

Some Constraints for Models of Timing: A Temporal Coding Hypothesis Perspective

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Most contemporary models of timing in animals were developed to account for the measurement of temporal intervals as they increase. Here we review growing evidence of timing in backward conditioning, which suggests that subjects exposed to Stimulus S1 followed by Stimulus S2 store information allowing the representation of S2 to retrieve both the occurrence and specific temporal location of S1. Such phenomena provide new and challenging constraints for models of timing. © 2002 Elsevier Science (USA)

The assumption that animals learn temporal relationships and intervals is not new. However, encoding of temporal information has been traditionally assumed to serve only as a catalyst in the formation of associations. Indeed, traditional theories of associative learning (e.g., Mackintosh, 1975; Pearce, 1987; Pearce & Hall, 1980; Rescorla & Wagner, 1972) view associations simply as mental links between the representations of events. The closer the two events are in time during training, the more robust the resulting association is assumed to be. Presumably, an organism acquires no representational knowledge about the temporal relationship of the paired events. That is, temporal information is not assumed to be encoded as part of the association; instead, it serves as a catalyst for the formation of the association. However, there has long been an awareness that conditioned responding (e.g., Pavlov's 1927 description of inhibition of delay; Smith, 1968) and instrumental responding (e.g., Skinner's 1938 description of scalloping on fixed interval schedules) both reflect encoded temporal information. Only in the past 20 years has there been any effort by learning theorists to model timing in animals. Most of this work has used operant preparations and been concerned

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with the mechanism that underlies timing rather than how the capacity to time intervals is used (e.g., Gibbon, 1977; Killeen & Fetterman, 1988; Stadon & Higa, 1999).

One contemporary model of how animals use temporal information is the so-called temporal coding hypothesis (e.g., Matzel, Held, & Miller, 1988; Savastano & Miller, 1998). Here, we review the assumptions of the temporal coding hypothesis and then turn to recent data illuminating the structure of learning in situations in which responding is notably dependent upon encoded temporal relationships. Specifically, we provide evidence that organisms learn backward and bidirectional associations, and we discuss the implications of these results for contemporary models of timing.

THE TEMPORAL CODING HYPOTHESIS

The temporal coding hypothesis (Barnet, Arnold, & Miller, 1991; Matzel *et al.*, 1988; Miller & Barnet, 1993; Savastano & Miller, 1998) represents a distinct departure from the traditional view of the role of temporal information in associative learning. In the framework of the temporal coding hypothesis, an association consists of more than a mental link between the representations of paired events. Indeed, the temporal relationship between the events is assumed to be encoded as part of the association. Thus, the temporal relationships between events (i.e., interstimulus intervals) are not mere catalysts for the formation of associations, but are also part of the content of learning. Animals are assumed to learn not only that a signal announces that an outcome will occur, but also when the outcome will occur. Our working definition of an association is that it is the total sum of all of the encoded relationships between two events, with the temporal relationship being of considerable importance, but not the sole content of the association (e.g., signals ordinarily indicate *where* as well as *when* an outcome will next occur).

The assumptions of the temporal coding hypothesis can be summarized as follows: (1) Good temporal contiguity (i.e., temporal proximity) between perceived events is both necessary and sufficient for the formation of an association; (2) The temporal relationship between the associated events (i.e., order and interval) is automatically encoded as part of the association (i.e., subjects act as if they create temporal maps that link events in memory [see Honig, 1981]); (3) This temporal information plays a critical role in the nature, magnitude, and timing of the responding elicited when one of the associates is subsequently presented; and finally, (4) Animals can superimpose temporal maps provided that they share a common element, thereby creating a temporal relationship between elements that were never physically paired. That is, temporal information from different training situations which have a common element can be integrated based on superpositioning of the common element in the different temporal maps. This last assertion is what takes the

temporal coding hypothesis beyond occasional statements of prior investigators.

TEMPORAL INTEGRATION AND TEMPORAL DIRECTIONALITY OF THE ASSOCIATIONS

According to the temporal coding hypothesis, robust associations can be acquired, provided there is good contiguity between the paired events, independent of whether the signal has a forward (signal \rightarrow outcome), simultaneous (signal + outcome), or backward (outcome \rightarrow signal) relationship to the outcome.

The existence of forward associations has been easy to demonstrate. In a Pavlovian conditioning preparation, the expression of a forward association requires only a predictive relationship between a conditioned stimulus (CS) and an unconditioned stimulus (US), at least when the traditional anticipatory response systems are assessed (e.g., fear conditioning to a tonal CS predicting the subsequent occurrence of a footshock US close in time). Thus, information about an immediately impending US supports anticipatory responding to the CS, which ordinarily prepares the organism for the occurrence of the US. In most laboratory preparations, "anticipation" is necessary to observe a behavioral change indicative of learning. Thus, conventional measures of Pavlovian conditioning are appropriate to investigate forward associations, but they are inadequate for the assessment of simultaneous and backward associations, which are situations in which the signal does not have an anticipatory relationship with the biologically relevant event (US). Indeed, simultaneous and backward pairings have long been known to result in little conditioned responding in situations in which an analogous forward relationship results in robust responding (e.g., Pavlov, 1927). Moreover, large numbers of backward conditioning trials result in inhibitory (rather than excitatory) behavioral control by the backward-trained CS (e.g., Cole & Miller, 1999; Heth, 1976).

