Classical conditioning, awareness, and brain systems

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Memory is composed of several different abilities that are supported by different brain systems. The distinction between declarative (conscious) and nondeclarative (non-conscious) memory has proved useful in understanding the nature of eyeblink classical conditioning – the best understood example of classical conditioning in vertebrates. In delay conditioning, the standard procedure, conditioning depends on the cerebellum and brainstem and is intact in amnesia. Trace conditioning, a variant of the standard procedure, depends additionally on the hippocampus and neocortex and is impaired in amnesia. Recent studies have sharpened the contrast between delay and trace conditioning by exploring the importance of awareness. We discuss these new findings in relation to the brain systems supporting eyeblink conditioning and suggest why awareness is important for trace conditioning but not for delay conditioning.

Memory is not a single faculty of the mind but is composed of different abilities that depend on different brain systems [1–3]. A fundamental distinction is between the capacity for conscious recollection of facts and events (declarative memory) and nondeclarative memory, which supports skill and habit learning and other forms of memory that are expressed through performance rather than recollection. Declarative memory depends on the integrity of the hippocampus and related structures and supports the flexible use of acquired knowledge; nondeclarative memory is supported by other brain systems.

In the past few years, the distinction between declarative and nondeclarative memory has proved useful in understanding the nature of classical conditioning. Classical conditioning is a simple form of associative learning that has been studied extensively in vertebrate and invertebrate animals [4–6]. The best-understood example of classical conditioning in vertebrates is conditioning of the eyeblink response [7,8].

In eyeblink classical conditioning a neutral conditioned stimulus (CS), such as a tone, is presented just before an unconditioned stimulus (US), such as a mild puff of air to the eye. After repeated pairings of the CS and the US, the CS elicits a learned or conditioned eyeblink response (CR) in advance of the US. The two most commonly studied forms of eyeblink conditioning are delay and trace conditioning (Fig. 1). In delay conditioning, the CS is presented and remains on until the US is presented. The two stimuli then overlap and co-terminate. In trace conditioning, an empty (or trace) interval separates the CS and US.

This review of classical conditioning and awareness focuses on delay and trace eyeblink classical conditioning for two reasons. First, the neural substrates of eyeblink conditioning are better understood than any other form of conditioning in the vertebrate. Second, the cognitive aspects of both delay and trace conditioning, including the role of awareness, have been more systematically investigated in the case of eyeblink conditioning than in other forms of classical conditioning. The conditioned eyeblink is an example of an aversively conditioned somatic motor response. The response is a highly specific motor movement that becomes adaptively timed to the presentation of the US. In other types of conditioning, like fear conditioning and autonomic conditioning, the conditioned response to the CS involves a broad change in emotional state. Further, unlike eyeblink conditioning, which depends especially on the cerebellum (as described in the next section), fear and autonomic forms of classical conditioning depend importantly on the amygdala. Systematic studies of fear and autonomic conditioning, in the context of awareness and delay and trace paradigms, could be of great interest (for studies of awareness and delay conditioning, see [9,10]; for studies of conditioning with subliminal CSs, see [11]).

Brain substrates for delay and trace eyeblink conditioning

Work with rabbits first demonstrated a clear distinction between delay and trace eyeblink conditioning. The acquisition and retention of delay eyeblink conditioning require the cerebellum and associated brainstem structures [12]; no forebrain structures (including the hippocampus) are required. Thus, decerebrate rabbits with no remaining forebrain tissue (i.e. after removal of cerebral cortex, basal ganglia, limbic system, thalamus, and hypothalamus) exhibited normal retention of delay eyeblink conditioning [13]. A putative circuit has been identified that includes the essential CS and US pathways, the regions where these pathways converge within the cerebellum to form the essential plasticity underlying the conditioned response, and the pathway that expresses the conditioned response [8]. Findings in humans are consistent with the animal work. Thus, delay eyeblink conditioning was impaired in patients with cerebellar [14–16] or brainstem lesions [17], but was intact in amnesic patients with damage that includes the hippocampus (and spares the cerebellum) [18,19]. Because delay conditioning is independent of the forebrain,

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and intact in amnesia, it appears to be a quintessential example of nondeclarative memory.

