Temporal integration and temporal backward associations in human and nonhuman subjects

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Two experiments are reported that demonstrate temporal integration of independently acquired temporal relationships, including backward associations, in both human (Experiment 1) and nonhuman (rats, Experiment 2) subjects. The experiments were designed and analyzed in the framework of the temporal coding hypothesis (e.g., Matzel, Held, & Miller, 1988; Savastano & Miller, 1998) as a strategy toward illuminating the use of temporal information and assessing the existence of temporal backward associations. Both experiments provided evidence of retrieval of associations to an event that was expected to occur prior to the moment in time at which a stimulus was presented (i.e., backward associations). In addition, Experiment 1 constitutes the first controlled demonstration of temporal integration by human subjects.

Many early theories of learning (e.g., Bush & Mosteller, 1951a, 1951b; Estes, 1950; Guthrie, 1930; Konorski, 1948) assumed that learning was simply based on contiguity. That is, when two events were in a close temporal (and spatial) relationship, an association was assumed to be established between them in such way that the presentation of one of the events would activate a representation of the other event. Presumably, the closer the two events were in time and space (i.e., the greater the contiguity), the stronger the association that would form between them. The construct of *association* was generally used to refer to the mechanism that linked representations of individual experiences according to the order in which they occurred. Those early theories assumed that when two stimuli were presented in close succession (e.g., Stimulus 1 [S1] followed by Stimulus 2 [S2]), a forward association developed between them such that later presentation of the first stimulus (S1) would retrieve a representation of the second stimulus (S2). However, there was continuing debate about whether, with serial presentations, organisms would build not only forward associations (from S1 to S2), but also backward associations (from S2 to S1), such that presentation of the second stimulus (S2) would retrieve a representation of the first one (S1).

In his well-known studies, Ebbinghaus (1885) concluded that, during the learning of a series of items, associations were formed not only from a given item to adjacent items that followed it in the series (i.e., forward associations), but also from that item to adjacent items that preceded it in the series (i.e., backward associations). Since that time, many studies have been conducted in which an attempt has been made to illuminate the problem of the directionality of associations. Some of these studies supported the conclusion that associations were bidirectional; that is, contiguous presentations of S1 and S2 resulted in the formation of an association that could be retrieved either in a forward direction (S1→S2) or in a backward direction (S1←S2; e.g., Asch & Ebenholtz, 1962; Asch & Lindner, 1963; Feldman & Underwood, 1957; Guthrie, 1933; Hermans, 1936; Houston, 1966; Hunt, 1959; Jantz & Underwood, 1958; Murdock, 1966; Richardson, 1960; Stoddard, 1929; Trowbridge, 1938; Wohlgenuth, 1912). However, many of these results were also subject to alternative explanations, leading to difficulties in viewing them as evidence of backward associations (see Ekstrand, 1966, for a review of these alternative explanations). Consequently, many researchers have assumed that backward associations were an “apparent,” rather than a “real,” phenomenon. Thus, although no one would deny that humans are capable of determining whether an event occurred earlier in time relative to another event, the question of whether such knowledge stems from the use of backward associations or from the use of other strategies remains mostly unanswered.

As Asch and Ebenholtz (1962) suggested in a classical study of forward and backward associations, there were several reasons for researchers to doubt the reality of

Support for this research was provided by NIMH Grant 33881. F.A. was supported by an F.P.I. fellowship from the Basque Government (Ref. BFI97.013). We thank Jeffrey Amundson, Raymond Chang, and Steven Stout for their comments on a preliminary version of this manuscript. Thanks are also due Amanda Ceraulo and Jennifer Dávila for their assistance with the collection of the data. Correspondence concerning this research should be addressed to R. R. Miller, Department of Psychology, SUNY-Binghamton, Binghamton, NY 13902-6000 (e-mail: rmiller@binghamton.edu).

backward associations and adhere to the tacit assumption that associations were only unidirectional in a temporally forward direction (i.e., $S1 \rightarrow S2$). One of the arguments supporting this unidirectional view was that our experience with events is unidirectional and we cannot reverse the temporal direction in which physical events occur. Because organisms are assumed to learn in the direction in which they might functionally use the information to prepare for $S2$ (i.e., $S1 \rightarrow S2$), it did not seem reasonable to entertain the possibility that backward associations are formed. That is, process was assumed to reflect function. A second premise of the unidirectional view was the conceptualization of association as a stimulus–response connection. For many years, learning was framed in terms of stimulus $\rightarrow$ response sequences, and it did not seem reasonable to assume the existence of backward response $\rightarrow$ stimulus associations. Forward directionality was viewed as an essential characteristic of the stimulus $\rightarrow$ response sequence; action proceeds in a determinate direction, and it cannot be reversed. A third argument supporting the unidirectional view was based on the presumed neurophysiological correlates of associations. Backward associations appeared to be inconsistent with the well-accepted law of forward neural conduction (from terminal buttons to dendrites) across synapses. These arguments explained in part why evidence of backward associations was viewed as reflecting “apparent” effects likely arising from underlying simultaneous and forward associations. Indeed, Jantz and Underwood (1958; see also Ekstrand, 1966, for a review) proposed that backward associations could be a consequence of subjects’ rehearsing the training items in the reverse order of the training sequence’s temporal arrangement; that is, subjects rehearsed an $S2 \rightarrow S1$ sequence despite their not having experienced an $S2 \rightarrow S1$ sequence during training. That is, associations were assumed to be formed in the forward direction, and backward associations were incidentally acquired through spontaneous $S2 \rightarrow S1$ practice during the $S1 \rightarrow S2$ experience.

Most modern theories of associative learning (e.g., Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972) are also incompatible with the existence of backward associations. These theories generally assume that the establishment of an association between two events requires not only that the two events occur in temporally proximity to one another, but also that the stimulus presented first in the event sequence ($S1$) *predicts* the subsequent stimulus event ($S2$). Thus, associations were viewed simply as temporally forward flowing mental links between the representations of associated events. This framework, also known as the *informational hypothesis* (Cantor, 1981; Egger & Miller, 1963; Kamin, 1969; Rescorla, 1968; Rescorla & Wagner, 1972), emerged as the most widely accepted alternative to the principle of contiguity, which, in its basic form, is indifferent to the temporal order of events and attends only to their temporal proximity. According to the informational hypothesis, the mere contiguous occurrence of two events is not sufficient for the formation of an association between their

representations. Instead, learning is presumed to occur only when one event (nonredundantly) predicts the occurrence of the other. The informational hypothesis is consistent with prevailing explanations of several well-established findings, such as stimulus-competition effects (e.g., Kamin, 1968; Wagner, Logan, Haberlandt, & Price, 1968), the degraded contingency effect (e.g., Rescorla, 1968), and the unconditioned stimulus (US)-preexposure effect (e.g., Randich & LoLordo, 1979). Although all of these models presume that temporal factors, such as the proximity of the stimuli, serve a facilitative role in the formation of the association, the common assumption has been that the temporal information itself does not become a part of that association. That is, organisms acquire no representational knowledge about the temporal relationship of the paired stimulus events.