Unlike most theories of associative learning (Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972; Wagner, 1981) which have tended to view performance as direct evidence of learning, the temporal coding hypothesis maintains a clear temporally based distinction between learning and the behavioral expression of that learning (see also Silva, Timberlake, & Cevik, 1998). In the framework of the temporal coding hypothesis, a predictive relationship is not essential for associative *acquisition*. Rather, the temporal coding hypothesis assumes that good contiguity (i.e., temporal proximity) is sufficient for the formation of an association, and the temporal information that is acquired during training is presumed to play a critical role in determining the nature, magnitude, and timing of the observed conditioned response. Consequently, the lack of responding typically observed after simultaneous or backward training reflects a measurement problem, not a lack

of learning. However, the assertion that simultaneous and backward associations are ordinarily latent requires that some means be identified to assess them. It is unclear whether a direct measure (i.e., first-order conditioning) is possible because response systems appropriate for the expression of simultaneous and backward associations have not yet been well characterized (e.g., Zentall, Sherburne, & Steirn, 1992; Silva & Timberlake, 2000).

Conditioned responding following backward conditioning training, a phenomenon considered to be problematic for traditional theories of learning (e.g., Mackintosh, 1975; Pearce, 1987; Pearce & Hall, 1980; Rescorla & Wagner, 1972), has been well established in Pavlovian conditioning (e.g., Ayres, Haddad, & Albert, 1987; Hearst, 1989; Heth, 1976; see Spetch, Wilkie, & Pinel, 1981, for a review) and in instrumental conditioning with choice behavior (e.g., Meck, 1985; Zentall *et al.*, 1992). However, responding to a backward-trained CS is almost invariably weaker than responding to a forward-conditioned CS. This weaker responding sometimes has been viewed as indicating that responding following backward conditioning results from the formation of forward and/or simultaneous associations between the late portions of the US (or its affective aftereffects) and the early portions of the CS (e.g., Romaniuk & Williams, 2000; Williams & Hulburt, 2000; see below for elaboration), thereby undermining the necessity of backward associations to explain responding in backward conditioning. However, a rejection of the existence of backward associations on these grounds might be criticized because the weaker responding in the case of the backward conditioning possibly reflects the inappropriateness of the measurement techniques selected.

One strategy that has been used to assess the existence of backward associations in conventional Pavlovian preparations involves an indirect evaluation of such associations through the use of a sensory preconditioning procedure. This procedure allows the creation of a predictive relationship to measure backward associations. In a sensory preconditioning procedure (Brogden, 1939), a stimulus (S1) is forward paired with another stimulus (S2) in Phase 1 (i.e., $S1 \rightarrow S2$). Subsequently, S2 is forward paired with the US in Phase 2 (i.e., $S2 \rightarrow US$). During testing, a strong conditioned response is observed to S1 (relative to control groups lacking either the Phase 1 or Phase 2 experience), even though S1 itself was never directly paired with the US. Using a sensory preconditioning procedure to study conditioned lick suppression after backward (as well as simultaneous and forward) conditioning trials, Matzel *et al.* (1988) initially exposed rats to forward $S1 \rightarrow S2$ pairings followed by backward pairings of S2 with the US ($US \rightarrow S2$). The expected backward response deficit was observed to S2. However, S1, which had been established as a predictor of S2 (and hence presumably a predictor of the US), evoked a strong conditioned response regardless of the manner in which S2 had been paired with the US. Figure 1A shows the design for the experiment on the left, the hypothetical temporal representation of the different