Like delay conditioning, successful trace eyeblink conditioning requires the cerebellum [20]. However, trace conditioning differs from delay conditioning in that it also requires the hippocampus and neocortex. Thus, acquisition and retention of trace conditioning were severely disrupted in rabbits and rats when the hippocampus was damaged [21–24]; and trace conditioning in rabbits was disrupted by damage to prefrontal cortex [25–27]. Again, findings in humans are consistent. In amnesic patients with damage that includes the hippocampus, trace eyeblink conditioning was mildly impaired with a trace interval of 500 ms and severely impaired with a trace interval of 1000 ms [28]. The effect of hippocampal damage is a function of the trace interval itself and does not occur because the interstimulus interval (ISI) is longer than in delay conditioning. For example, the same patients who exhibited impaired trace conditioning when the ISI was as short as 600 ms [28] performed normally in a delay paradigm with an ISI of 750 ms [19]. Another distinctive feature of trace conditioning is that the importance of the hippocampus is time-limited. When hippocampal lesions were made in rabbits 1 day after acquisition, trace conditioning was abolished, whereas lesions made 30 days after acquisition had no effect [21]. Thus, trace conditioning exhibits two important characteristics of declarative memory. First, trace conditioning requires the hippocampus. Second, in trace conditioning, as in other forms of declarative memory, the hippocampus has a time-limited role [29].

The difference between delay and trace eyeblink conditioning has recently been brought into sharper focus by studies that have explored the importance of awareness. Declarative memory typically includes knowledge (or awareness) about what has been learned. By contrast, nondeclarative memory does not require awareness of any memory content and, when awareness is present, it appears to be epiphenomenal to task performance [30]. With respect to eyeblink conditioning, the questions of interest are: When conditioning occurs, do individuals become aware of the relationship between the CS and US; namely, that the CS precedes and predicts the US? Is awareness of the stimulus contingencies necessary for successful conditioning to occur? Does the importance of awareness differ for delay and trace conditioning? These questions have a long history, focusing on delay conditioning and assessments of awareness through interview [31,32]. More recent studies have involved both delay and trace conditioning, either single-cue conditioning or differential conditioning (see below), and also more objective methods for assessing awareness. In addition, recent studies have often involved older individuals (50 to 80 years of age), who do not become aware of the CS–US relationship as readily as the young adults who are usually studied. If all participants became aware, the importance of awareness could not be evaluated.

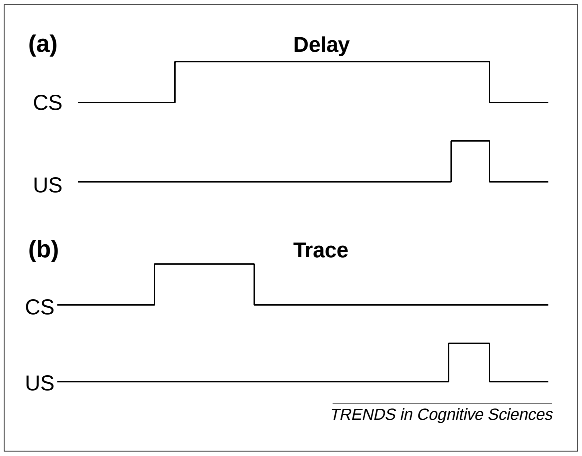

Fig. 1. Schematic representation of delay classical conditioning and trace classical conditioning. (a) In delay conditioning, the conditioned stimulus (CS) (for example a tone) is presented and remains on (upwards deflection) until the unconditioned stimulus (US) is presented (for example a puff of air to the eye). The two stimuli then overlap and co-terminate. (b) In trace conditioning, the CS is presented and then terminated. A silent or trace interval then follows before the presentation of the US. Single-cue conditioning involves a single CS, as illustrated here. Differential conditioning involves a CS^+ (e.g. a tone), which precedes the US, and a $CS^–$ (e.g. a static noise), which occurs in the absence of the US.

Awareness and differential eyeblink conditioning

In delay and trace differential conditioning, the CS^+ (e.g. a tone) is followed by the US whereas the $CS^–$ (e.g. a static noise) is presented alone. Successful differential conditioning occurs when more CRs are elicited by the CS^+ than by the $CS^–$. In differential conditioning, the participant can in principle learn several different facts about the stimulus contingencies (for example, the CS^+ predicts the US, the $CS^–$ does not predict the US, and the CS^+ and $CS^–$ are unrelated), and knowledge (awareness) of all these facts can be assessed.

Individuals (mean age = 67 years) were given a 17-item, true or false test [33] after conditioning (e.g. '*I believe the tone usually came immediately after the static noise*'). From this test, awareness (initially defined as a score ≥13 correct; chance = 8.5 correct; probability of a score ≥13 occurring by chance, $P = 0.05$) was found to be important for successful trace conditioning but not for successful delay conditioning [34]. Only those participants who became aware of the temporal contingencies of the conditioning stimuli successfully acquired differential trace conditioning. Further, four amnesic patients, who had damage that included the hippocampus bilaterally, failed to become aware and also failed to acquire differential trace conditioning (Fig. 2a). By contrast, in the case of differential delay conditioning, awareness of the stimulus contingencies had no relationship to acquisition of the differential conditioned response. That is, participants who did not become aware conditioned as well as participants who did become aware.