Several timing models of conditioning, in which the temporal relationship between events is in some way encoded as part of the association, have been formulated in the last quarter century (e.g., Church & Broadbent, 1990; Gibbon, 1977; Grossberg, 1991; Killeen & Fetterman, 1988; Machado, 1997; Schmajuk, 1997; Staddon & Higa, 1999; Sutton & Barto, 1990). However, because most of these models were derived from information theory, they too are hindered by the constraint that an anticipatory (i.e., predictive) relationship is necessary for associative acquisition. Indeed, they share the assumption that time perception requires the use of so-called *time markers* (e.g., stimulus onset, reinforcement, events during the inter-stimulus interval, etc.), the occurrence of which initiates an interval to be timed. Thus, measurement of time is assumed to occur only in the forward direction, from the presentation of the time marker toward a later event that terminates the interval (see Arcediano & Miller, 2002, for a review).

In contrast to timing models of conditioning, which assume that only forward temporal relationships are encoded, and conventional associative models of conditioning, which assume that animals do not learn about the temporal properties of the stimulus events, there is the recently proposed *temporal coding hypothesis* (Barnet, Arnold, & Miller, 1991; Matzel, Held, & Miller, 1988; Miller & Barnet, 1993; Savastano & Miller, 1998). This is not a model of timing processes but simply a model that assumes the relative *time* (and *location*) of an event is as fundamental to the event representation as *what* the event is. The temporal coding hypothesis assumes that an association consists of more than a mental link between the representations of two paired events in which activation of the representation of one event in turn activates the representation of the other event. Rather, the temporal relationship between the events during training is encoded as part of the association (i.e., it is part of the content of learning).

The assumptions of the temporal coding hypothesis can be summarized in the following four tenets: (1) Temporal contiguity between perceived events is both necessary and sufficient for the formation of an association, with greater

temporal contiguity resulting in stronger associations; (2) the temporal relationship between the associated events (i.e., order and interval) is 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 (4) animals can superimpose temporal maps, provided 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 that have a common element can be integrated on the basis of a superpositioning of the common element in the different temporal maps. This last assertion is what takes the temporal coding hypothesis beyond the views of prior investigators.

It is important to note that, unlike many theories of associative learning (e.g., Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972; Wagner, 1981), which have tended to treat performance as direct evidence of learning, the temporal coding hypothesis maintains a clear distinction between learning and the behavioral expression of that learning. According to the temporal coding hypothesis, encoding and retrieval of two events can occur in any temporal direction (i.e., backward, simultaneous, and forward) as long as there is some degree of contiguity between them. However, whether such learning will be observed in behavior and, if that is the case, how that learning will be expressed will depend on multiple variables, such as the species, experimental preparation, motivation to respond, and so on, and, centrally for the present discussion, the temporal relationships between events. Thus, some preparations encourage the subject to respond at the time at which the outcome is expected, which might be during or after the test cue. In other preparations, the nature of the response system assessed requires a predictive relationship between the conditioned stimulus (CS) and the US for learning to be evidenced in overt behavior. Pavlovian conditioning preparations often involve assessment of anticipatory response systems (e.g., fear conditioning to a tone CS that predicts the impending occurrence of a footshock US). That is, in the framework of the temporal coding hypothesis, a predictive relationship is not essential for associative acquisition. The problem is that conventional measures of Pavlovian conditioning usually assess forward associations but are rather inadequate for assessing backward associations, because these associations establish a diagnostic (i.e., $US \leftarrow CS$), rather than a predictive (anticipatory; i.e., $CS \rightarrow US$), relationship between the events. Thus, the question is how backward associations can be assessed through the observation of overt behavior.

One strategy that can be 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 (e.g., Matzel et al., 1988). This procedure allows for the

assessment of simultaneous situations (e.g., the present Experiment 1, with humans, achieved through instructions) and predictive situations (e.g., the present Experiment 2, with rats, achieved through anticipation of an impending footshock) to reveal learned backward associations. In a traditional sensory preconditioning procedure (Brogden, 1939), a stimulus (S2) is forward-paired with another stimulus (S1) in Phase 1 (i.e., $S2 \rightarrow S1$). Subsequently, S1 is forward-paired with a US in Phase 2 (i.e., $S1 \rightarrow US$). During testing, a conditioned response is observed to S2 (relative to control groups lacking either the Phase 1 or the Phase 2 pairings), even though S2 itself was never directly paired with the US. In the two experiments reported here, we examined the occurrence of temporal backward associations, using a modified sensory preconditioning procedure, in which the order of the stimuli during Phase 2 was reversed (i.e., $US \rightarrow S1$, instead of $S1 \rightarrow US$). Superpositioning a $US \rightarrow S1$ temporal map on an $S2 \rightarrow S1$ temporal map, with the two S1 representations aligned, presumably gives S2 a simultaneous (in Experiment 1) or anticipatory (in Experiment 2) relationship to the US that is dependent on the *backward* $US \rightarrow S1$ association.

EXPERIMENT 1

Experiment 1 was performed to determine whether human subjects were able to integrate temporal information from different phases of learning, as assumed by the temporal coding hypothesis (e.g., Matzel et al., 1988; Savastano & Miller, 1998). Moreover, this experiment used temporal integration as a strategy to obtain evidence bearing on the use of backward temporal associations in a human preparation.

The subjects were assigned to one of three experimental groups: an experimental group to test for temporal integration and to provide evidence concerning backward associations (Group Bw), a control group for temporal integration (Group ConTI), and a control group for backward associations (Group ConBw; see the lower panel of Figure 1). All the groups received pairings of S2 and S1 in Phase 1, with S2 occurring immediately before S1 (i.e., termination of S2 coincided with onset of S1, $S2 \rightarrow S1$). Then, in Phase 2, Group Bw received [backward] outcome $\rightarrow$ S1 pairings, Group ConTI received [backward] outcome $\rightarrow$ S3 pairings, and Group ConBw received simultaneous presentations of the outcome and S1. Then all the groups were tested for responding during and after the presentation of S2. The treatment given to Groups Bw and ConBw was expected to result in integration of the memories of Phase 1 and Phase 2 training, due to S1's having been presented in both phases of training. Presumably, if temporal integration occurs and the representations of events are temporally specific, responding would be expected during the presentation of S2 in Group Bw and after the presentation of S2 in Group ConBw. No temporal integration was expected in Group ConTI, because there was no event common to Phases 1 and 2; thus, responding was expected to be equally low during and after

Figure 1. Design and hypothetical temporal representations of Experiment 1. The left side of the top panel presents the practice trials (common to all the participants), and the left side of the bottom panel presents the treatment phases for each group. The right sides of the top and bottom panels present the hypothetical temporal representations that result after temporal integration based on superposition of elements common to the treatment phases and the use of backward (as well as simultaneous and forward) associations. Open rectangles and letters represent cues; the black rectangles represent the outcome.

presentation of S2 (see the lower right panel of Figure 1 for a graphic representation of the expected temporal integration and the Results section for elaboration).

