern of activation across these units (collectively labeled as the “temporal US representation”). At the moment of US presentation it is assumed that inputs from the CS representation that converge on the various units that comprise the US temporal representation will develop strong connections with those units that are especially active (e.g., colored nodes). As conditioning proceeds the CS units should come to produce a pattern of activation within these temporal US representation units that closely resembles the pattern produced by the oscillatory units at the moment of US delivery, and, in this sense, the CS, upon its presentation, activates an “abstract temporal code” of the CS-US interval. Notice, however, that this abstract temporal code merely reflects the status of the oscillators at the moment of US delivery. Temporally organized conditioned responding, then, can be seen to reflect a

comparison process where the activation pattern within the temporal US representation produced by the CS inputs is contrasted with that produced by the oscillatory units on any given conditioning trial. These two sources of activation will become closely aligned as the moment of reward or its anticipation approaches. Notice also that in circumstances where different stimuli are trained with different CS-US intervals, the two CSs will develop strong connections with different subsets of units within the “temporal US representation” and so different CR timing when there is training with different CS-US intervals would be possible.

While this account is similar to existing multiple oscillator approaches to interval timing, there is an interesting difference as well. In the striatal beat frequency theory (Buhusi & Oprisan, 2013; Matell & Meck, 2004; Oprisan & Buhusi, 2011), for instance, a multiple oscillator representation of time emanating from frontal cortical cells is assumed to converge on a much more limited number of neurons in the striatum. At the time of reward delivery dopamine release in the striatum from input from the substantia nigra is thought to result in the strengthening of connections between those strongly activated cortical oscillator neurons and striatal neurons which, ultimately, will control responding in the task. In this way, temporally organized responding will emerge once the specific array of cortical oscillators that were strongly active during the time of reinforcement is approached. One potentially important difference between this model and the approach advanced here is that in the striatal beat frequency model there is no sense in which a cue might activate a representation of the reinforced time interval in advance of that interval having already elapsed. Instead, behavior is stimulated at the moment that the oscillator array matches the reinforced time because of the strong connections learned. In other words, a memory for the reinforced interval is in the connection weights, and this memory is in no sense activated prior to the time at which the relevant neurons are activated. In contrast, in the present approach the CS is thought to activate a representation of the oscillator array at the moment that it is presented. Responding will only emerge once that representation is approximated by the status of the actively running oscillators on a given trial. Thus, there is a sense in which the CS conveys information about the reinforced CS-US interval prior to that interval having elapsed. This bears a strong resemblance to the idea in the classic timing model of Gibbon, et al (1984) that a cue can activate a reference memory of the reinforced time but that responding develops only once the currently running representation of time matches that reference memory. The present approach, however, is an attempt to capture that idea within an associative framework (see also Church & Broadbent, 1990).

One of the main ways in which the present approach differs from others is in its assumption that learning about temporal aspects of the US (or, more properly, the CS-US interval) reflects a single module of learning. A complete description of Pavlovian learning would include other associative contents, such as the sensory and temporal qualities of reward. One interesting implication is that the rules governing learning about distinct US features may differ. For instance, consider a blocking experiment in which a pretrained cue signals reward with a 10 s CS-US interval, and during a blocking phase that cue is combined with a second cue and the stimulus compound signals reward with a 10 s CS-US interval in one condition or a 30 s CS-US interval in another condition. We expect the second cue to be blocked only when the CS-US intervals are the same in the two phases. In the present perspective this follows from the fact that the first cue will activate the same multiple-oscillator representation of the reinforced time that actually occurs at the time of reward. Thus, there will be no discrepancy between these activation arrays, and, thus, no “surprise.” Notice, however, that if the sensory and temporal aspects of reward are learned about in separate modules (as perhaps occurs with limited Pavlovian training), then it would be possible for blocking to occur with the sensory-specific qualities of reward even when the CS-US interval is changed since the same reward would be predicted by the cue in the two phases

independent of their times. These and other implications will need further experimental evaluation.

The ideas expressed above provide a mere sketch of how one might begin to entertain some sort of synthesis of ideas taken from associative and interval timing traditions, and many theoretical details will surely need to be worked out. Nevertheless, in the present paper we have tried to resist the temptation of interpreting associative and temporal learning processes within the confines of a single reductionist framework. The present approach, while it retains an essentially associationistic flavour, explicitly combines major elements of both traditions. It remains to be seen how such an approach may yield new discoveries. However, the empirical work we have presented here, we believe, strongly points to the need to consider theoretical approaches that combine elements from both the associative and interval timing traditions in grappling with the important problem of how time might be understood within the confines of a basic learning theory. Learning about specific sensory qualities of reward and about reward timing appears to involve distinct modules, and the major challenge will be to understand how such processes interact. The empirical and theoretical ideas presented here should provide some important additional constraints in reaching such an understanding.