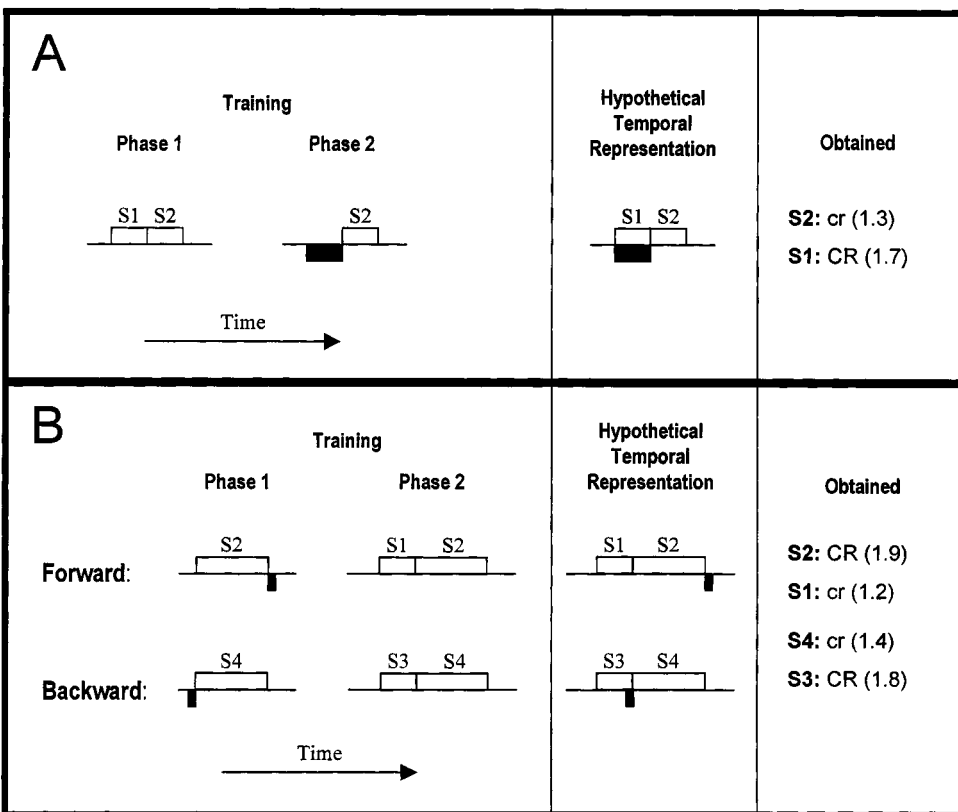


FIG. 1. Backward conditioning in sensory preconditioning and second order conditioning. (A and B) The experimental design, hypothetical temporal representations, and expected and observed results of Matzel, Held, and Miller (1988, Experiment 2) and Barnet, Cole, and Miller (1997, Experiment 1), respectively. CR indicates expected strong responding; cr indicates expected weak responding. See text for an explanation of the designs and temporal representations. Latencies to drink for five cumulative seconds in the presence of the test stimulus are presented in parentheses in log *s* (the log transformation was necessary to allow the use of parametric statistics).

phases of training after integration in the center, and the behavioral results on the right.

Another procedure that is useful for detecting backward (and simultaneous) associations is second-order conditioning, a procedure similar to sensory preconditioning, except that the order of the training phases is reversed (i.e., S2 → US pairings, followed by S1 → S2 pairings). During testing, a strong conditioned response is observed to S1 (relative to control groups lacking either the Phase 1 or Phase 2 experience), even though S1 itself was never directly paired with the US. For example, Barnet, Cole, and Miller

(1997) exposed rats to forward $S2 \rightarrow US$ as well as backward $US \rightarrow S4$ pairings followed by forward second-order $S1 \rightarrow S2$ and second-order $S3 \rightarrow S4$ pairings. Responding to $S2$ and $S4$ showed the usual differences observed between forward and backward conditioning (i.e., responding to $S4$ was weaker than to $S2$). However, responding to the second-order stimuli was reversed: $S3$ elicited more responding than $S1$, presumably indicative of backward associations formed during the $US \rightarrow S4$ pairings and temporal integration between Phase 1 and Phase 2 of training based on the common element ($S4$) to both experiences yielding better (forward) contiguity between $S3$ and the US than $S1$ and the US . Figure 1B depicts the design for this experiment on the left, the hypothetical integrated temporal maps in the center, and the predicted and observed behavioral results on the right.

One popular account of sensory preconditioning that is sometimes also applied to second-order conditioning assumes that at test the representation of the first-order CS mediates between the second-order CS that is presented at test and the representation of the US which immediately supports responding (e.g., Holland, 1981; Ward-Robinson & Hall, 1996). The mediation process assumed by such models consists of the first-order CS simply passing on its excitatory value to the second-order CS. This sort of mediational process is able to account for excitatory responding to a first-order backward CS ($US \rightarrow CS$). That is, the US presumably activates a US representation that remains active for some time after termination of the physical US (i.e., a US trace) and during which time the CS is presented, thereby critically allowing a representation of the CS to be active immediately before the (continuing) activation of the US trace. Hence, in this framework, a forward association (i.e., $CS \rightarrow US$) is formed despite the physical events having been presented backward (i.e., $US \rightarrow CS$). However, such a view fails to account for the stronger responding observed to the second-order CS than the first-order CS in the Barnet *et al.* (1997) and Matzel *et al.* (1988) backward conditioning studies described above. The temporal coding hypothesis, which we previously noted accounts for these observations, also attributes a mediational role to the first-order CS, but the temporal relationship between the first-order CS and the US as well as the first-order CS's excitatory value is assumed to be transferred to the second-order CS.

Recently, however, Williams and Hulburt (2000) proposed a mediational account for the observations of Barnet *et al.* (1997) and Matzel *et al.* (1988) that does not require temporal integration. Specifically, they examined whether different temporal components of a CS, which as a whole did not support strong behavioral control through backward conditioning, could support the development of excitatory second-order conditioned responding. Williams and Hulburt suggested that second-order conditioning with a backward first-order CS could be explained without invoking any special mechanism such as integration of temporal maps; instead, they assumed that CSs are divided into components such as CS onset and termination, which can

be separately conditioned. If so, the onset of a backward first-order CS might become excitatory because it is present during the primary affective reaction evoked by the recently presented US, whereas the termination of the same CS becomes inhibitory because it is not paired with the affective reaction evoked by the US. Thus, backward and forward first-order CSs might serve as second-order reinforcers for the same reason, the onset of both CSs might be excitatory, and there would be no need for temporal integration as assumed by Miller and colleagues (Barnet & Miller, 1996; Barnet, et al., 1997; Miller & Barnet, 1993). Williams and Hulburt observed responding consistent with their expectations: The early but not the late portion of the backward-conditioned first-order CS supported second-order excitatory responding.

