PSYCHOLOGICAL SCIENCE

Research Article

TRACE AND DELAY EYEBLINK CONDITIONING: Contrasting Phenomena of Declarative and Nondeclarative Memory

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Abstract—*We tested the proposal that trace and delay eyeblink conditioning are fundamentally different kinds of learning. Strings of one, two, three, or four trials with the conditioned stimulus (CS) alone and strings of one, two, three, or four trials with paired presentations of both the CS and the unconditioned stimulus (US) occurred in such a way that the probability of a US was independent of string length. Before each trial, participants predicted the likelihood of the US on the next trial. During both delay (*n *= 20) and trace (*n *= 18) conditioning, participants exhibited high expectation of the US following strings of CS-alone trials and low expectation of the US following strings of CS-US trials—a phenomenon known as the gambler's fallacy. During delay conditioning, conditioned responses (CRs) were not influenced by expectancy but by the associative strength of the CS and US. Thus, CR probability was high following a string of CS-US trials and low following a string of CS-alone trials. The results for trace conditioning were opposite. CR probability was high when expectancy of the US was high and low when expectancy of the US was low. The results show that trace and delay eyeblink conditioning are fundamentally different phenomena. We consider how the findings can be understood in terms of the declarative and nondeclarative memory systems that support eyeblink classical conditioning.*

Classical conditioning of the eyeblink response is a form of associative learning whereby a neutral, conditioned stimulus (CS; typically a tone) is repeatedly paired with an unconditioned stimulus (US; typically a puff of air to the eye). Initially, the CS does not elicit an eyeblink response, whereas the US initially and reliably elicits a reflexive eyeblink unconditioned response (UR). However, with repeated pairing of the CS and US, the CS begins to elicit a learned, or conditioned, response (CR). In delay conditioning, the CS is presented and remains on until the US is presented. The two stimuli overlap and then co-terminate. In trace conditioning, the CS is presented first. A silent, or trace, interval then follows before the presentation of the US.

The nature of trace and delay eyeblink conditioning has been illuminated by the distinction between declarative and nondeclarative knowledge (Clark & Squire, 2000). We found previously that declarative knowledge of the stimulus contingencies (i.e., awareness that the CS predicts the US) is critical for acquisition of trace conditioning but not for acquisition of delay conditioning (Clark & Squire, 1998). After 120 trials of differential conditioning with a CS+ and a CS−, only participants who were aware that the CS+ predicted the US exhibited successful trace conditioning. (The CS+ is followed by the US; the CS− is not.) Awareness was unrelated to differential delay conditioning. Further, using a trial-by-trial measure of awareness, we found that awareness and successful differential trace conditioning emerged concurrently (Manns, Clark, & Squire, 2000b). In other studies, informing participants about the stimulus contingencies before the conditioning session facilitated trace conditioning (Clark & Squire, 1999). In contrast, interfering with the development of awareness by distracting participants during the conditioning session prevented the acquisition of trace conditioning but not the acquisition of delay conditioning (Clark & Squire, 1999).

Finally, awareness that the CS predicts the US is important for single-cue trace conditioning (i.e., with a single CS), just as it is for differential conditioning. Participants who were aware of the stimulus contingencies exhibited better single-cue trace conditioning than participants who were not aware of this relationship (Manns, Clark, & Squire, 2000a). Furthermore, the degree of awareness after the first 10 conditioning trials predicted the overall success of trace conditioning across the entire conditioning session (Manns et al., 2000a).

These findings imply that in the case of trace conditioning, individuals who develop declarative knowledge of the stimulus contingencies may be successful because they expect the US when the CS is presented. In contrast, delay conditioning has the automatic and reflexive features that are characteristic of nondeclarative memory. Delay conditioning may therefore be a simple function of the associative strength between the CS and the US.