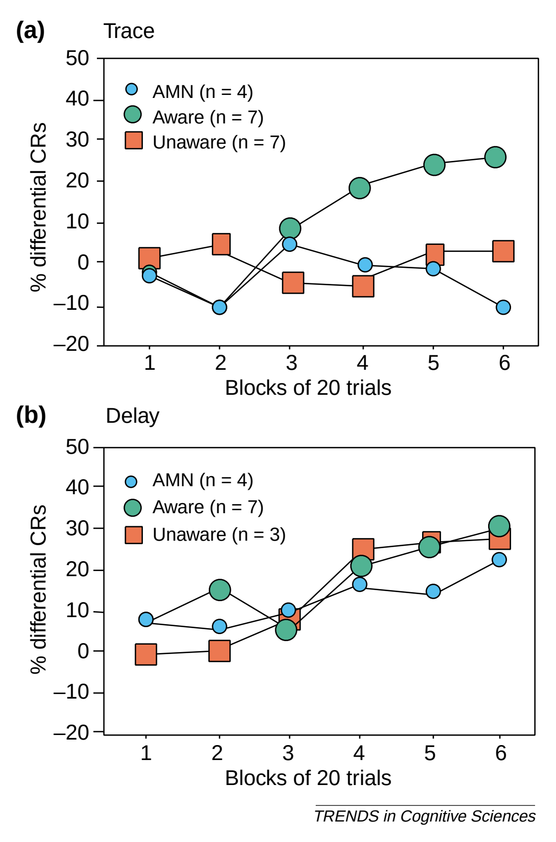

Fig. 2. Percentage of differential conditioned responses (CRs) across six blocks of 20 trials for participants given differential trace conditioning (a) and differential delay conditioning (b). For trace conditioning, a trace interval of 1000 ms was interposed between a 250 ms conditioned stimulus (CS) and a 100 ms unconditioned stimulus (US). For delay conditioning, the CS remained on for 1250 ms before co-termination with the 100 ms US. Green circles indicate participants who became aware of the stimulus contingencies (≥13 out of 17 items correct on a post-conditioning questionnaire; chance = 8.5), red squares indicate participants who failed to become aware, and blue circles show the performance of four amnesic (AMN) patients with bilateral damage to the hippocampal formation. For differential trace conditioning, only the participants who became aware of the stimulus contingencies exhibited successful acquisition (for blocks 4–6, the aware subjects performed greater than chance and better than the unaware and amnesic patients; all *P*s < 0.05). For differential delay conditioning, awareness was unrelated to successful acquisition, and the amnesic patients also conditioned normally [34].

In addition, the same amnesic patients who could not acquire trace conditioning acquired delay conditioning at a normal rate (Fig. 2b). Even when a more generous criterion was adopted for designating participants as aware (>9 questions out of 17 correct), the results were identical: those designated as unaware conditioned as well as those who were designated as aware [35].

In related studies, also with older participants, awareness was manipulated directly by fully explaining the stimulus contingencies before conditioning [33]. The explanation facilitated trace conditioning and also improved post-conditioning awareness scores (participants obtained 16.0 items correct on the 17-item questionnaire versus 13.3 items correct when no explanation was given; Fig. 3a). Other participants were asked to engage in a secondary (distraction) task during the conditioning session. Specifically, they saw a sequence of single digits (one every 1.5 s for a 1-s duration) throughout the session and pressed a button whenever they saw three consecutive odd digits. These individuals failed to develop awareness (9.1 items correct out of 17) and also failed to exhibit differential trace conditioning (Fig. 3b). By contrast, participants given this same distraction task during differential delay conditioning performed as well as participants who were not distracted (Fig. 3c).

In the case of successful differential trace eyeblink conditioning, the question arises of whether awareness of the stimulus contingencies precedes, follows, or parallels the acquisition of differential trace conditioning. This question was addressed using a trial-by-trial (‘on-line’) measure of awareness during the course of differential trace conditioning [36]. Specifically, participants (mean age = 67 years) were asked to push a button whenever they believed the US was about to appear. With this procedure, differential button pushes (that is, pushes following the CS^+ but not the $CS^−$) provide direct evidence that the stimulus contingencies have been identified. Figure 4 shows the percentage of differential responses across the conditioning session for button presses and conditioned eyeblink responses. Successful differential trace eyeblink conditioning and awareness of the stimulus contingencies emerged approximately in parallel. However, the percentage of differential button presses reached much higher levels than the percentage of differential eyeblink responses. This observation suggests that awareness was not directly causing the conditioned eyeblinks. One way to understand the relationship between awareness and trace conditioning follows from the finding that successful trace conditioning depends on the cerebellum [20]. The contribution of the cerebellum to differential trace eyeblink conditioning apparently progresses to the asymptote more slowly than the development of voluntary button pushes. The button pushes are limited only by developing awareness of the stimulus contingencies.