Williams and Hulburt (2000) noted that their results were consistent with Wagner's SOP model (Wagner, 1981), which assumes that excitatory responding results only from situations in which two event representations are simultaneously in a primary state of activation. Because only the early portion of the first-order backward CS (S2) could be processed simultaneously with some aspects of the US trace, only the initial segments of the backward CS acquire excitatory properties, which might then become associated with the second-order CS (S1) during the $S1 \rightarrow S2$ pairings. The late portions of the S2 representation become inhibitory because, while they are in a primary state of activation, the US representation is already in a state of low activation. Responding following backward conditioning in situations using a sensory preconditioning procedure can be explained in similar way. During Phase 1 ($S1 \rightarrow S2$), S1 and the first portion of S2 develop an excitatory association because both events are simultaneously represented in a primary state of activation. In Phase 2 ($US \rightarrow S2$), the first portions of S2 develop an excitatory relationship with the US because both are simultaneously represented in a primary state of activation. Therefore, when S1 is presented at test, it activates the representation of the early portion of S2, which in turn will activate the representation of the US, resulting in conditioned responding. Thus, the Williams and Hulburt mechanism can account for the data viewed by Miller and colleagues as evidence of backward associations without recourse to the use of temporal integration and backward associations.

In order to test for temporal integration and the use of backward associations, Arcediano, Escobar, and Miller (2001b), using water-deprived rats in a conditioned lick suppression preparation, controlled for the Williams and Hulburt (2000) alternative account. Figure 2 shows the design for the relevant groups in their Experiment 2 (left), the hypothetical temporal representation of the stimuli based on the assumptions of the temporal coding hypothesis (middle), and the predictions derived from temporal integration and the obtained results (right). Two of their groups are represented: An experimental group in which temporal integration anticipates responding to their sec-

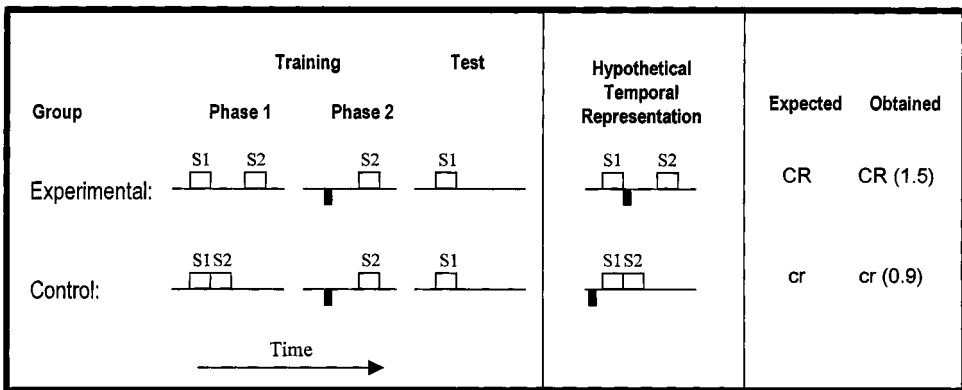


FIG. 2. Backward associations. Experimental design (left), hypothetical temporal representations (middle), and expected and obtained results (right) of Arcediano, Escobar, and Miller (2001b, Experiment 2). Group Experimental provides a test for temporal integration and backward associations. CR indicates expected strong responding; cr indicates expected weak responding. Refer to text for an explanation of the design and temporal representations. Latencies to drink for five cumulative seconds in the presence of the test stimulus are presented in parentheses in log s (the log transformation was necessary to allow the use of parametric statistics).

ond-order CS (S1) and a control group in which temporal integration anticipates weaker responding to S1 but the Williams and Hulburt account predicts stronger responding to S1. The two groups of rats were administered S1 → S2 trials in Phase 1. For Group Experimental, there was a 5-s gap between the termination of S1 and the onset of S2. For Group Control, there was no gap between the termination of S1 and the onset of S2. During Phase 2, both groups received US → S2 trials with a 4-s gap between the termination of US and the onset of S2. All animals received one test trial with S1. S1 and S2 were auditory cues 3 s in duration; the US was a 1-s, 1.0-mA footshock. The test scores are presented in Fig. 2 (right). As can be seen, Group Experimental responded more strongly than Group Control.