Method

Subjects

Fifty-three undergraduate students at SUNY-Binghamton participated in this study, in partial fulfillment of a course requirement. The subjects were randomly assigned to the experimental groups, yielding 17 subjects in Group Bw, 19 subjects in Group ConTI, and 17 subjects in Group ConBw.

Apparatus and Procedure

The subjects performed the experiment using personal computers located in three small rooms. Two of the rooms had two computers, each separated by an opaque screen, and the third room had only one computer.

In order to evaluate temporal integration and the use of backward associations by human subjects, we developed a novel behavioral task that measured the learning of specific temporal relationships between different stimuli through time spent pressing the space bar on a computer keyboard. In this task, different colored shapes were presented on a 14-in. monitor screen. One of these shapes (a red star) was designated (through instructions) as the target stimulus for the

subjects (i.e., the outcome). During training, the subjects were asked to observe the relationship between the other colored shapes (*cue* stimuli) and the outcome in order to be able to anticipate during testing whether, when, and for how long the outcome should be expected on the screen. All the cues and the outcome were 5 sec in duration. The computer screen always displayed two light gray rectangles (aligned on the central vertical axis) over a dark gray background across the entire screen. The cues were presented in the top rectangle. The outcome was presented in the bottom rectangle.

The subjects were presented with four different *situations*. The first three situations were labeled as *practice situations* and were identical for all the subjects. The fourth situation consisted of our relevant experimental manipulation. For each practice situation, there was a learning, or observational, phase followed by a test phase. During the observational phase, participants were asked to observe how different cues were related to the presence of the outcome. In the test phase, the subjects were presented with the test cue and were asked to hold down the space bar of their computer's keyboard during the entire time they believed the outcome should appear on the screen, and not during any other time. That is, the subjects should infer, on the basis of the information presented during the observational phase, not only whether the outcome should appear, but also when and for how long. The outcome was not programmed to occur during testing, but depressing the space bar by the subjects at any moment during testing made the outcome appear on the screen. The purpose of this action was to facilitate the subjects in re-creating the expected test cue–outcome temporal relationship (if any) and to provide the subjects with feedback about their pressing the space bar. The subjects' responses were recorded on a second-by-second basis during the entirety of each 25-sec test phase.

The top panel of Figure 1 summarizes the three practice situations. During the observation phase of the first practice situation, the subjects received one simultaneous presentation of Cue S4 (a green plus sign) and the outcome (the red star). At test, Cue S4 was displayed, and the subjects were expected to press the space bar during the entire time of presentation of S4. During the observation phase of the second practice situation, the subjects received one presentation of Cue S5 (an orange triangle) followed immediately by the outcome. At test, Cue S5 was displayed, and the subjects were expected to press the space bar for approximately 5 sec, not during but immediately after S5 was terminated. Finally, during the observation phase of the third and last practice situation, the subjects received one presentation of Cue S6 (a pink square) followed immediately by the outcome. At test, a different cue, S7 (a light blue rectangle), was displayed on the screen, and the subjects were expected not to respond at any time. After completing each practice situation, the subjects received feedback concerning their performance, which included a graphic representation of their expected performance, based on the observational phase, and their actual execution during testing.

The fourth situation (lower panel of Figure 1) was the relevant experimental manipulation and consisted of two (rather than one) observation phases and one test phase. The subjects were informed through an instructions screen that they should remember the relationships between the stimuli in both observational phases, because the information from one phase might complete the information from the other phase. During the first observation phase (Phase 1), the subjects in all the groups received one presentation of Cue S2 followed immediately by Cue S1. During the second observation phase (Phase 2), the subjects in Group Bw received one presentation of the outcome immediately followed by S1, the subjects in Group ConTI received one presentation of the outcome immediately followed by Cue S3, and the subjects in Group ConBw received one simultaneous presentation of the outcome and S1. For all groups, the outcome (i.e., the red star) was presented 11 sec into the second observation phase. All the groups were then tested with one presentation of Cue S2. Cue S2 was a blue X; Cues S1 and S3 were a yellow

circle and a brown diamond, counterbalanced within groups. The subjects performed the experimental (fourth) situation described above three times (i.e., three cycles of training, each followed by testing). They received no feedback in any of these repetitions. In pilot experiments, we observed that the subjects seemed to have problems in apprehending the temporal intervals presented during training and responding in accord with these relationships after experiencing the training relationships once. In order to further analyze whether these difficulties were coming from the complex nature of the procedure or from the inability of human subjects to encode specific temporal intervals from the different phases of training and integrate them on the basis of a common element, we decided to present them with three cycles of training with the same experience (it seemed plausible that the learning of specific temporal relationships and their integration requires more training than does the learning of contingencies). Testing occurred after each one of these cycles in order to observe the progressive learning of the temporal relationships. Because the subjects received no feedback concerning their performance, it was not expected that these tests would have an impact on what was learned during training.

According to the temporal integration tenet of the temporal coding hypothesis, the subjects in Groups Bw and ConBw should have been able to integrate the information separately learned during the two observational phases, because the temporal representations could be integrated using the common element, S1 (see the lower right panel of Figure 1). Thus, at test, the subjects in Group Bw should have expected the outcome *during* the presentation of S2; however, in Group ConBw responding was expected *after*, not *during*, the presentation of S2 (i.e., temporal integration maintains the specific temporal order of presentation of the events). In contrast, no responding was expected in Group ConTI, because there was no common element that allowed integration of the two phases of training.

A data selection criterion was established, such that only the data from the subjects who, during the second practice situation, pressed the space bar for at least 1 sec more after than during the presentation of the test cue (S5) were considered for the study. This criterion, based on a simple temporal discrimination, was established to determine whether the subjects attended to both the instructions and the simple and direct temporal relationship between the cue and the outcome presented during training. After the instructions and the feedback given following the first (hence, novel) practice situation, it was expected that the subjects would not have a problem (if they were attending to the task) in determining, during the second practice trial, that termination of S5 was immediately followed by the outcome (see the top panel of Figure 1) and that, during testing, they should hold down the space bar immediately after (but not during) S2, when the outcome should be expected to occur. The third practice trial was added because in pilot experiments, we observed that the subjects had a strong tendency to respond throughout testing in situations in which they were not able to determine, on the basis of their experiences during training, whether and when the outcome should be expected to occur. Thus, we wanted to make clear to them that, in situations in which time of occurrence of the outcome could not be determined on the basis of the observational phase, they were expected not to respond. This third practice trial was not selected as a criterion of elimination, because it did not allow the observation of temporal discrimination (responding was not expected during or after test cue presentation). Data from 23 subjects (7 from Group Bw, 9 from Group ConTI, and 7 from Group ConBw) were eliminated from the analyses due to their failing to pass the data selection criterion. Thus, the final *n* was of 10 subjects per group.