A method for evaluating the relative importance of expectancy and associative strength in delay eyeblink conditioning was described by Perruchet (1985). A sequence of trials was presented so that the US followed the CS only 50% of the time. Strings of one, two, three, or four CS-alone trials were intermixed with strings of one, two, three, or four CS-US trials. In this circumstance, expectancy of the US tended to increase during strings of CS-alone trials and to decrease during strings of CS-US trials, a phenomenon known as the gambler's fallacy. However, the probability of a CR was not related to US expectancy. Instead, CR probability mirrored the strength of the CS-US association. That is, CRs were more likely as the number of consecutive CS-US trials increased, and less likely as the number of consecutive CS-alone trials increased.

In contrast to delay conditioning, trace conditioning depends on declarative knowledge of the stimulus contingencies. If expectancy of the US is one aspect of this declarative knowledge, then in trace conditioning the probability of a CR might mirror the subjective expectancy of the US. Figure 1 illustrates how delay and trace conditioning might be influenced differently by the recent history of CS-alone and CS-US trials. In the experiment we report here, we used Perruchet's (1985) method to evaluate how expectancy of the US develops during both delay and trace eyeblink conditioning and to determine the relationship between expectancy and conditioned responding. The results demonstrate a fundamental contrast between these two forms of classical conditioning.

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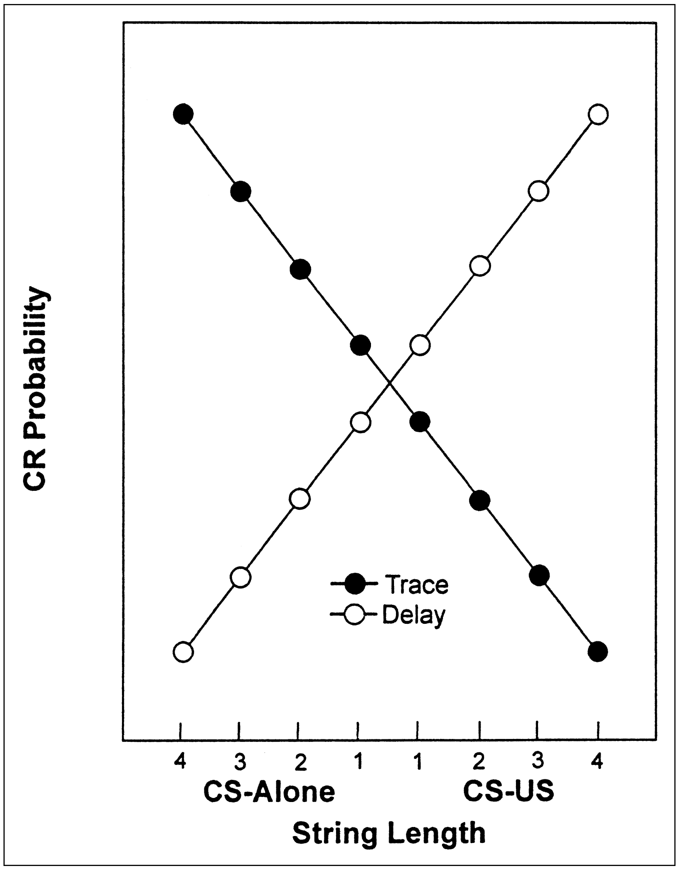

Fig. 1. Contrasting predictions of the probability of a conditioned response (CR) for delay (white circles) and trace (black circles) conditioning as a function of the recent history of CS-alone (conditioned stimulus alone) and CS-US (conditioned stimulus and unconditioned stimulus) trials (adapted from Perruchet, 1985).

METHOD

Participants

The participants were either students at the University of California, San Diego, who received credit toward a course requirement for their participation, or respondents to notices posted at the university. Participants were assigned to one of two groups. The first group (delay) consisted of 20 individuals (10 men and 10 women) who were given delay eyeblink conditioning. They averaged 24.0 years of age (range: 18–41) and 15.1 years of education. The second group (trace) consisted of 18 individuals (7 men and 11 women) who were given trace eyeblink conditioning. They averaged 21.7 years of age (range: 18–29) and 14.7 years of education.