The differences in responding between Groups Experimental and Control are difficult to explain from a perspective that does not assume temporal integration and the use of backward associations. According to the temporal coding hypothesis, subjects learned during Phase 1 not only the association between S1 and S2, but also the temporal relationships between these stimuli; that is, subjects learned not only that S2 followed S1 (S1 → S2), but also that S1 preceded S2 (S1 ← S2). Similarly, during Phase 2, subjects learned the temporal relationships (forward and backward) between the US and S2. Thus, when S1 was presented at test to Group Experimental, these subjects retrieved a representation of S2 with an 8-s temporal gap between the onset of S1 and the onset of S2. Similarly, the representation of S2 onset activated a representation of the onset of the US 5 s back in time. According to the

temporal coding hypothesis, the US was expected to occur immediately after termination of S1 (see Fig. 2, middle). That is, after integration of the temporal maps from Phases 1 and 2, S1 predicted the occurrence of the US, and consequently it elicited strong conditioned responding. In contrast, when S1 was presented at test to Group Control, these subjects retrieved a representation of S2 occurring immediately after termination of S1 because there had been no temporal gap between S1 termination and S2 onset during Phase 1. As a result of Phase 2 training, like in Group Experimental, the representation of S2 activated a representation of the onset of the US 5 s back in time. Thus, after integration of these two temporal maps, the US was expected to occur *before* onset of S1. That is, in Group Control the onset of the US was expected to occur 2 s before S1 onset. Thus, S1 did not predict the occurrence of the US; instead, it indicated that the US should have occurred before the onset of S1 (see Fig. 2, middle). Because there was no anticipation of the US in this group, little or no conditioned responding was expected. An experiment performed with human participants using analogous experimental groups replicated these results (see Arcediano *et al.*, 2001b, Experiment 1).

The Williams and Hulburt (2000) extension of Wagner's (1981) SOP model seems unable to account for the above observations. As a result of Phase 2 training, activation of the representation of the US by S2 should have been identical in the two groups. Thus, if an excitatory association was established between the US and the early portion of S2, it should have been of similar degree for both groups. As a result of Phase 1 training, S1 should have activated a stronger representation of S2 in the Control group than in the Experimental group because there was no temporal gap between S1 and S2. Thus, the Williams and Hulburt account predicts stronger responding to S1 by the Control group, a pattern of results opposite to the one we observed.

The results obtained by Arcediano *et al.* (2001b) are compatible with the temporal coding hypothesis in that temporal integration of all relevant temporal associations (backward and forward) can account for these results. Importantly, the temporal coding hypothesis account assumes that backward associations encode the specific backward temporal relationship, and not merely temporally nonspecific associations as a result of backward pairings. The Arcediano *et al.* data support this assumption of the temporal coding hypothesis (which is similar to that suggested by Logan, 1977, 1979). Temporally nonspecific associations are predicated by models such as Wagner's SOP (1981) in that backward pairings presumably cause the two stimuli to be simultaneously in a high activation state of memory. Notably, in the framework of SOP, these associations do not encode the temporal order of the stimuli; they encode only the strength of that association.

One implication of the temporal coding hypothesis is that associations between stimuli are in some sense bidirectional (see, e.g., Savastano & Miller, 1998). Consider the case of the S1 \rightarrow S2 association in the Experimental group of Fig. 2. The temporal coding hypothesis assumes that associa-

tive learning depends on contiguity rather than prediction, and furthermore it assumes that temporal relationships are encoded as part of the association. Consequently, it suggests that presenting one stimulus (e.g., S1) will activate the representation in memory of the other stimulus (S2), as well as its temporal location relative to S1. For this to occur, the association between S1 and S2 must be functionally bidirectional ($S1 \leftrightarrow S2$). Thus, presentation of S1 alone should activate a prospective (predictive) representation of S2, and testing on S2 alone should activate a retrospective (diagnostic) representation of S1. However, such functional bidirectionality could be implemented either through a single bidirectional association ($S1 \leftrightarrow S2$) or two unidirectional associations ($S1 \rightarrow S2$ and $S1 \leftarrow S2$).

In order to differentiate between these two possibilities, Arcediano, Escobar, and Miller (2001a) performed an experiment similar to that of Arcediano *et al.* (2001b), but added a new posttraining treatment (Phase 2) in which either S1 or S2 was presented alone in order to analyze the nature of temporal associations underlying the responding observed by Arcediano *et al.* (2001b). Figure 3 shows the design (left) for the relevant groups of Arcediano *et al.* (2001a, Experiment 2), the hypothetical representation of the stimuli and their temporal relationships based on either two unidirectional forward and backward associations or one single bidirectional association along with the behavioral predictions for each possibility (middle), and the obtained results (right). The stimuli were similar to those used by Arcediano *et al.* (2001b, Experiment 2).

If memory of the temporal relationship between the two stimuli (S1 and S2) is based on two unidirectional links, one forward ($S1 \rightarrow S2$) and one backward ($S1 \leftarrow S2$), then Phase 2 presentation of S1 alone should have weakened (or built up inhibition for) the $S1 \rightarrow S2$ association but not the $S1 \leftarrow S2$ association, and vice versa for posttraining presentation of S2 alone. Thus, if S1-S2 pairings established two unidirectional associations, we should not have observed a weakening of conditioned responding to S1 in Group Exp-Ext-S2 in which S2 was presented alone and, presumably, the $S1 \leftarrow S2$ association was extinguished. For Group Exp-Ext-S1, when S1 was presented at test, it presumably did not activate a representation of S2 because of the $S1 \rightarrow S2$ extinction treatment during Phase 2. Without the activation of the S2 representation, it is not possible to accomplish the temporal integration of the information acquired in Phases 1 and 3; hence and not surprisingly, no responding to S1 was expected. However, when S1 was presented at test to Group Exp-Ext-S2, it activated a representation of S2 because the $S1 \rightarrow S2$ association remained intact assuming that the S1-S2 pairings of Phase 1 had produced two unidirectional associations. These subjects received extinction of S2, which should have weakened the $S1 \leftarrow S2$ association, but this extinction treatment should not have affected the $S1 \rightarrow S2$ association. Thus, temporal integration should have occurred and strong conditioned responding to S1 would be expected in this group.