Results and Discussion

Mean times of space bar depression during and after the 5-sec presentation of the test cue, S2, for each of the three repetitions of the target manipulation are displayed in

Table 1
Group Means During and After the Test Cue Within Each of the Three Repetitions
of the Target Situation After Applying the Data Selection Criterion

Trial	Group Bw				Group ConTI				Group ConBw			
	During		After		During		After		During		After	
	<i>M</i>	<i>SEM</i>	<i>M</i>	<i>SEM</i>	<i>M</i>	<i>SEM</i>	<i>M</i>	<i>SEM</i>	<i>M</i>	<i>SEM</i>	<i>M</i>	<i>SEM</i>
1	1.32	0.68	1.21	0.57	0.15	0.15	0.84	0.56	0.44	0.44	1.23	0.58
2	2.13	0.72	1.36	0.56	0.40	0.40	0.38	0.37	0.26	0.13	2.46	0.64
3	2.08	0.70	0.63	0.31	0.46	0.33	0.51	0.37	0.09	0.06	1.92	0.68

Note—Mean ($\pm$ SEM) time of space bar depression during the 5 sec of the test cue presentation and 5 sec after the test cue presentation.

Table 1. As can be seen in the table, as training progressed, the subjects in Group Bw learned to expect the outcome during (and not after) S2 presentation, the subjects in Group ConTI appeared not to know when to expect the outcome, and the subjects in Group ConBw learned to expect the outcome after (and not during) S2 presentation.

Figure 2 (right panel) depicts the distribution of the groups' responses on a second-by-second basis during the test phase of the last (third) cycle of training. Presumably, this test reflected maximal learning and integration of the temporal relationships between the events presented during training. As can be seen, the subjects in Group Bw

Figure 2. Mean responses during the practice and test situations of Experiment 1. The left panel presents the distribution of responses, on a second-by-second basis, during the entirety of the practice test sessions, after and before the data selection criterion is applied (vertical bars and line graphs, respectively). The right panel presents the distribution of responses, on a second-by-second basis, during the entirety of the last trial of the target manipulation, after and before the data selection criterion is applied (vertical bars and line graphs, respectively). Brackets represent the standard error of the mean. The 5-sec intervals during and after presentation of the test cue are delimited by vertical dot lines.

held down the space bar *during* the presentation of S2 for longer than the subjects in Groups ConTI and ConBw. That is, the subjects in Group Bw appear to have been able to integrate temporal information from the different phases of training and to use backward associations in order to anticipate whether, when, and for how long to respond. Moreover, the subjects in Group ConBw held down the space bar *after* the presentation of S2 for longer than the subjects in Groups ConTI and Bw, providing further evidence of temporal integration and the use of temporally appropriate patterns of responding.

A one-way analysis of variance (ANOVA) performed on the number of seconds that the subjects held down the space bar during Cue S2 presentation on the third test trial yielded a main effect of group [$F(2,27) = 5.64, MS_e = 1.98, p < .01$]. Planned comparisons revealed that Groups Bw and ConTI differed [$F(1,27) = 6.62, p < .05$]. That is, the subjects in Group Bw seemingly were able to integrate the temporal information from the two observation phases on the basis of the common element, S1. Groups Bw and ConBw also differed [$F(1,27) = 9.96, p < .01$]. That is, the subjects apparently were able to use backward associations in order to know when to expect the outcome. However, lower responding during S2 by Group ConBw than by Group Bw could have been due to the simultaneous presentations of S1 and the outcome, resulting in a masking effect—that is, a deficit in processing or attending to stimuli presented simultaneously. In order to assess this alternative explanation, we performed an additional comparison within Group ConBw, which revealed that responding during S2 was lower than responding after S2 [$t(9) = 2.83, p < .05$]. That is, low responding during S2 in Group ConBw did not result from a deficit in processing or attending simultaneously to S1 and the outcome during the second phase of learning. Instead, the subjects in this group appear to have learned that the outcome should be expected not *during* S2, but *after* S2. Further support for our assumption that the subjects encoded the specific temporal location of the outcome is provided by a 3 (group: Bw vs. ConTI vs. ConBw) $\times$ 2 (time of responding: during S2 vs. after S2) ANOVA. This analysis revealed a group $\times$ time of responding interaction [$F(2,27) = 5.79, p < .01$]. Thus, we can conclude that the subjects were able to encode and retrieve specific temporal information and use backward (as well as simultaneous and forward) associations in order to integrate the different temporal maps and predict when the outcome should be expected to occur.

One might argue that our human subjects were able to anticipate the occurrence of the outcome by timing the duration from onset of the task to onset of the outcome through *chronometric counting* (i.e., “counting” the seconds until the presentation of the expected outcome; e.g., Fetterman & Killeen, 1990; Gilliland & Martin, 1940; Killeen, 1991; Wilkening, Levin, & Druyan, 1987). The outcome was presented 11–15 sec into the training sessions, and the test cue was presented to all the subjects during that same range of time. Thus, we must consider whether responding during S2 in Group Bw could be explained in terms of a counting strategy without recourse to backward associations. However, detailed analysis indicates that such a strategy could not explain the between-group and within-group differences observed in this experiment. The subjects in Group ConTI could not anticipate the occurrence of the outcome on the basis of the test cue, because there was no a common element to allow integration of the two phases of training. Thus, for this group, the only way to predict the moment of occurrence of the outcome was to use a counting strategy with respect to the start of the test trial. Mean responding by Group ConTI during the time the outcome should have been expected on the basis of a counting strategy (11–15 sec into the session) was 0.46 sec; for Group Bw, it was 2.08 sec. In addition, responding during the presentation of S2 in Group ConBw was 0.09 sec, as compared with 1.92 sec after S2 presentation (16–20 sec into the session).

As was previously stated, in order to increase the sensitivity of our measures, we used a data selection criterion to eliminate data from the subjects who seemed to have difficulties in understanding or attending to the task. However, due to the large number of subjects that met the data selection criterion, we also analyzed the data of all the subjects, without applying the criterion. Responding during and after the 5-sec-long test cue for each one of the practice situations, without applying the criterion of elimination and after applying the criterion of elimination, is presented in Table 2. The distribution of the subjects' space bar depression times on a second-by-second basis during the practice test sessions before and after applying the data selection criterion is displayed in the left panel of Figure 2. There were no differences between groups in responding during or after the test cue presentation during any of the three practice situations, regardless of whether or not the data selection criterion was applied (all F s < 1.49 , all p s $> .24$). Table 3 displays the average time that

Table 2
Mean Responding During and After the Test Cue Within the Three Practice Situations With and Without Applying the Data Selection Criterion

Situation	All Participants				Criterion			
	During		After		During		After	
	<i>M</i>	<i>SEM</i>	<i>M</i>	<i>SEM</i>	<i>M</i>	<i>SEM</i>	<i>M</i>	<i>SEM</i>
Practice 1	3.50	0.20	0.81	0.16	4.00	0.17	0.63	0.16
Practice 2	1.47	0.24	2.60	0.23	0.24	0.08	3.87	0.13
Practice 3	0.58	0.17	2.31	0.27	0.11	0.06	2.25	0.37

Note—Mean ($\pm$ SEM) time of space bar depression during the 5 sec of the test cue presentation and 5 sec after the test cue presentation.