Procedure

The procedure was modeled after one described by Perruchet (1985). Participants gave informed consent and then were seated in a darkened room, approximately 0.7 m in front of a computer monitor. One hundred fifty-six conditioning trials were administered. The CS was a 70-dB, 1-kHz tone presented through earphones. The US was a 100-ms, 2-psi airpuff delivered to the left eye through a nozzle attached to modified sunglasses that were worn by the participants. The sunglasses also held an infrared emitter detector for measuring eyeblinks.

Half the trials were CS-alone trials on which the US was omitted. On the other half of the trials, the CS was followed by the US. For the delay group, the US was presented (on half the trials) 1,250 ms after the onset of the CS. The CS and US then overlapped for 100 ms and co-terminated. When the US was omitted, the CS was presented alone for 1,350 ms. For the trace group, the CS was presented for 250 ms and was then followed by a 1,000-ms trace interval. At the end of the trace interval, the US was presented for 100 ms. When the US was omitted, the CS was presented alone for 250 ms.

Eyeblinks were scored as CRs when they occurred between 750 ms after the onset of the CS and before the onset of the US. This criterion was used to filter out nonassociative responding and voluntary responding (purposeful or volitional blinking; for a similar scoring method, see Daum et al., 1993; Finkbiner & Woodruff-Pak, 1991). For an eyeblink to be scored as a CR, the participant's maximum eyeblink amplitude in response to the CS had to be 20% of the same participant's maximum eyeblink amplitude in response to the first 10 US presentations of the session.

The 156 conditioning trials were presented as strings of one, two, three, or four CS-alone trials and an equal number of strings of one, two, three, or four CS-US trials (Table 1). Five different orders that met the conditions described in Table 1 were constructed. Within each order, the probability of a US was independent of string length. Each order was used four times within the delay group. For the trace group, three of the orders were used four times, and two were used three times.

At the beginning of the session, participants were told that an airpuff would be delivered on 50% of the trials. Before each trial, participants used a horizontal scale on a computer screen to indicate how likely or unlikely it was that an airpuff would be presented on the next trial. The scale contained seven evenly spaced hash marks. A plus sign appeared above the right-most hash mark, and a minus sign appeared above the left-most hash mark. Participants made their predictions by pressing one of two keys to move an indicator bar to the left or right along the scale (five key presses moved the indicator bar a distance of one hash mark). Participants were instructed to place the indicator bar on the center hash mark if they were completely unsure whether an airpuff would be delivered on the next trial. Alternatively, they were told to move the indicator bar toward the right the more sure they were that an airpuff would be presented, and toward the left the more sure they were that an airpuff would not be presented. The indicator bar could occupy any of 30 positions along the scale, and responses were scored from −3.0 (to reflect high confidence that the US would not appear) to +3.0 (to reflect high confidence that the US would appear). After making a prediction, which

Table 1. *Distribution of CS-alone and CS-US trials*

Parameter	CS-alone trials				CS-US trials			
String length	4	3	2	1	1	2	3	4
Number of strings	3	6	12	24	24	12	6	3
Number of trials	12	18	24	24	24	24	18	12

Note. String length refers to the number of consecutive trials with the conditioned stimulus (CS) alone or with paired presentations of both the CS and the unconditioned stimulus (US). The number of trials refers to the number of trials dedicated to each string length. A total of 156 trials was presented.

required 2 to 3 s, participants pressed the space bar to begin the next trial, which occurred 5 to 10 s later ($M = 7.5$ s). Thus, the intertrial interval was about 10 s, on average. At the completion of each trial, the indicator bar automatically reset to the center of the scale, where it remained until the participants made their next prediction.