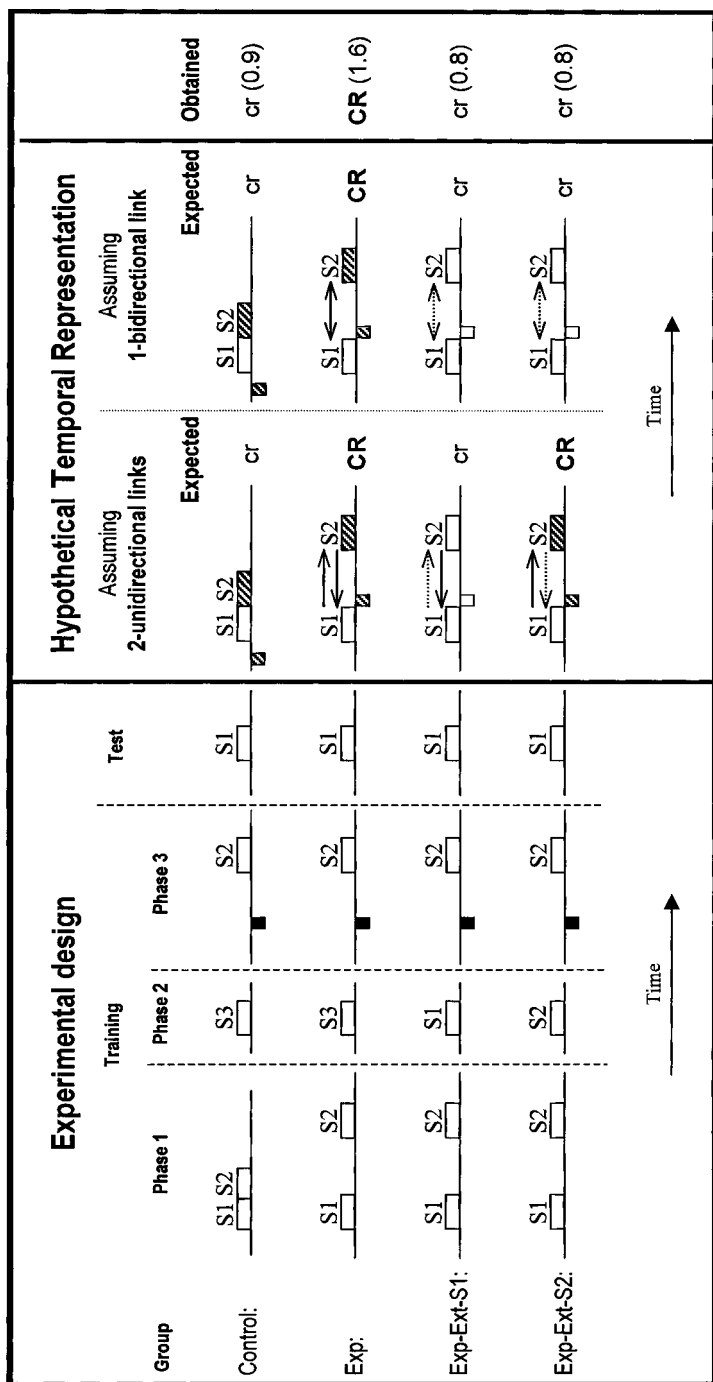


FIG. 3. Bidirectionality of associations. Experimental design (left), hypothetical temporal representations and expected results (middle), and obtained results (right) of Arcediano, Escobar, and Miller (2001a, Experiment 2). The expected results are presented both for the hypotheses of there being two unidirectional (forward and backward) links and one (bidirectional) link. CR indicates expected strong responding; cr indicates expected weak responding. Refer to text for an explanation of the design and temporal representations. Latencies to drink for five cumulative seconds in the presence of the test stimulus are presented in parentheses in log s (the log transformation was necessary to allow the use of parametric statistics).

In contrast, if the two stimuli were linked by a single bidirectional link (i.e., $S1 \leftrightarrow S2$), we would not expect to observe conditioned responding to $S1$ in Group Exp-Ext- $S2$ because presentation of $S2$ alone should have extinguished the $S1$ - $S2$ association to the same degree as the $S1$ alone presentations given to Group Exp-Ext- $S1$ (i.e., extinction of the association in one direction should extinguish the association in both directions). The results obtained in this experiment (Fig. 3, right column) support the view that the associations between $S1$ and $S2$ were based on a single bidirectional link. An experiment performed with human participants using analogous experimental groups replicated these results (see Arcediano *et al.*, 2001a, Experiment 1; for further recent evidence of bidirectional associations with humans, see Gerolin & Matute, 1999). Notably, there is an obvious alternative interpretation of the data presented here. Phase 2 extinction at $S2$ in Group Exp-Ext- $S2$ may not have extinguished the $S1$ - $S2$ association; instead, it might have served as latent inhibition treatment that impaired acquisition of stimulus control by $S2$ during the US- $S2$ pairings of Phase 3. However, this possibility was precluded through appropriate control groups.