Acknowledgments

The research reported here was supported by National Institute on Drug Abuse (034995) and Professional Staff Congress – City University of New York (64638-00 42) grants awarded to the author. The authors would like to thank Vincent LoLordo and two anonymous reviewers for helpful comments on an earlier version of this manuscript.

References

- Balleine BW, Killcross S. Parallel incentive processing: an integrated view of amygdala function. *Trends Neurosci.* 2006; 29:272–279. [PubMed: 16545468]
- Balsam PD, Gallistel CR. Temporal maps and informativeness in associative learning. *Trends in Neurosciences.* 2009; 32:73–78. [PubMed: 19136158]
- Balsam PD, Drew MR, Gallistel CR. Time and associative learning. *Comp Cogn and Behav Rev.* 2010; 5:1–22. [PubMed: 21359131]
- Buhusi CV, Oprisan SA. Time-scale invariance as an emergent property in a perceptron with realistic, noisy neurons. *Behavioural Processes.* 2013; 95:60–70. [PubMed: 23518297]
- Buhusi CV, Schmajuk NA. Timing in simple conditioning and occasion setting: a neural network approach. *Behav. Process.* 1999; 45(1–3):33–57.
- Church RM, Broadbent HA. Alternative representations of time, number, and rate. *Cognition.* 1990; 37:55–81. [PubMed: 2269008]
- Davis M, Schlesinger LS, Sorenson CA. Temporal specificity of fear conditioning: effects of different conditioned stimulus-unconditioned stimulus intervals on the fear-potentiated startle effect. *J Exp Psychol: Anim Behav Process.* 1989; 15:295–310. [PubMed: 2794867]
- Delamater AR. The role of the orbitofrontal cortex in sensory-specific encoding of associations in Pavlovian and instrumental conditioning. *Annals of the New York Academy of Sciences.* 2007; 1121:152–173. [PubMed: 17872387]
- Delamater AR. At the interface of learning and cognition: An associative learning perspective. *International Journal of Comparative Psychology.* 2011; 24:389–411.
- Delamater AR. Issues in the extinction of specific stimulus-outcome associations in Pavlovian conditioning. *Behavioural Processes.* 2012a; 90:9–19. [PubMed: 22465262]
- Delamater AR. On the nature of CS and US representations in Pavlovian learning. *Learning & Behavior.* 2012b; 40:1–23. [PubMed: 21786019]