Table 3
Group Means During and After the Test Cue Within Each of the Three Repetitions
of the Target Situation Without Applying the Data Selection Criterion

Trial	Group Bw				Group ConTI				Group ConBw			
	During		After		During		After		During		After	
	<i>M</i>	<i>SEM</i>	<i>M</i>	<i>SEM</i>	<i>M</i>	<i>SEM</i>	<i>M</i>	<i>SEM</i>	<i>M</i>	<i>SEM</i>	<i>M</i>	<i>SEM</i>
1	1.28	0.50	0.75	0.36	0.79	0.36	0.98	0.39	0.65	0.37	1.14	0.42
2	2.01	0.54	1.06	0.37	1.12	0.41	0.31	0.20	1.09	0.42	1.94	0.46
3	1.95	0.52	0.81	0.31	1.08	0.37	0.89	0.34	0.64	0.33	1.83	0.47

Note—Mean ($\pm$ SEM) time of space bar depression during the 5 sec of the test cue presentation and 5 sec after the test cue presentation.

the subjects pressed the space bar during and after the presentation of S2, without applying the data selection criterion. As can be seen in the table, within the test phase of the third training cycle, responding during S2 in Group Bw was higher than that in Group ConBw [$F(1,50) = 4.92$, $MS_e = 2.97$, $p < .05$]. A similar comparison between Groups Bw and ConTI fell short of significance, although the tendency for higher responding in Group Bw than in Group ConTI remained [$F(1,50) = 2.27$, $MS_e = 2.97$, $p = .13$]. Finally, a within-subjects t test on Group ConBw revealed a significant difference between responding during and after S2 [$t(16) = 2.09$, $p = .05$]. That is, the data from all the subjects (without applying a data selection criterion) retained the basic differences between groups. Differences between Groups Bw and ConBw supported evidence of temporal integration and the formation of backward (Group Bw) and simultaneous (Group ConBw) associations between the outcome and S2. Importantly, the failure to observe statistical differences between Groups Bw and ConTI seemed to be mostly related to a high level of responding throughout the test phase exhibited by the subjects in Group ConTI, who could not anticipate the occurrence of the outcome, when all the the subjects were included in the analyses (see the middle right panel of Figure 2).

The differences in responding between Groups Bw and ConBw are difficult to explain from a view that does not assume temporal integration and the use of backward associations. According to the temporal coding hypothesis, during Phase 1, the subjects learned not only the association between S2 and S1, but also the temporal relationships between these stimuli; that is, the subjects learned not only that S1 followed S2 ($S2 \rightarrow S1$), but also that S2 preceded S1 ($S2 \leftarrow S1$). Similarly, during Phase 2, the subjects learned the temporal relationships (backward in Group Bw and simultaneous in Group ConBw) between the outcome and S1. Thus, when S2 was presented at test to Group Bw, these subjects retrieved a representation of S1 occurring immediately after termination of S2 (i.e., $S2 \rightarrow S1$). Similarly, the representation of the onset of S1 activated a representation of the onset of the outcome 5 sec back in time (i.e., $US \leftarrow S1$). Consequently, according to the temporal coding hypothesis, the subjects in Group Bw should have expected the outcome to occur simultaneously with S2 (see the lower right panel of Figure 1). That is, after integration of the temporal maps from

Phases 1 and 2, S2 signaled the occurrence of the outcome simultaneously with S2, and consequently, it elicited strong responding *during* S2, but not *after* S2. When S2 was presented at test to Group ConBw, these subjects retrieved a representation of S1 occurring immediately after termination of S2 (i.e., $S2 \rightarrow S1$), just as did those in Group Bw. However, in contrast with Group Bw and as a result of the simultaneous S1–outcome training of the Phase 2, integration of the Phase 1 and the Phase 2 temporal maps resulted in an expectation of the outcome occurring *after* (not *during*) termination of S2, the time at which S1 (and hence, the outcome) was expected.

Explanations based only on simultaneous or forward associations appear unable to account for the above observations. In this framework, as a result of Phase 1 training, S2 should have activated a similarly strong representation of S1 in both groups. However, as a result of Phase 2 training, activation of the representation of the outcome through S1 should have been similar or stronger in Group ConBw than in Group Bw, because of the greater contiguity between the outcome and S1 in Group ConBw. Thus, on the basis of this account, we should expect no responding during the S2 test presentation in either group (unless we assume that there was generalized responding to S2; but in that case, responding should have been similar in both groups or stronger in Group ConBw, because of the greater temporal contiguity between S1 and the outcome). The actual pattern of results was not consistent with that expected from associative accounts based only on simultaneous or forward associations.

In summary, the results of Experiment 1 support the predictions from the hypothetical temporal representations shown in Figure 1 (lower right panel), which are based on the assumption that the subjects can encode backward associations and can integrate temporal maps from different training experiences on the basis of their common elements.

EXPERIMENT 2

The results of Experiment 1 appear to provide evidence of temporal integration and temporal backward associations. However, these results with human subjects are subject to alternative explanations because humans are regarded as capable of using so-called higher order processes of learning. Specifically, responding in Experiment 1 could

have reflected the temporal arrangement of the stimuli on the basis of the use of linguistic labels, such as *before*, *during*, and *after*, and thereby, possibly depended on higher order cognitive processes, rather than on simple associations that encoded temporal relationships. Moreover, humans can use what is called *episodic memory* to encode and retrieve what, when, and where an event occurred in the past (Tulving, 1972), and it is arguably assumed that this type of memory is beyond the memory capabilities of nonhuman animals (see Clayton, Griffiths, & Dickinson, 2000, for a review). These higher order interpretations of the human data of Experiment 1 are not inconsistent with the use of temporal integration strategies based on superpositioning of common elements and knowledge of specific temporal intervals (backward, simultaneous, and forward). However, these interpretations appear to be inconsistent with the possibility that nonhuman animals can encode and use specific backward associations. It was not the purpose of this research to address the basis of linguistic temporal labels or to determine how humans use episodic memory. Our primary interest was to determine whether human and nonhuman subjects use forward and backward associations in a similar manner, which would suggest the possibility that the same basic process of learning associations over time operates in humans and (at least some) nonhuman species, consistent with the principle of parsimony. In order to further address this problem, in Experiment 2 we conducted a study analogous to Experiment 1 but used nonhuman subjects (i.e., rats), in order to illuminate the generality of these associative processes.

The procedure used in Experiment 2 was conditioned lick suppression, with footshock as the US. As in Experi-

ment 1, there were three treatment groups (see Figure 3). Group Bw was the critical experimental group to be tested for temporal integration and backward associations, Group ConTI was a control group for temporal integration, and Group ConBw was a control group for backward associations. The three groups of rats were administered S2–S1 trials in Phase 1. For Groups Bw and ConTI, there was a 5-sec gap between the termination of S2 and the onset of S1. For Group ConBw, there was no gap between the termination of S2 and the onset of S1. During Phase 2, US–S1 trials were presented to Groups Bw and ConBw, and US–S3 trials were presented to Group ConTI. There was a 4-sec gap between termination of the US and onset of the CS for all three groups. All the CSs were 3 sec in duration, and the US was 1 sec in duration. All the animals received one test trial with S2.