Although the temporal coding hypothesis is quite successful in accounting for the experiments described above which collectively indicate that associations are bidirectional and encode specific temporal relationships, the hypothesis is challenged by the observation in first-order backward conditioning (i.e., $US \rightarrow CS$) that the backward CS often acts as an excitor with few pairings and as inhibitor with many pairings. With the US preceding the CS, the CS seemingly has no predictive relationship to the US; hence, in the framework of the temporal coding hypothesis it should not support excitatory responding. However, Chang, Blaisdell, and Miller (2001) have recently found that posttraining extinction of the training context attenuates excitatory responding to the CS. Thus, a CS made excitatory through a few backward pairings may not be a first-order cue, but a second-order cue linked to the US by an excitatory mediating context. Moreover, with more training and a relatively large minimum intertrial interval, subjects may learn that the context immediately following the CS is free of the US (safe in the case of footshock as the US), which could account for the CS becoming an inhibitor with many backward pairings (Moscovitch & LoLordo, 1968).

IMPLICATIONS FOR MODELS OF TIMING

The evidence described above concerning temporally specific backward associations and the bidirectionality of these associations challenges the assumptions of most contemporary theories of timing. Most theories of timing require a representation of the time elapsed between two stimuli, a process that increases as a function of time since the occurrence of an event. This incremental process has been described in various ways for different timing theories. In the scalar expectancy theory of timing (SET; Gibbon, 1977; Gibbon & Church, 1984; also see Treisman, 1963), a pacemaker emits a series

of pulses in time. A time marker (CS onset) opens an accumulator that counts the pulses until the reinforcer occurs and closes the accumulator, at which point the value of the accumulator is stored in a reference memory and the accumulator is reset to zero. To generate behavior, the stored value of the accumulator is compared with the current value of the accumulator, and when the difference falls below a threshold, responding at a steady rate begins. In the behavioral theories of timing (Killeen & Fetterman, 1988; Machado, 1997), the onset of a stimulus initiates a sequence of behavioral states the passage of which serves as the representation of time. In some versions of this model, a pacemaker with a variable rate determined in part by reinforcement drives the system through these various states. Sutton and Barto (1981, 1990) proposed that the representation of time since stimulus onset is encoded as the degree of activation of a memory trace, which gradually increases as a function of time that the stimulus has been present and gradually decreases as a function of time that the stimulus has been absent.

Although many real-time conditioning models use stimulus trace strength as the mechanism by which the passage of time is represented (e.g., Machado, 1997; Moore & Choi, 1998; Wagner, 1981), there are other ways in which time has been represented. For example, the spectral theory of timing (Grossberg & Schmajuk, 1989; Schmajuk, 1997) assumes that the onset of a stimulus initiates a cascade of traces that peak and then decay at different times following stimulus presentation. Traces that are maximally active at the time that the US is presented become preferentially associated with that US. The multiple-oscillator theory of timing (Church & Broadbent, 1990) posits that time is represented as the interaction of multiple (parallel) periodic functions. The multiple-time-scale model (MTS; Staddon & Higa, 1999) proposes that time is represented by the decay of stimulus representations in short-term memory. In this model, the effects of stimulus presentation change with time through habituation. Temporal control arises from a comparison of a cascade of differentially habituating stimulus representational units with memory (of trace strength immediately after stimulus onset). Every discriminable stimulus is assumed to have its own trace that works as a timing mechanism. Any variable that changes monotonically with time elapsed since a stimulus event (i.e., a time marker) can serve to measure time.

In all these and other contemporary theories of timing, there is a common assumption: All intervals are timed using some stimulus that acts as time marker (e.g., CS onset, reinforcement, events during the interstimulus interval, etc.), the occurrence of which initiates the interval to be timed. Measurement of time is always assumed to occur in the forward direction, from the presentation of the time marker toward the later event that terminates the interval. This commonality is depicted simply in Fig. 4A. When S1 is presented, its onset acts as a time marker for timing its relationship with S2. In this way, the organism can calculate the temporal interval between S1

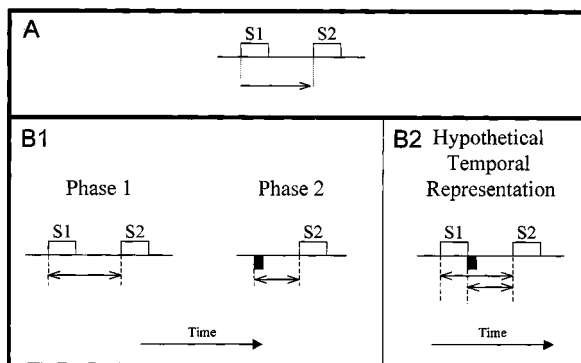


FIG. 4. Timing and temporal integration. (A) A trace relationship between S1 and S2. S1 acts as a time marker that starts the timing process to determine the temporal location of the occurrence of S2. (B) An example of temporal integration based on bidirectional links. (B1) Two phases of training in which a trace relationship between S1 and S2 is trained during Phase 1, and a backward trace relationship between the US and S2 is trained in Phase 2. (B2) The result of the temporal integration of the two phases of training. The two temporal maps are superimposed with S2 as the common element, resulting in an expectation of the US immediately after S1.

and S2 and know when to expect or anticipate the occurrence of S2 based on later presentations of S1. However, this timing, based on an internal clock, trace memory, habituation, or any other mechanism, is assumed to start at some point (typically, the onset of a stimulus is the starting point) and continue timing in a forward direction (e.g., with counts or pulses in an accumulator, decay of a memory over a trace interval, or habituation process).