- Delamater AR, Holland PC. The influence of CS–US interval on several different indices of learning in appetitive conditioning. *Journal of Experimental Psychology: Animal Behavior Processes*. 2008; 34:202–222. [PubMed: 18426304]
- Delamater AR, Oakeshott S. Learning about multiple attributes of reward in Pavlovian conditioning. *Annals of the New York Academy of Sciences*. 2007; 1104:1–20. [PubMed: 17344542]
- Drew MR, Zupan B, Cooke A, Couvillon PA, Balsam PD. Temporal control of conditioned responding in goldfish. *Journal of Experimental Psychology Animal Behavior Processes*. 2005; 31:31–39. [PubMed: 15656725]
- Durlach PJ, Shane DO. The effect of intertrial food presentations on anticipatory goal-tracking in the rat. *Quarterly Journal of Experimental Psychology*. 1993; 46B:289–318. [PubMed: 8210453]
- Gallistel CR, Gibbon J. Time, rate, and conditioning. *Psychological Review*. 2000; 107:289–344. [PubMed: 10789198]
- Galtress T, Kirkpatrick K. Reward value effects on timing in the peak procedure. *Learning and Motivation*. 2009; 40:109–131.
- Gibbon, J.; Balsam, P. Spreading association in time.. In: Locurto, CM.; Terrace, HS.; Gibbon, J., editors. *Autoshaping and conditioning theory*. Academic Press; New York: 1981.
- Gibbon J, Church RM, Meck WH. Scalar timing in temporal memory. *Annal. NY Acad. Sci.* 1984; 423:52–77.
- Gottlieb DA. Is number of trials a primary determinant of conditioned responding? *Journal of Experimental Psychology: Animal Behavior Processes*. 2008; 34:185–201. [PubMed: 18426303]
- Grossberg S, Schmajuk NA. Neural dynamics of adaptive timing and temporal discrimination during associative learning. *Neural Netw.* 1989; 2(2):79–102.
- Jenkins, HM.; Barnes, RA.; Berrera, FJ. Why autoshaping depends on trial spacing.. In: Locurto, CM.; Terrace, HS.; Gibbon, J., editors. *Autoshaping and Conditioning Theory*. Academic Press; New York: 1981. p. 255–284.
- Kehoe EJ, Horne PS, Macrae M, Horne AJ. Real-time processing of serial stimuli in classical conditioning of the rabbit's nictitating membrane response. *Journal of Experimental Psychology: Animal Behavior Processes*. 1993; 19:265–283. [PubMed: 8340769]
- Killeen PR, Fetterman JG. A behavioral theory of timing. *Psychological Review*. 1988; 95:274–295. [PubMed: 3375401]
- Kirkpatrick K, Church RM. Are separate theories of timing and conditioning necessary? *Behavioral Processes*. 1998; 44:163–182.
- Kirkpatrick K, Church RM. Independent effects of stimulus and cycle duration in conditioning: The role of timing processes. *Animal Learning & Behavior*. 2000; 28:373–388.
- Kruse JM, Overmier JB, Konz WA, Rokke E. Pavlovian conditioned stimulus effects upon instrumental choice behavior are reinforcer specific. *Learning & Motivation*. 1983; 14:165–181.
- Lindblom LL, Jenkins HM. Responses eliminated by noncontingent or negatively contingent reinforcement recover in extinction. *Journal of Experimental Psychology: Animal Behavior Processes*. 1981; 7:175–190. [PubMed: 7241053]
- LoLordo, VM.; Fairless, JL.; Stanhope, KJ. The effect of context upon responses to conditioned inhibitors.. In: Brush, FR.; Overmier, JB., editors. *Affect, conditioning, and cognition: Essays on the determinants of behavior*. Lawrence Erlbaum Associates; Hillsdale, NJ: 1985. p. 131–144.
- LoLordo VM, Williams DA, McPhee JE. Overshadowing of situational cues with variable but not fixed intertrial intervals. *Animal Learning & Behavior*. 2001; 29:143–152.
- Ludvig EA, Sutton RS, Kehoe EJ. Evaluating the TD model of classical conditioning. *Learning & Behavior*. 2012; 40:305–319. [PubMed: 22927003]
- Machado A. Learning the temporal dynamics of behavior. *Psychological Review*. 1997; 104:241–265. [PubMed: 9127582]
- Mackintosh, NJ. Stimulus selection: Learning to ignore stimuli that predict no change in reinforcement.. In: Hinde, RA.; Hinde, JS., editors. *Constraints on learning*. Academic Press; London: 1973. p. 75–96.
- Matell MS, Meck WH. Cortico-striatal circuits and interval timing: coincidence-detection of oscillatory processes. *Cogn. Brain Res.* 2004; 21:139–170.