Remaining issues concerning differential eyeblink conditioning

These studies suggest that awareness of the stimulus contingencies is important for successful differential trace conditioning but is unnecessary for differential delay conditioning. Nevertheless, it is possible to construct differential delay conditioning protocols where awareness is related to successful conditioning. Particularly interesting are two studies where tones (800 Hz and 2100 Hz), rather than a tone and static noise, served as the CS^+ and $CS^−$. Individuals who were identified as aware of the stimulus contingencies performed better than those who were identified as unaware [37,38]. Distractor tasks also reduced conditioning performance independently of their effects on awareness (also see [39]). Importantly,

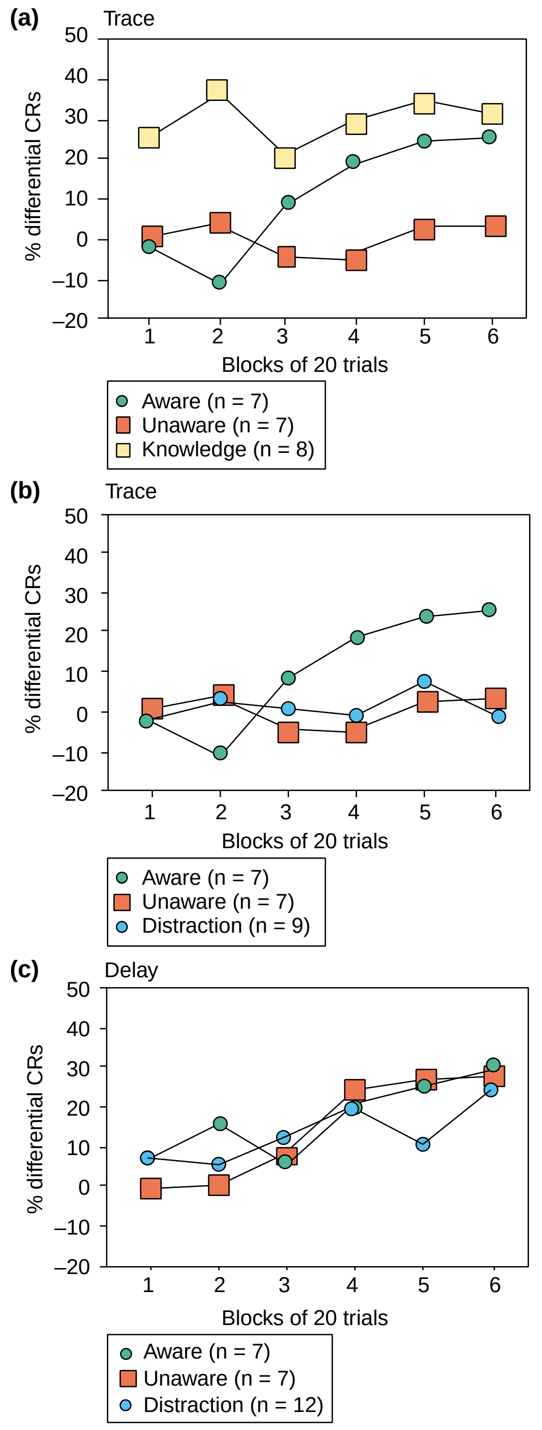

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Fig. 3. Percentage of differential conditioned responses (CRs) across six blocks of 20 trials for participants given differential trace conditioning (a,b) and differential delay conditioning (c). The groups labeled 'Aware' and 'Unaware' in the three panels are replotted from Fig. 2. (a) Shows that participants who were made aware of the stimulus contingencies before conditioning (Knowledge, yellow squares) performed better than the 14 participants (Aware and Unaware) who were not given any explicit information about the stimulus contingencies. Performance of the Knowledge group approximated the performance of the seven participants who on their own became aware of the stimulus contingencies during the conditioning session. (b) Shows that participants who were prevented from becoming aware by a concurrent distraction task during trace conditioning (blue circles) performed like participants who did not become aware. (c) Shows that participants who were prevented from becoming aware by a concurrent distraction task during differential delay conditioning (blue circles) conditioned successfully.

although unaware participants did perform more poorly than aware participants in each task condition, those designated unaware nevertheless achieved a substantial level of differential conditioning performance in the no-distraction condition (35.8% CRs; [37]; compare with Fig. 2b). In any case, it appears that under some conditions awareness can be important for differential delay conditioning.