Each prediction was recorded as a function of how long a string of CS-alone trials or CS-US trials had occurred when the prediction was made. Thus, a total of 6 predictions was recorded after string lengths of four (3 after strings of CS-alone trials and 3 after strings of CS-US trials; see Table 1). In the case of string lengths of three, a total of 18 predictions was recorded (6 after strings of three CS-alone trials, 6 after strings of three CS-US trials, plus 6 after the third trial of each string of four; see Table 1). Similarly, 42 predictions were recorded after string lengths of two (24 after string lengths of two, 12 after the second trial of each string of three, and 6 after the second trial of each string of four). Finally, 89 predictions were recorded after string lengths of one (the prediction made before the first trial was not recorded). Altogether, there were 156 trials, and 155 predictions were recorded (89 + 42 + 18 + 6).

RESULTS

Figure 2 shows the mean prediction scores for the two groups as a function of how many CS-alone or CS-US trials had just occurred. The finding of interest was that in both the delay and the trace group, participants were less likely to expect an airpuff to be delivered on the next trial if they had just experienced a series of trials in which an airpuff was delivered (CS-US trials). In addition, participants were more likely to expect an airpuff on the next trial if they had just experienced a series of trials in which an airpuff was not delivered (CS-alone trials). Moreover, the longer the string of immediately preceding CS-US (or CS-alone) trials, the more confident was the prediction that the next trial would not include (or include) the US; the linear trend across string lengths was significant for both the delay group, $F(1, 19) = 10.9, p < .01$, and the trace group, $F(1, 17) = 4.91, p < .05$. The effect of string length on predictions was similar in the two groups (Fs $<$ 1.31, ps $>$ .10, for the effect of group and the Group × String Length interaction). These findings extend the observations of Perruchet (1985), who used a similar procedure for studying delay conditioning. The findings for both delay and trace conditioning illustrate the phenomenon known as the gambler's fallacy.

Despite the fact that the predictions about the US made by the two groups were influenced in the same way by the recent history of CS-alone trials and CS-US trials, the CRs emitted by the two groups were influenced very differently. Figure 3 shows the median percentage of CRs as a function of string length. (Medians were used because the percentage of CRs at every string length was positively skewed.) For the delay group, conditioning performance reflected the recent strength of the CS-US association. That is, participants in the delay group were most likely to emit a CR when they had just experienced a consecutive series of CS-US trials. They were least likely to emit a CR when they had just experienced a consecutive series of CS-alone trials. Using the method of least squares, we determined the best linear fit for the delay group's medians in Figure 3. The slope of the best-fitting line was +1.96.

A randomization procedure (Edgington, 1987; Westfall & Young, 1993) was used to evaluate the delay group's performance statistically. We randomly sampled (with replacement) 10,000 different orders for the eight values in Figure 3, out of the 8! (40,320) possible ways in which these values could be ordered. A slope more extreme than the slope that we obtained (i.e., > +1.96) was obtained in fewer than 1% of the sampled orders. That is, using this procedure, the p value for the slope of the line fit through the data for the delay group in Figure 3 was .009. The same procedure was implemented two additional times, and p values of .010 and .009 were obtained.