Although temporal integration was expected to occur in Groups Bw and ConBw because S1 was an event common to the two phases of training, responding was expected only in Group Bw. In Group Bw, temporal integration of the two phases of training was expected to result in an expectation of the US immediately after S2. In contrast, in Group ConBw, temporal integration would result in the US's being expected before S2. Owing to the anticipatory nature of conditioned lick suppression, responding was expected only in the group in which temporal integration resulted in anticipation of the US. Temporal integration and, consequently, responding were not expected in Group ConTI, because there were no events common to Phases 1 and 2. Figure 3 shows a summarized design of Experiment 2 (left panel) and the hypothetical temporal representations for each group (right panel).

Figure 3. Design and hypothetical temporal representations of Experiment 2. The left side of the figure presents treatment trials given to each group. The right side of the figure presents the hypothetical temporal representations that result after temporal integration based on superposition of elements common to the treatment phases. Open rectangles and letters represent conditioned stimuli; the black rectangles represent the footshock unconditioned stimulus.

Method

Subjects

The subjects were 18 male and 18 female experimentally naive Sprague–Dawley descended rats bred in our colony. Weight ranges were 205–341 g for the males and 185–264 g for the females. The subjects were individually housed in stainless steel, wire-mesh cages in a vivarium maintained on a 16:8-h light:dark cycle. Experimental sessions occurred approximately midway through the light component of that cycle. The subjects were allowed free access to food in the home cage. A progressive water deprivation schedule was imposed over the week prior to the beginning of the experiment until water availability was limited to 30 min per day, given approximately 2 h after any scheduled treatment. All the rats were handled for 30 sec three times per week from weaning until the initiation of the experiment.

Apparatus

Twelve experimental chambers of two different types were used: rectangular (R) and V-shaped (V). The use of two different chambers was due to the available apparatus and was not relevant to the problem being addressed. Chamber R was a clear Plexiglas chamber rectangular in shape, measuring $23.0 \times 8.25 \times 13.0$ cm ($l \times w \times h$). The floor was constructed of stainless steel rods 0.5 cm in diameter, spaced 1.5 cm apart center to center. The rods were connected by NE-2 neon bulbs that allowed a constant-current footshock to be delivered by means of a high-voltage AC circuit in series with a 1.0-M Ω resistor. Each of six copies of Chamber R was housed in a separate light- and sound-attenuating environmental isolation chest, which was dimly illuminated by a 2-W (nominal at 120 VAC, driven at 60 VAC) incandescent houselight mounted on the ceiling of the environmental chest, approximately 26 cm from the center of the experimental chamber.

Chamber V was a 22.1-cm-long box vertically shaped like a truncated V (height, 25.3 cm; width, 21.3 cm at the top, 5.1 cm at the bottom). The floor and sides were constructed of stainless steel sheets, and the ceiling was constructed of clear Plexiglas. The floor of each chamber consisted of two parallel metal plates, each 2.0 cm wide, with a 1.1-cm gap between them. Each of six copies of Chamber V was housed in its own environmental isolation chest, which was dimly illuminated by a 7.5-W (nominal at 120 VAC, driven at 60 VAC) incandescent houselight mounted on an inside wall of the environmental chest, approximately 30 cm from the center of the experimental chamber. The light entering the animal chamber was primarily that reflected from the roof of the environmental chest. The light intensities in the two chambers were approximately equal, due to the differences in opaqueness of the walls in Chambers R and V.

Each chamber (R and V) was equipped with a water-filled lick tube that extended about 1 cm from the rear of a cylindrical niche, 4.5 cm in diameter, left–right centered in one short wall, with its axis perpendicular to the wall, and positioned with its center 4 cm above the floor of the chamber. Each niche had a horizontal infrared photobeam transversing it parallel to its mounting wall 1 cm in front of the lick tube. In order to drink from the tube, the subjects had to insert their heads into the niche, thereby breaking the infrared photobeam. Thus, the amount of time that the test stimulus caused the subject to cease breaking the photobeam (i.e., interrupt drinking) could be monitored; this served as our dependent variable.

Each chamber (R or V) was also equipped with three speakers mounted widely separated on the inside walls of the environmental chest. Each speaker could deliver a different auditory stimulus—specifically, a click train (6/sec), a white noise, and a complex tone of high frequency (3000 and 3200 Hz presented simultaneously). Ventilation fans in each chest provided a constant 76-dB (C scale) background noise. When delivered, the auditory stimuli were all approximately 6 dB (C scale) above this background noise.

Procedure

The subjects were randomly assigned to one of three groups: Bw, ConTI, and ConBw, counterbalanced for sex ($n_s = 12$). CS S2 was

the click train; CSs S1 and S3 were the white noise and the tone, counterbalanced within groups. All CSs were 3 sec in duration. The US was a 1-sec, 1.0-mA footshock. The type of training chamber (R or V) was counterbalanced within groups. All the sessions were 60 min in duration, except where otherwise noted.

Acclimation. All the subjects were exposed to the experimental context. No nominal stimuli were programmed to occur, and the subjects had free access to the water-filled lick tubes.

Phase 1 training. On Days 2 and 3, all the subjects were presented with six daily S2–S1 pairings. For Groups Bw and ConTI, there was a 5-sec gap between the termination of S2 and the onset of S1. For Group ConBw, there was no gap; that is, S2 termination was followed immediately by S1 onset. On Day 2, onsets of S2 occurred at 8, 14, 22, 32, 44, and 58 min into the session; on Day 3, onsets of S2 occurred at 6, 18, 28, 34, 48, and 56 min into the session (mean intertrial interval [ITI] was 10 min). The water-filled lick tubes were not available during Phase 1 training.

Phase 2 training. On Days 4 and 5, all the subjects received trace backward conditioning trials, with a 4-sec gap between US termination and CS onset. Groups Bw and ConBw received four daily US–S1 pairings, and Group ConTI received four daily US–S3 pairings. On Day 4, US onsets occurred at 9, 21, 36, and 51 min into the session; on Day 5, US onsets occurred at 7, 22, 34, and 49 min into the session (mean ITI was 14 min). The water-filled lick tubes were not available during Phase 2 training.

Restabilization. On Days 6 and 7, all the subjects were exposed each day to the training context for 60 min and again, 3 h later, for an additional 30 min. The subjects had free access to the water-filled lick tubes, and no nominal stimuli were programmed to occur. These sessions were intended to reestablish a stable rate of drinking behavior, which might have been disrupted by the footshock US administered during training, thereby providing similar baseline behavior across the three groups upon which conditioned lick suppression could be assessed.

Testing on S2. On Day 8, all the subjects were tested for conditioned lick suppression to S2. Time spent drinking by each subject was recorded. After 5 cumulative seconds of licking in the absence of any nominal stimulus, CS S2 was presented. Thus, all the subjects were drinking at the time of S2 onset. Time to complete an additional 5 cumulative seconds of licking after the onset of S2 was recorded. The latencies recorded during the presentation of S2 were interpreted as reflecting the expectancy that the US would follow S2. The test session was approximately 16 min in duration, with a ceiling score of 15 min imposed on the time to complete 5 cumulative seconds of drinking in the presence of S2.