One possibility is that awareness is relevant to differential delay conditioning only when the two cues are relatively similar to each other. Interestingly, neither intact nor hemispherectomized cats were able to acquire differential delay conditioning with 800-Hz and 2100-Hz tones [40], the same cues used in the human studies that found awareness to be important [37,38]. Yet differential conditioning was successful in intact and operated cats when a 2100-Hz tone and static noise were used, and also when more distinct tone pairs were used (100 vs 1000 Hz and 200 vs 3000 Hz). In addition, rabbits with hippocampal lesions acquired differential delay conditioning at a normal rate when distinct tones served as stimuli (1000 Hz versus 10 000 Hz) [41]. Note also that our studies of differential delay conditioning in humans, which found awareness to be irrelevant [33,34], used a tone and static noise as conditioned stimuli.

Despite this evidence that differential delay conditioning can be acquired without awareness when the cues are distinct (and can also be acquired at normal rates in hemispherectomized cats and rabbits with hippocampal lesions when the cues are sufficiently different), awareness was recently reported to correlate with differential delay conditioning even when a tone and static noise served as stimuli [42] (contrast this with Figs 2b and 3c). An issue that is potentially relevant to all studies of eyeblink conditioning concerns the difficulty in identifying voluntary eyeblink responses and distinguishing them from conditioned responses [43,44]. If voluntary eyeblinks sometimes occurred in response to the CS^+, and were scored as true CRs, then the performance of aware individuals (who would be capable of voluntary eye closures) would necessarily be better than the performance of unaware individuals (who would not exhibit voluntary eye closures). It is not clear that voluntary responses were a factor in this recent study [42]. However, according to classical criteria for identifying voluntary responses (early onset, large amplitude, response maintained until the US, no increase in amplitude with onset of the airpuff US [43]), the average responses illustrated in figure 3 of that study [42] have the characteristics of voluntary eyeblinks. Additional studies of differential delay conditioning under different cue conditions will be helpful.

It is also noteworthy that subsequent work from the same group [45] found that eight amnesic patients

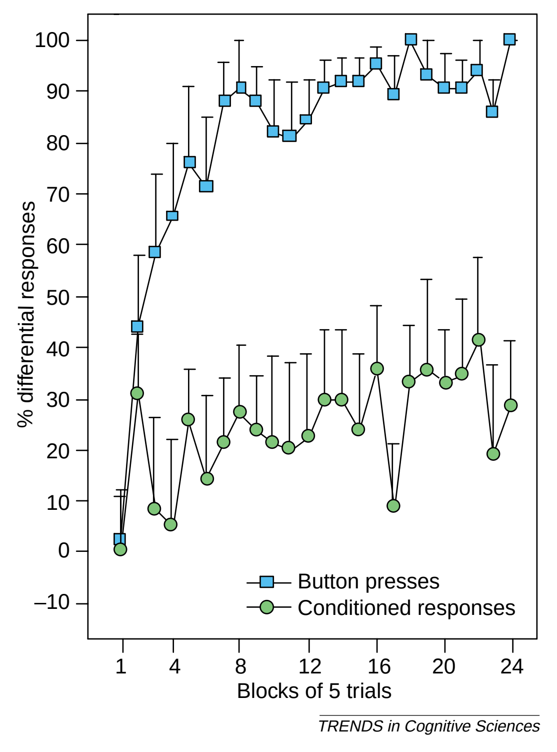

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Fig. 4. Percentage differential button presses (presses to the CS^+ minus presses to the CS^-) and percentage differential conditioned responses (eyeblinks elicited by the CS^+ minus eyeblinks elicited by the CS^-) during trace eyeblink conditioning ($n = 14$). During the conditioning session participants pressed a button whenever they thought the unconditioned stimulus (US) was about to appear. Awareness of the stimulus contingencies and differential trace eyeblink conditioning developed approximately in parallel. Lines show the standard error of the mean.

with hippocampal lesions acquired differential delay conditioning (1000-Hz and 5000-Hz tones) nearly as well as controls, in agreement with our earlier report [34]. Further, four patients who were reported to develop some declarative knowledge (awareness) about the task conditioned no better than the remaining patients who did not. These findings support the idea that differential delay conditioning can proceed automatically and reflexively, and that awareness can be epiphenomenal to successful conditioning.

Awareness and single-cue eyeblink conditioning

In single-cue conditioning, only one CS is presented, and the level of conditioning is determined by the number of trials in which a CR occurs. The relationship of awareness to single-cue conditioning was not evaluated systematically in earlier studies of eyeblink conditioning because most participants (especially the young adults typically studied) became aware of the simple contingency (the CS predicts the US). Nevertheless, early investigators viewed single-cue delay conditioning as simple and straightforward, and unrelated to awareness [31,32]; subsequent studies reached the same conclusion [46–48]. As single-cue trace conditioning seems nearly as simple and straightforward as single-cue delay conditioning, it is natural to ask what the role of awareness in single-cue trace conditioning is?