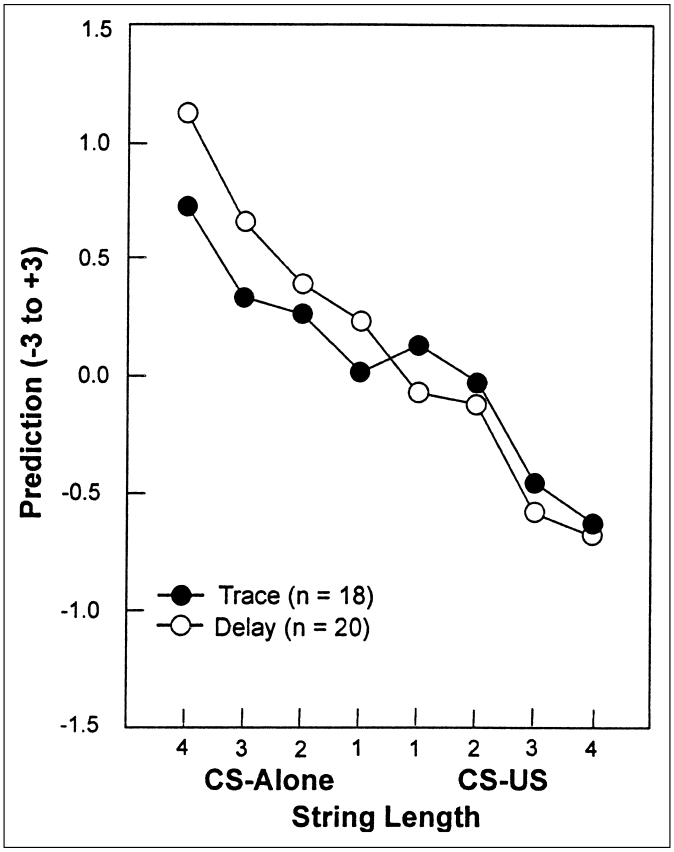

Fig. 2. Participants' judgments (on a scale from −3.0 to + 3.0) of how likely they thought it was that the airpuff unconditioned stimulus (US) would appear on the next trial. String length (1 to 4) refers to the number of consecutive trials, immediately prior to the trial on which a prediction was made, in which the conditioned stimulus (CS) alone had been presented or both the CS and the US had been presented. (The appearance of the US was in fact independent of string length.)

For the trace group, in contrast to the delay group, conditioning performance paralleled the predictions that were made about whether a US would appear on the next trial. That is, participants in the trace group were most likely to emit a CR on trials that they had predicted would include an airpuff. They were least likely to emit a CR on trials that they had predicted would not include an airpuff. Using the method of least squares, we determined that the best-fitting line for the medians in Figure 3 had a slope of −2.73. The same randomization procedure described for the delay group indicated that the slope obtained for the trace group was significant. On three implementations of this procedure, p values of .049, .050, and .050 were obtained.

Finally, the randomization procedure was used to determine if the delay and trace groups differed from each other with respect to the slopes of the lines that best fit their data. We randomly sampled with replacement from the total of 3.36×10^{10} possible combinations by which sets

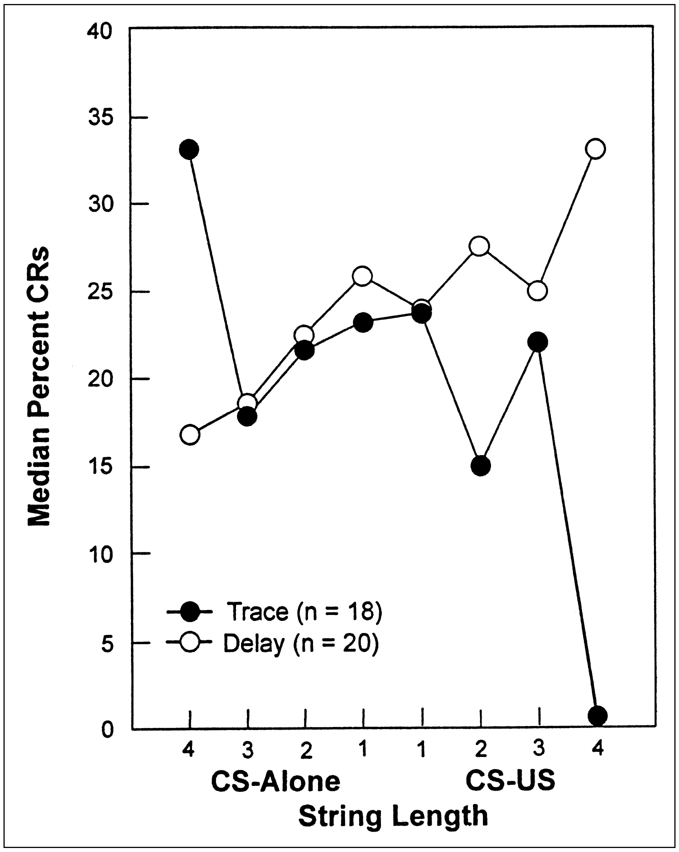

Fig. 3. Median percentage of conditioned responses (CRs) as a function of string length. String length refers to the number of consecutive trials, immediately prior to the trial on which a prediction was made, in which the conditioned stimulus (CS) alone had been presented or both the CS and the unconditioned stimulus (US) had been presented.