Following the convention of our laboratory, the data from any animal that took longer than 60 sec to complete its first 5 cumulative seconds of licking in the test day (i.e., prior to CS onset) were excluded from the experimental analysis, because they were considered to reflect unusually high fear of the context. The data from 1 subject from Group Bw were excluded from the analyses because of this criterion. All test scores were converted to log times (base 10), in order to better approximate the within-group normal distributions assumed by parametric statistics.

Results and Discussion

Figure 4 depicts the mean suppression at test for each group. As can be seen in the figure, the subjects in Group Bw suppressed drinking at test more than did the subjects in Groups ConTI and ConBw. That is, only the subjects in Group Bw appeared to anticipate the occurrence of the US on the basis of the presentation of S2, which is consistent with integration of temporal information from the two different phases of learning and the use of backward associations.

Figure 4. Results of Experiment 2: Mean lick suppression during presentation of the target conditioned stimulus. Brackets represent the standard error of the mean.

A one-way ANOVA performed to assess possible differences in drinking behavior prior to the test CS presentation was not significant [$F(2,32) = 2.85, p > .05$], suggesting that there were no large differences between groups in fear of the context. A similar ANOVA conducted on the data recorded during the test CS presentation yielded a main effect of group [$F(2,32) = 19.71, MS_e = 0.10, p < .0001$]. Planned comparisons using the error term of this ANOVA revealed that Group Bw differed from Groups ConTI and ConBw [$F_s(1,32) = 35.62$ and 22.78 , respectively; both $p_s < .0001$]. Groups ConTI and ConBw did not differ [$F(1,32) = 1.41, p > .10$].

As in the experiment with humans, the differences in responding between Groups Bw and ConBw are difficult to explain from a view that does not assume temporal integration and the use of both forward and backward associations. According to the temporal coding hypothesis, the subjects learned during Phase 1 not only that S1 occurred when S2 occurred, but also the specific temporal relationships between these stimuli; that is, the subjects learned not only that S1 followed S2 ($S2 \rightarrow S1$), but also that S2 preceded S1 ($S2 \leftarrow S1$). Similarly, during Phase 2, the subjects learned the temporal relationships (forward and backward) between the US and S1 (i.e., $US \rightarrow S1$ and $US \leftarrow S1$). Thus, when S2 was presented at test to Group Bw, these subjects retrieved a representation of S1, which started 8 sec after the onset of S2 (S2 lasted for 3 sec; thus, the representation of S1 was activated 5 sec after termination of S2). Similarly, the representation of the onset of S1 activated a representation of the onset of the US 5 sec *back in time*. Temporal integration of the Phase 1 and the Phase 2 experiences by Group Bw resulted in an

expectation of the US's occurring immediately after termination of S2 (see the right panel of Figure 3). That is, S2 elicited strong conditioned responding because it predicted an impending footshock. In contrast, when S2 was presented at test to Group ConBw, these subjects retrieved a representation of S1's occurring immediately after termination of S2, because there was no temporal gap between S2 termination and S1 onset during Phase 1. As a result of Phase 2 training, as in Group Bw, the representation of S1 activated a representation of the onset of the US 5 sec back in time. After integration of these two temporal maps, the US was expected to occur 2 sec before the onset of S2. Thus, because S2 indicated that the US should have occurred already, there was no anticipation of the US in this group, and little or no conditioned responding should be observed. Finally, no conditioned responding was observed in Group ConTI, because there was no common element that allowed integration of the two phases of training.

Explanations based only on simultaneous or forward associations seem to be unable to account for the above observations. In this framework, as a result of Phase 2 training, activation of the representation of the US by S1 should have been identical in Groups Bw and ConBw. As a result of Phase 1 training, S2 should have activated a stronger representation of S1 in Group ConBw than in Group Bw, because there was no temporal gap between S2 and S1 (i.e., delay pairings in Group ConBw, as compared with trace pairings in Group Bw). Thus, accounts based on simultaneous or forward associations predict stronger responding to S2 by Group ConBw, a pattern of results opposite to the one that we observed.

In summary, the results of Experiment 2 are consistent with the predictions of the temporal coding hypothesis (see the hypothetical temporal representation in the right panel of Figure 3). The subjects behaved as if they had integrated temporal maps from the different phases of training, and the pattern of responding observed is consistent with their having used backward associations.

GENERAL DISCUSSION

Experiment 1 with human subjects and Experiment 2 with nonhuman (i.e., rat) subjects provided evidence of temporal integration of two different training experiences on the basis of superpositioning of an element common to both experiences. Furthermore, this temporal integration suggests the use not only of forward associations (e.g., $S2 \rightarrow S1$), but also of backward associations (e.g., $US \leftarrow S1$).

The Mediation Process

To provide evidence of temporal integration and the use of backward associations, we used a modified sensory preconditioning procedure. One popular account of sensory preconditioning (i.e., $S2 \rightarrow S1$ followed by $S1 \rightarrow US$, testing on S2; Brogden, 1939) assumes that at test the representation of the first-order CS (S1) mediates between the second-order CS (S2) and the representation of the

US, which immediately supports responding (e.g., Holland, 1981). This mediation process consists of the first-order CS's simply "passing on" its excitatory value to the second-order CS. A similar explanation has also been used to account for excitatory responding in backward sensory preconditioning procedures (e.g., $S1 \rightarrow S2$ followed by $S1 \rightarrow US$, testing on $S2$; Ward-Robinson & Hall, 1996). Ward-Robinson and Hall assumed that during the second phase of a backward sensory preconditioning procedure (i.e., $S1 \rightarrow US$ trials), $S1$ activates a representation of $S2$ that remains active for some time, thereby critically allowing a representation of $S2$ to be associated with the US representation. In this framework, a $S2$ -US association is formed despite the first-order and the second-order stimuli having been presented in a backward (i.e., $S1 \rightarrow S2$) arrangement during the first training phase. However, such a view fails to account for reports of stronger responding to the second-order CS ($S2$) than to the first-order CS ($S1$; Barnet, Cole, & Miller, 1997, $US \rightarrow S1$ followed by $S2 \rightarrow S1$; Matzel et al., 1988, $S2 \rightarrow S1$ followed by $US \rightarrow S1$). That is, if $S1$ is "passing on" its excitatory value to $S2$, similar or stronger responding to $S1$ than to $S2$ should be expected.