Participants (aged 47–78 years) were given single-cue trace conditioning (tone CS, 1000 ms trace interval) while watching a silent movie or while performing an attention-demanding digit-monitoring task. Participants who watched the movie emitted more CRs, and also performed better on a 7-item post-conditioning questionnaire that assessed awareness, than participants who were distracted by the digit-monitoring task [49]. Other participants (aged 51–75 years) watched the silent movie during single-cue conditioning and took the 7-item questionnaire after the first 10 conditioning trials, again after 60 trials, and finally after all 120 trials were completed. Those who became aware of the CS–US relationship early in the session (after 10 trials) conditioned to a greater extent than those who became aware of the relationship later in the session or who never became aware at all (Fig. 5a). Further, performance on the questionnaire after the first 10 conditioning trials predicted the magnitude of single-cue trace conditioning over the entire 120-trial conditioning session (Fig. 5c) [49]. In a similar study of single-cue trace conditioning, individuals aged 15–30 years who were designated as aware after the session produced more conditioned responses during the first 10 conditioning trials than those designated unaware [50].

Unlike these findings for single-cue trace conditioning, awareness was found to be unrelated to single-cue delay conditioning. Thus, participants (aged 50–76 years) who became aware of the stimulus contingencies early in the conditioning session conditioned no better than participants who became aware later in the session or who did not become aware (Fig. 5b) [51]. Further, there was no relationship between awareness scores obtained early in conditioning and the magnitude of conditioning across the 120-trial conditioning session (Fig. 5d) [51].

Expectancy of the US and delay and trace conditioning

The findings reviewed here suggest that delay and trace eyeblink conditioning are fundamentally different kinds of learning. Successful trace conditioning is related to the development of awareness (declarative knowledge) about the stimulus contingencies. By contrast, successful delay conditioning is unrelated to the development of awareness, at least in standard delay (or differential) paradigms where the CS (or the CS^+ and CS^-) can be processed easily. Individuals who develop awareness of the stimulus contingencies might be successful at trace conditioning because they have acquired a representation that allows them to expect the US when the CS is presented.

A method for evaluating the relationship of expectancy to conditioning performance was developed by Perruchet [52]. A sequence of trials is presented such that the US follows the CS only 50% of the time. Strings of one, two, three or four CS-alone