This general view of timing being an *anticipatory* process is challenged by evidence of temporally specific backward associations and the bidirectionality of the associations. In order to explain the results of Arcediano *et al.* (2001a,b), subjects seemingly need the capacity to time not only the interval between S1 and S2 in a forward fashion (e.g., encode that onset of S1 was followed after X s by onset of S2), but also to time the interval between S2 and S1 in a backward fashion (e.g., encode that onset of S2 was preceded for X s by onset of S1; see Fig. 4B1). The same process seems to apply during Phase 2 of training in Arcediano *et al.* (2001b) and Phase 3 of training in Arcediano *et al.* (2001a). The behavior of rats and humans indicated that they had encoded the specific intervals from S1 to S2 and from the US to S2, and that they had been able to retrieve the backward temporal location of the US with respect to S2 when S1 was presented at test. The conclusion here is that subjects encode the order in which two stimuli occurred as well as the interval between them, and importantly they can activate this ordinal and interval information as a result of activation (through physical presentation of an associate) of *either stimulus*.

A seeming example of animals encoding and retaining into the future information about the occurrence of a temporally and spatially *specific* set of events was provided recently by Clayton and Dickinson (1999) in studies with scrub jays. In their experiments, scrub jays were permitted to store perishable and nonperishable food (worms and peanuts, respectively), and then one half of them were allowed to recover the food after 4 h and the other half after 124 h. The birds searched preferentially for the worms in the first condition, but they searched preferentially for peanuts, avoiding decayed worms, in the second condition. Clayton and Dickinson considered this temporal control of behavior showed by the scrub jays problematic for associative timing models and viewed this behavior as indicative of episodic-like memory. Episodic memory refers to acquisition and recall of what, where, and when an event occurred in the past (Tulving, 1972). The Clayton and Dickinson results seem to contrast with the widely accepted assumption that the acquisition and subsequent retrieval of episodic information is beyond the memory capabilities of nonhuman animals and the view that the presence of episodic memory is untestable in the absence of human language (for a review, see Clayton, Griffiths, & Dickinson, 2000). These results might be viewed as parallel on a larger temporal scale to the demonstrations of the use of backward temporal associations we previously described (Arcediano *et al.*, 2001a,b), in which rats were able to encode and retrieve what and when an event occurred in the past. We would note that evidence of the use of backward associations demonstrates that animals are able to remember what specific event occurred at a specific moment of time in the past.

Recently, Gallistel and Gibbon (2000) proposed a model called rate expectancy theory (RET), which greatly extends the temporal coding hypothesis and is centrally predicated upon organisms forming, integrating, and comparing temporal maps. "The ability to remember temporal intervals and to add, subtract, and divide them—the central capabilities assumed in our timing models—gives the animal such a [temporal] map" (Gallistel & Gibbon, 2000, p. 318). Like the temporal coding hypothesis, RET explains the results reported by Arcediano *et al.* (2001a,b) based on the expected interval to the US at the onset of S1. What distinguishes RET from other models of animal timing is that, in addition to assuming that intervals can be timed down, it allows one previously timed and stored interval to be *subtracted* from another with the difference being used as the comparison value in reference memory for deciding when an impending event will occur. Applied to the Experimental group of Arcediano *et al.* (2001b), when S1 was presented at test to Group Experimental, the expected interval to the US was 3 s (from S1 onset to US onset; see Fig. 2) and this resulted in strong conditioned responding relative to the group for which the expected interval to the US is -2 s. According to the decision rule of RET, the expectation of the US in $+3$ s should support more responding than -2 s. In this way, Gallistel and Gibbon are able to

explain the results described above. However, it is still unclear how RET implements subtraction of temporal intervals.

Although the temporal coding hypothesis is unusual in that it is a model of behavioral timing that is not a real-time model and posits no underlying mechanisms of how animals perceive time, it makes testable predictions based on qualitative tenets 1–4 (see Introduction); hence, it brings to the study of animal timing some challenging insights. The temporal coding hypothesis assumes that organisms encode the signed (i.e., forward and backward) temporal relationships between all possible pairs of stimuli, neutral as well as biologically significant, and have bidirectional access to this information. These stimuli are associatively linked in memory through not only a temporally forward link, but also a temporally backward link. Moreover, these two links apparently reflect two different access points to a single bidirectional association. The hypothetical temporal representations assumed by the temporal coding hypothesis and RET (i.e., “temporal maps” and their integration; see Fig. 4B2) seem to provide, at least at this point, the only plausible account of these results.

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