- Matzel LD, Held FP, Miller RR. Reexamination of simultaneous and backward conditioning: implications for contiguity theory. *Learn. Motiv.* 1988; 19:317–344.
- Meck WH, Church RM. Abstraction of temporal attributes. *J. Exp. Psychol., Anim. Behav. Processes.* 1982; 8:226–243.
- Medina JF, Garcia KS, Nores WL, Taylor NM, Mauk MD. Timing mechanisms in the cerebellum: testing predictions of a large-scale computer simulation. *J. Neurosci.* 2000; 20:5516–25. [PubMed: 10884335]
- Miller, RR.; Schachtman, TR. Conditioning context as an associative baseline: Implications for response generation and the nature of conditioned inhibition.. In: Miller, RR.; Spear, NE., editors. *Information processing in animals: Conditioned inhibition.* Erlbaum; Hillsdale, NJ: 1985.
- Ohyama T, Gibbon J, Deich JD, Balsam PD. Temporal control during maintenance and extinction of conditioned keypecking in ring doves. *Animal Learning & Behavior.* 1999; 27:89–98.
- Oprisan SA, Buhusi CV. Modeling pharmacological clock and memory patterns of interval timing in a striatal beat-frequency model with realistic, noisy neurons. *Front. Integr. Neurosci.* 2011; 5:52. <http://dx.doi.org/10.3389/fnint.2011.00052>. [PubMed: 21977014]
- Pavlov, IP. *Conditioned reflexes* (G.V. Anrep, Trans.). Oxford University Press; London: 1927.
- Randich A, LoLordo VM. Associative and nonassociative theories of the CS preexposure phenomenon: Implications for Pavlovian conditioning. *Psychological Bulletin.* 1979; 86:523–548. [PubMed: 377357]
- Rescorla RA. Pavlovian conditioning and its proper control procedures. *Psychological Review.* 1967; 74:71–80. [PubMed: 5341445]
- Rescorla RA. Probability of shock in the presence and absence of CS in fear conditioning. *Journal of Comparative & Physiological Psychology.* 1968; 66:1–5. [PubMed: 5672628]
- Rescorla RA. Redundant treatments of neutral and excitatory stimuli in autoshaping. *Journal of Experimental Psychology: Animal Behavior Processes.* 1989; 15:212–222.
- Rescorla RA. Associative changes with a random CS-US relationship. *Quarterly Journal of Experimental Psychology.* 2000; 53B:325–340. [PubMed: 11131789]
- Rescorla, RA.; Wagner, AR. A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement.. In: Black, AH.; Prokasy, WF., editors. *Classical conditioning: II. Current research and theory.* Appleton-Century-Crofts; New York: 1972. p. 64-99.
- Roberts S. Isolation of an internal clock. *Journal of Experimental Psychology: Animal Behavior Processes.* 1981; 7:242–268. [PubMed: 7252428]
- Staddon JER, Higa JJ. Time and memory: Towards a pacemaker-free theory of interval timing. *Journal of the Experimental Analysis of Behavior.* 1999; 71:215–251. [PubMed: 10220931]
- Trapold MA, Carlson JG, Myers WA. The effect of noncontingent fixed- and variable-interval reinforcement upon subsequent acquisition of the fixed-interval scallop. *Psychonomic Science.* 1965; 2:261–262.
- Vogel EH, Brandon SE, Wagner AR. Stimulus representation in SOP: II. An application to inhibition of delay. *Behavioural Processes.* 2003; 62:27–48. [PubMed: 12729967]
- Ward, RD.; Gallistel, CR.; Balsam, PD. It's the information! *Behavioural Processes.* 2013. <http://dx.doi.org/10.1016/j.beproc.2013.01.005>
- Ward RD, Kellendonk C, Simpson EH, Lipatova O, Drew MR, Fairhurst S, Kandel ER, Balsam PD. Impaired timing precision produced by striatal D2 receptor overexpression is mediated by cognitive and motivational deficits. *Behavioral Neuroscience.* 2009; 123:720–730. [PubMed: 19634929]
- Williams DA, LoLordo VM. Time cues block the CS, but the CS does not block time cues. *Quarterly Journal of Experimental Psychology.* 1995; 48B:97–116. [PubMed: 7597196]
- Williams DA, Frame KA, LoLordo VM. Discrete signals for the unconditioned stimulus fail to overshadow contextual or temporal conditioning. *Journal of Experimental Psychology: Animal Behavior Processes.* 1992; 18:41–55.

Highlights

1. Zero contingency training results in a learning, not a performance, deficit.
2. Learning sensory and temporal features of the US affect PIT differently.
3. US preexposure and devaluation effects recruit associative and timing processes.
4. A dual process multiple oscillator timing + associative model is proposed.

Figure 1.

Mean magazine responding is displayed during CS and Pre CS periods across 6 extinction sessions for the groups given zero or positive contingency (Zero, Pos) training followed by context extinction or not (Ctx Ext, No Ext).

Figure 2.

Data from Pavlovian-to-instrumental transfer tests showing instrumental responding in 5 successive intervals during the Pre stimulus period and also during the stimulus but separated in terms of the response that was previously reinforced with the same or different outcome as that signaled by the CS. The data are shown for separate groups of rats given a different amounts of Pavlovian training in which the US was always presented either early or late in the CSs.

Figure 3.

Mean magazine responding during CS presentations in the extinction test sessions after one of the USs had been devalued (CS dev) or not (CS not dev). Responding is shown in 12, successive 5-s intervals within the CS. Mean % time in the food magazine is shown in the upper panel while those data were expressed as a ratio of baseline responding in the lower panel.

Figure 4.

Three different models for approaching timing in Pavlovian learning. Panel A shows a multi-component model where the CS is assumed to form distinct associations with sensory (US_S) and emotive (US_E) features of the US as well as with a representation of the time of occurrence of the US (US_T). Panel B displays a multiple oscillator model where different oscillators are assumed to have different periodicities. Panel C shows a dual process model where associations are assumed to be formed between the CS and a temporal US representation that itself is established through input from separate oscillators (Osc 1, 2, 3). The degree of activation of these temporal units is coded by their degree of shading.