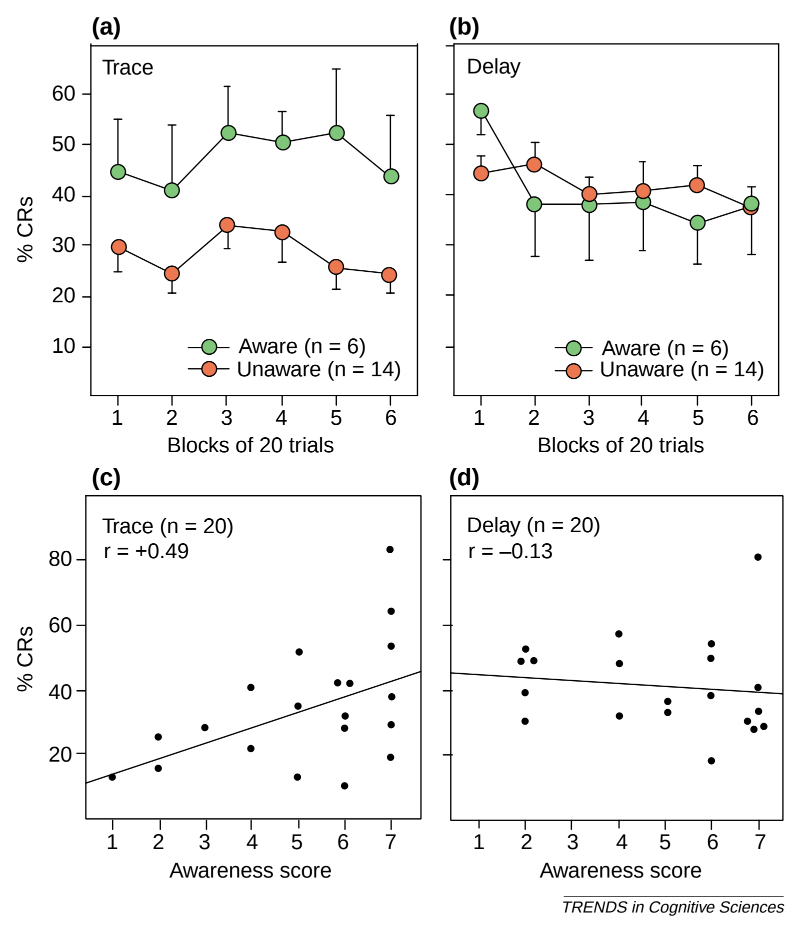

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Fig. 5. (a) Trace conditioning: percentage conditioned responses (CRs) across six blocks of 20 trials by participants who were classified as aware or unaware after the first 10 trials on the basis of their answers to seven true or false questions given after the first 10 trials. (b) Delay conditioning: percentage CRs across six blocks of 20 trials by participants who were classified as aware or unaware after the first 10 trials on the basis of their answers to the same seven questions. Lines show the standard error of the mean. (c,d) Relationship between the awareness score obtained after the first 10 trials and the strength of conditioning (percentage CRs) across all 120 conditioning trials: (c) performance of participants who received trace conditioning ($r = 0.49$, $P < 0.05$); (d) performance of participants who received delay conditioning ($r = –0.13$, $P > 0.1$).

trials are intermixed with strings of one, two, three or four CS–US trials. Before each trial, participants are asked to rate how much they ‘expect’ the US (airpuff) to appear on the next trial. In this circumstance, expectancy of the US increases during strings of CS-alone trials and decreases during strings of CS–US trials, a phenomenon known as the gambler’s fallacy. For example, a string of CS-alone trials increases the expectation that a US will occur on the next trial, despite the fact that the probability of a US is always 50%.

For individuals presented with single-cue delay conditioning trials, the probability of a CR was dissociated from expectancy and instead mirrored the strength of the CS–US association [52]. That is, CRs became more likely as the number of consecutive CS–US trials increased and became less likely as the number of consecutive CS-alone trials increased. Using this same method, we compared the performance of participants given delay conditioning to the performance of those given trace conditioning [53]. For both groups, expectancy of the US varied in accordance with the gambler’s fallacy. Figure 6 shows the percentage of conditioned responses as a function of the recent history of CS-alone and CS–US trials. The findings for delay conditioning fully confirmed the findings reported previously [52]. That is, the probability of a CR was related not to expectancy but to the associative strength of the CS and US. The results for trace conditioning were the opposite: The probability of a CR was positively related to expectancy of the airpuff US. That is, CR probability was high when expectancy of the US was high and low when expectancy of the US was low. These findings show that expectation of the US has a different role in trace conditioning than in delay conditioning and support the idea that trace conditioning and delay conditioning are fundamentally different in their dependence on higher-order cognitive processes like awareness. Accordingly, these data demonstrate the inadequacy of unitary views of classical conditioning that propose awareness to be important for all conditioned performance [54].

Conclusion

The studies outlined above can be understood in terms of the declarative and nondeclarative memory systems that support eyeblink classical conditioning. In both delay and trace conditioning paradigms, individuals sometimes develop declarative (conscious) knowledge about the stimulus contingencies, and sometimes do not. For the most commonly studied forms of delay conditioning, declarative knowledge is superfluous to the acquisition of the CR and conditioned performance can be supported by cerebellar and brainstem circuits [12]. Trace conditioning is fundamentally different. It resembles delay conditioning in that it also depends on the cerebellum [20], but it is additionally dependent on the hippocampus [21–24,28] and neocortex [25–27]. Further, unlike delay conditioning, trace conditioning is strongly related to the acquisition of declarative knowledge (awareness) of the CS–US contingencies and to the degree to which the US is expected.

We suggest that the cerebellum is responsible for the acquisition, storage and generation of the conditioned response in both trace and delay conditioning. Trace conditioning might additionally require declarative knowledge because the trace interval makes it difficult for the cerebellum to process the CS and the US and form a motor memory. Electrophysiological studies have not detected activity in the cerebellum for longer than 100 ms following the termination of a single input pulse [55]. In trace conditioning, because the US follows the CS by as much as 1000 ms, the cerebellum might not be able to maintain a representation of the CS across the trace interval. If, however, the hippocampus and neocortex have represented the stimulus contingencies, then it is possible that processed

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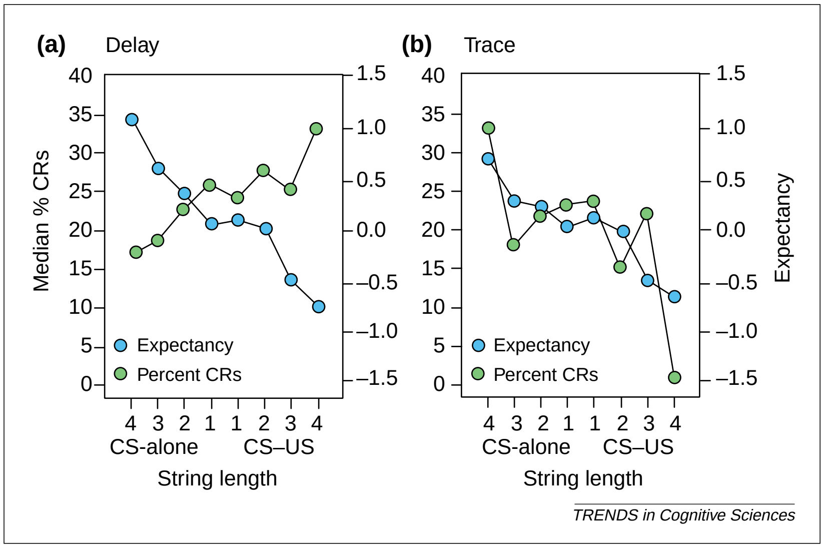