Recently, however, Romaniuk and Williams (2000) proposed a mediational mechanism, consistent with Wagner's (1981) SOP model, which does not require temporal integration of specific temporal intervals and accounts for the stronger responding observed to the second-order CS than to the first-order CS, as reported by Barnet et al. (1997) and Matzel et al. (1988). Romaniuk and Williams assumed that CSs are divided into components, such as CS onset and termination, which can be separately conditioned, and noted that in the SOP model excitatory responding results only from situations in which two event representations are simultaneously activated into a primary state of activation ($A1$ - $A1$ learning in Wagner's SOP terminology). Consequently, they suggested that 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 paired with the secondary affective reaction evoked by the US. That is, because only the early components of the first-order backward CS ($S1$) could be processed simultaneously with the primary affective aspects of the US trace, only the initial segments of the backward CS should acquire excitatory properties, which might then become associated with the second-order CS ($S2$) during the $S2 \rightarrow S1$ pairings. The late components of the $S1$ representation presumably become inhibitory because, while they are in a primary state of activation ($A1$), the US representation is already in a state of low activation ($A2$; $A1$ - $A2$ learning in Wagner's SOP terminology). Thus, the stronger responding to the second-order CS than to the first-order backward CS reported by Barnet et al. (1997) and Matzel et al. (1988) could be explained without recourse to the use of temporal integration. In this view, previous data in the literature supportive of temporal integration and of the

use of temporal backward associations could be explained by assuming the principles of the SOP model and by assuming that different temporal components of a stimulus can be distinctively conditioned with respect to another stimulus.

The Temporal Coding Hypothesis

The main purpose of Experiments 1 and 2 was to obtain additional support for temporal integration with human and nonhuman animals and provide evidence of subjects' using backward associations. Previous experiments supporting backward associations have been criticized because, in one or another way, they were subject to alternative explanations (e.g., different availability for retrieval of the stimuli, familiarization of the items to be retrieved, or incidental rehearsal in the reverse order to training; see Asch & Ebenholtz, 1962, and Ekstrand, 1966, for reviews). More recent experiments with animals, using Pavlovian conditioning (e.g., Barnet et al., 1997; Hearst, 1989; Matzel et al., 1988) and instrumental conditioning (e.g., Hogan & Zentall, 1977; Richards, 1988; Zentall, Sherburne, & Steirn, 1992), and with humans (e.g., Gerolin & Matute, 1999) have provided additional data indicative of backward associations. However, each of these new observations could also have been explained in terms of purely simultaneous and forward associations (e.g., through simultaneous overlapping trace representations and mediational representations; see, e.g., Holland, 1981; Romaniuk & Williams, 2000; Ward-Robinson & Hall, 1996). In order to preclude these alternative explanations, our experiments were designed to control for the specific temporal order of the associations. In our view, a common confound in the literature has been to identify the temporal arrangement of the stimuli provided by the experimenter with the temporal order of the associations. As experimenters, we can present $S2$, followed serially by $S1$, and then, at test, present $S1$ in order to find out if the subjects are able to retrieve $S2$. Although, traditionally, retrieval of $S2$ given $S1$ at test has been considered to be evidence of the use of backward associations, there are alternative explanations that can account for these results without recourse to the construct of backward associations. Our strategy to avoid these alternative explanations was to show that our subjects were able to encode the *specific* intervals from $S2$ to $S1$ and from the US to $S1$ and that they were able to retrieve the *specific* backward temporal location of the US with respect to $S1$ when $S2$ was presented at test. This is the novel finding of the present research.

The temporal coding hypothesis attributes a mediational role to the first-order CS ($S1$), as do the mediational process accounts, but it assumes that this mediational role is effected through temporal integration of the representations of $S2 \rightarrow S1$ and $US \rightarrow S1$ training on the basis of their common element ($S1$). The results obtained in Experiments 1 and 2 are difficult to explain from a perspective that does not assume the encoding of the temporal relationship between proximate stimuli, using both forward

and backward associations, and their temporal integration on the basis of superpositioning of common elements. Explanations based on mediational processes that assume the existence of only simultaneous or forward associations (e.g., Romaniuk & Williams, 2000; Ward-Robinson & Hall, 1996) are unable to account for the present observations. For example, as a result of Phase 2 training in Experiment 2, activation of the representation of the US by S1 should have been identical in Groups Bw and ConBw (see Figure 3). Thus, if an excitatory association was established between the US and the early components of S1, it should have occurred to a similar degree in both groups. As a result of Phase 1 training, S2 should have activated a stronger representation of S1 in Group ConBw than in Group Bw, because there was no temporal gap between S2 and S1 in the former group. That is, the temporal contiguity between S2 and S1 was greater in Group ConBw, thereby allowing the representation of more elements of S2 to be simultaneous with elements of S1; in SOP terms, in the Bw group more S2 elements would have declined from A1 to A2 state by the time that S1 is presented than in the ConBw group (i.e., the S2–S1 association would be weaker in Group Bw than in Group ConBw). Thus, mediation accounts based exclusively on simultaneous or forward associations predict similar or stronger responding to S2 by Group ConBw than by Group Bw, a pattern of results opposite to the one that we observed.

Rate Expectancy Theory

Gallistel and Gibbon's (2000; also see Gallistel, 1990) recently proposed rate expectancy theory (RET), which can be viewed as a [major] complement to the postulates of the temporal coding hypothesis. RET assumes that animals have the ability to encode temporal intervals and to add, subtract, and even divide the resulting temporal information. Like the temporal coding hypothesis, RET explains the results reported in Experiments 1 and 2 in terms of the expected interval to the US at the onset of S2. What distinguishes RET from other models of animal timing is that, in addition to assuming that intervals can be timed in the forward direction, 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 Group Bw in Experiment 2, when S2 was presented at test, the expected interval to the US was +3 sec (from S2 onset to US onset; see Figure 3), and this resulted in strong conditioned responding relative to Group ConBw, for which the expected interval to the US was –2 sec. According to the decision rule of RET, the expectation of the US in +3 sec should support more responding than does –2 sec. In this way, Gallistel and Gibbon are also able to explain the results described above.

Episodic-Like Memories

A seeming example of animals' encoding and retaining information about the occurrence of a temporally *specific* set of events was provided recently by Clayton and Dick-

inson (1999) in experiments with scrub jays, which cache food. 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 shown by the scrub jays as raising problems 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). Clayton and Dickinson's results seem to contrast with both the widely accepted assumption that the acquisition and subsequent retrieval of episodic information is beyond the memory capabilities of nonhuman animals and the related but slightly different view that the presence of episodic memory is untestable in the absence of human language (for a review, see Clayton et al., 2000). Clayton and Dickinson's observations might be viewed as parallel, on a larger temporal scale, to the results we report in this paper, in which rats were able to encode and retrieve the *what* and *when* of an event that occurred in the past. The present evidence that animals use backward associations to remember which specific event occurred at a specific moment in time parallels the now widely accepted evidence that animals use forward associations to retrieve representations of specific events anticipated in the future (i.e., expectations).

In summary, the present experiments provide evidence of integration of temporal memories and of the simultaneous encoding of forward and backward associations in both human and nonhuman subjects. Although future research still needs to determine whether the ability to use backward associations is related to a single (e.g., temporal integration) or multiple (e.g., higher order logical deduction in humans and memory integration in rats) underlying mechanisms, the similarity of the results of Experiments 1 and 2 suggest the existence of a single mechanism that is similar across different mammal species (in this case, humans and rats).

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(Manuscript received July 25, 2002;
revision accepted for publication February 1, 2003.)