of eight data points (eight from each of 38 participants) can be partitioned into two different groups ($n = 20$ and $n = 18$). In 10,000 samples, an absolute difference in slopes greater than the observed difference (4.69) was obtained in fewer than 2.8% of the samples. That is, using this procedure, the two-tailed p value for the difference in slopes that we obtained was .0278. The randomization procedure was implemented two additional times, and p values of .027 and .034 were obtained.

The overall conditioning performance was similar in the two groups (25.8% and 23.0% for the delay and trace groups, respectively). (Medians were used because the distribution of percentage of CR scores was positively skewed in both groups.) The level of conditioning was relatively low overall, presumably because the US was omitted on half the trials. Thus, the CS-alone trials would have served as extinction trials and attenuated the strength of the CS-US association. In any case, even though the overall level of conditioning was similar for the delay and trace groups, the probability of emitting a CR was influenced differently in the two groups by the recent history of CS-alone and CS-US trials.

DISCUSSION

Participants in the delay and trace conditioning groups exhibited the same pattern of predictions when they were asked whether a US would occur on the next trial. In both groups, expectation of the US increased as the string length of CS-alone trials increased, and expectation of the US decreased as the string length of CS-US trials increased (Fig. 2). This pattern of predictions, which is known as the gambler's fallacy, occurred despite the fact that the probability of a US on each trial was unrelated to the string length. These results confirm Perruchet's (1985) finding for delay eyeblink conditioning and extend the results to trace conditioning.

The striking finding concerned how strings of CS-alone and CS-US trials affected conditioned responding (Fig. 3). As Perruchet (1985) found, participants given delay conditioning exhibited more CRs following longer runs of CS-US trials (i.e., acquisition of the CR was stronger), and they exhibited fewer CRs following strings of CS-alone trials (i.e., extinction of the CR was stronger). The finding that conditioned responding was influenced not by expectancy but by the recent frequency of CS-alone and CS-US trials provides particularly strong evidence that delay eyeblink conditioning in humans is an example of nondeclarative memory and is unrelated to awareness (Clark & Squire, 1998; Grant, 1973; Papka, Ivry, & Woodruff-Pak, 1997). This view of delay conditioning is similar to earlier accounts of classical conditioning that emphasized the importance of associative strength (Bush & Mosteller, 1951; Prokasy & Kumpfer, 1969).

The results from trace conditioning were opposite those from delay conditioning. Participants in the trace group exhibited more CRs following longer runs of CS-alone trials (when expectancy of the US was higher), and they exhibited fewer CRs following strings of CS-US trials (when expectancy of the US was lower). These findings show that trace conditioning was related to expectation of the US, that is, to the subjective belief that the US would occur. Thus, the results for trace conditioning are reminiscent of earlier accounts of classical conditioning that emphasized the importance of expectancy (Bolles, 1972; Bolles & Fanselow, 1980).

For delay conditioning, the results were closely related to the strength of the CS-US association. Indeed, this relationship was nearly monotonic (Fig. 3). The results for trace conditioning were opposite to those for delay conditioning and were related to expectation rather than to associative strength. However, the results for trace conditioning depended mainly on the long strings (four consecutive CS-alone trials and four consecutive CS-US trials), and there was little effect of string lengths of one, two, or three. Associative strength appears to increase with each consecutive CS-US trial, and to decrease with each consecutive CS-alone trial, and delay conditioning exhibits corresponding increments and decrements. By contrast, in the case of trace conditioning, expectation may need to exceed some threshold for performance to be affected.