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Fig. 6. The relationship between expectancy of the unconditioned stimulus (US) and conditioning performance for delay (a) and trace (b) conditioning. Blue circles indicate each group's expectancy of the US (on a –3 to +3 scale) as a function of the recent history of conditioned stimulus (CS)-alone and CS–US trials. 'String length' refers to the number of consecutive trials, immediately before the trial on which a prediction was made, in which the CS had been presented alone or both the CS and the US had been presented. For both delay and trace conditioning, the subjective expectation of the US was highest after four CS-alone trials and lowest after four CS–US trials. Green circles indicate the median percentage of conditioned responses (CRs) as a function of the recent history of CS-alone and CS–US trials. The performance of the group given delay conditioning ($n = 20$) was inversely related to expectation of the US. Thus, the probability of a CR was related to the associative strength of the CS and US (highest after a string of paired CS–US trials and lowest after a string of CS-alone trials). The results for trace conditioning ($n = 18$) were opposite. That is, conditioning performance mirrored the expectation of the US. CR probability was highest when expectation of the US was highest and lowest when expectation of the US was lowest.

information about the CS can be transmitted to the cerebellum at a time during each trial that is optimal for cerebellar plasticity (immediately before and during the US). Thus, an interesting possibility is that in trace conditioning the cerebellum receives reformatted information, such that CS and US information arrive at the cerebellum in the temporally overlapping fashion that the cerebellum can use. By this view, awareness of the contingencies, although not directly driving the acquisition of the conditioned response by the cerebellum, serves as an indicator that the hippocampus and related structures are effectively engaged by the task and working with the cerebellum so that the trace conditioned response can be acquired.

The close correspondence of findings in humans and experimental animals suggests that the characteristics of eyeblink classical conditioning and its neural substrates are highly similar across vertebrate species. The advantage of studies with humans is that the cognitive aspects of conditioning can readily be related to performance. As it becomes possible to identify more precisely the circumstances when knowledge of the stimulus contingencies (i.e. awareness) is crucial for conditioning, it also becomes possible to specify when the same or similar cognitive processes are likely to be occurring in experimental animals. The advantage of studies with experimental animals is that they are amenable to electrophysiological investigations, permanent and reversible lesions to selected anatomical areas, and molecular methods for manipulating genetically identifiable populations of neurons. Such work would seem to hold great promise for animal studies that could then be interpreted not only with respect to traditional topics like learning and memory, but within a larger framework of higher cognitive functions like awareness. These ideas are only now beginning to be addressed as legitimate problems for experimental neuroscience [56].

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The dynamics of standing balance

Ramesh Balasubramaniam and Alan M. Wing

The control of standing is a complicated task that involves the action of muscles distributed over the whole body. Forces arising from gravity, external events or our own actions all tend to disturb the unstable equilibrium that preserves posture. For the central nervous system the problem of standing can be cast in terms of finding appropriate relations among body segments to maintain the desired position of the body as a whole with respect to the environment. In this review we evaluate some recent discoveries on the effects of predictable and unpredictable perturbations, and the role of perceptual information, attention and cognitive processes in the control of upright stance.

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Standing straight is not as simple a task as one might think. It involves keeping several distributed joints and muscle groups in a geometric relationship with respect to the environment. Except for soldiers commanded to do so, most of us are always doing something else when we stand. When disturbed from an upright standing position we typically use certain strategies to recover balance and these strategies are almost always affected by what we are doing at that time (anything from walking the dog to singing in the shower). In this article we will review some recent developments in posture control studies that have shed some light on cognitive and perceptual factors that can affect balance in various contexts and environments.

Posture is defined as the geometric relation between two or more body segments (e.g. arm-trunk). The relation is expressed in terms of joint angle(s) between segments (e.g. ankle and knee angles describe the posture of the leg). A complete geometry defining the posture of the whole body should include the relation of the body to the environment (e.g. body relative to support surface) [1,2]. An issue for the central nervous system is that posture must be actively maintained because joints between body segments are free to move under external forces. The external force field might be constant (e.g. gravity), or variable (e.g. the pull of a boisterous dog on a leash). The effect of several simultaneous external forces acting around any given joint can be characterised in

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