The present findings can be understood in terms of the declarative and nondeclarative memory systems that support eyeblink classical conditioning. In both delay and trace conditioning sessions, participants sometimes develop declarative (conscious) knowledge about the stimulus contingencies and sometimes do not. For delay conditioning, declarative knowledge is superfluous to the acquisition of the CR (Clark & Squire, 1998, 1999; Papka et al., 1997). Results from studies in the rabbit indicate that the cerebellum and associated brain stem structures are necessary and sufficient to accomplish delay eyeblink conditioning and that conditioning can in fact proceed normally in the absence of the forebrain (Thompson & Krupa, 1994). Further, patients with cerebellar lesions are deficient at delay eyeblink conditioning (Daum et al., 1993).

Trace conditioning also depends on the cerebellum (Woodruff-Pak, Lavond, & Thompson, 1985) but is additionally dependent on the hippocampus (Kim, Clark, & Thompson, 1995; McGlinchey-Berroth, Carrillo, Gabrieli, Brawn, & Disterhoft, 1997; Moyer, Deyo, & Disterhoft, 1990; Solomon, Vander Schaaf, Thompson, & Weisz, 1986). Unlike delay conditioning, trace conditioning depends on acquiring declarative knowledge (or awareness) of the CS-US contingencies (Clark & Squire, 1998, 1999; Manns et al., 2000a, 2000b) and is strongly influenced by whether the US is expected (present study). Most forms of declarative knowledge develop together with awareness. Thus, declarative knowledge may develop naturally whenever the hippocampus and related structures are engaged in their normal function of binding together the elements of an episode for long-term memory storage (Eichenbaum & Cohen, 2000; Squire, 1992). In this view, trace conditioning requires the hippocampus (and declarative knowledge) because the trace interval between the CS and the US makes it difficult to process the CS-US relationship in an automatic, reflexive way. Instead, the neocortex is required to represent the CS-US relationship, and the hippocampus and related structures work conjointly with the neocortex to achieve the representation.

Although hippocampal-cortical interaction (and declarative knowledge) promotes the development of the CR in the cerebellum, this knowledge or expectancy does not appear to directly drive or produce the CR. Two findings support the idea that the cerebellum itself drives the CR, and that the hippocampal formation provides input that the cerebellum needs. First, in a recent study that tracked trial-by-trial awareness during differential trace conditioning (Manns et al., 2000b), participants pressed a button when they believed the US was about to occur. As a group, participants came to exhibit highly reliable differential button pushes in excess of 90% (percentage of button pushes in response to the CS+ minus percentage of button pushes in response to the CS−). Yet button-press performance was far better than differential eyeblink responses, which never exceeded 45% as a group. Thus, trace eyeblink CRs did not result directly from knowing that the US was about to occur. Second, in the present study, the level of CR responding for the trace group was related to expectation of the US, but was nevertheless not highly correlated with the prediction score on a trial-by-trial basis (mean point biserial correlation across participants = .04).

We suggest that in the case of trace conditioning, the cerebellum is responsible for the acquisition, storage, and generation of the CR, and the hippocampal formation provides input to the cerebellum that is essential for the acquisition process. One possibility is that the hippocampus provides temporally shifted information to the cerebellum so that the CS and US arrive at the cerebellum in the temporally overlapping fashion that the cerebellum can use. In this view, declarative knowledge of the CS-US contingencies (Clark & Squire, 1998), the ability to predict the US (Manns et al., 2000b), and expectancy of the US (present study) are all good indicators that the hippocampal system is effectively engaged by the task and working with the cerebellum so that the cerebellum can generate the CR.

Acknowledgments—This work was supported by the Medical Research Service of the Department of Veterans Affairs, National Institute of Mental Health Grant MH 24600, the National Alliance for Research on Schizophrenia and Depression (NARSAD), and the Metropolitan Life Foundation. We thank Craig Stark, Mark Appelbaum, and Shauna Stark for assistance.

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(RECEIVED 9/7/00; ACCEPTED 10/24/00)