Biological Psychology 87 (2011) 393–400

Contents lists available at ScienceDirect

Biological Psychology

journal homepage: www.elsevier.com/locate/biopsycho

Awareness is necessary for differential trace and delay eyeblink conditioning in humans

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ARTICLE INFO

Article history:
Received 2 September 2010
Accepted 2 May 2011
Available online 14 May 2011

Keywords:
Eyeblink conditioning
Awareness
Learning
Delay
Trace

ABSTRACT

Squire et al. have proposed that trace and delay eyeblink conditioning procedures engage separate learning systems: a declarative hippocampal/cortical system associated with conscious contingency awareness, and a reflexive sub-cortical system independent of awareness, respectively (Clark and Squire, 1998; Smith et al., 2005). The only difference between these two procedures is that the conditioned stimulus (CS) and the unconditioned stimulus (US) overlap in delay conditioning, whereas there is a brief interval (e.g., 1 s) between them in trace conditioning. In two experiments using the same procedure as Clark and Squire's group, we observed differential conditioning only in participants who showed contingency awareness in a post-experimental questionnaire, with both trace and delay procedures. We interpret these results to suggest that, although there may be multiple brain regions involved in learning, these regions are organized as a coordinated system rather than as separate, independent systems.

1. Introduction

A popular view of human behavior proposes two independent and competing systems, one that is unconscious, intuitive, parallel and automatic, and another that is conscious, reflective, serial and verbal. In the case of associative learning, it is almost universally believed that conditioning, particularly Pavlovian conditioning, is carried out by a reflexive, unconscious mechanism that is quite distinct from higher cognitive processes associated with language and conscious contingency learning. However, empirical reviews of human associative learning have shown that there is surprisingly little evidence for dual learning systems organized along these lines. Conditioned responding is closely associated with conscious awareness of contingencies, is sensitive to verbal and reasoning manipulations, and is impaired by cognitive load (Brewer, 1974; Dawson and Schell, 1985; Lovibond and Shanks, 2002).

An apparent exception to this pattern is the evidence presented by Clark et al. that differential Pavlovian eyeblink conditioning with a delay procedure (in which the conditioned stimulus, CS, and the unconditioned stimulus, US, overlap in time) can be observed in participants who show no conscious awareness of the CS-US contingency (Clark and Squire, 1998, 1999; Smith et al., 2005). By contrast, these researchers have found that eyeblink conditioning with a trace procedure (in which there is a temporal gap between CS and US) is only observed in participants who are aware of the CS-US contingency (see Fig. 1). They have interpreted this data pattern as supporting Squire's (1994) distinction between declarative learning, mediated by a conscious hippocampal/cortical circuit, and non-declarative learning, mediated by an unconscious cerebellar/sub-cortical circuit.

In Clark and Squire's procedure, participants were shown a silent movie and told that they would be asked questions about the movie after it had finished. Superimposed on this task were presentations of two auditory stimuli, a tone and white noise, as well as presentations of an airpuff to one eye. A differential conditioning design was used in which one of the auditory stimuli (CS+) was always paired with the airpuff US, whereas the other stimulus (CS−) was always presented alone. Eyeblink conditioned responses (CRs) were recorded with an infrared reflective system. After 120 trials (60 each of CS+ and CS−, intermixed), participants were given a post-experimental awareness questionnaire that assessed their conscious knowledge of events in the silent movie as well as the differential contingency between the two CSs and the US. Using this procedure, Clark and Squire have found that trace conditioning is only observed in participants classified as contingency aware, whereas delay conditioning is observed both in participants classified as aware and those classified as unaware (Clark and Squire, 1998, 1999; Smith et al., 2005).

Lovibond and Shanks (2002) drew attention to several limitations of the research by Clark and Squire's group and the conclusions that could be drawn from it. In particular, they criti-

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doi:10.1016/j.biopsycho.2011.05.002

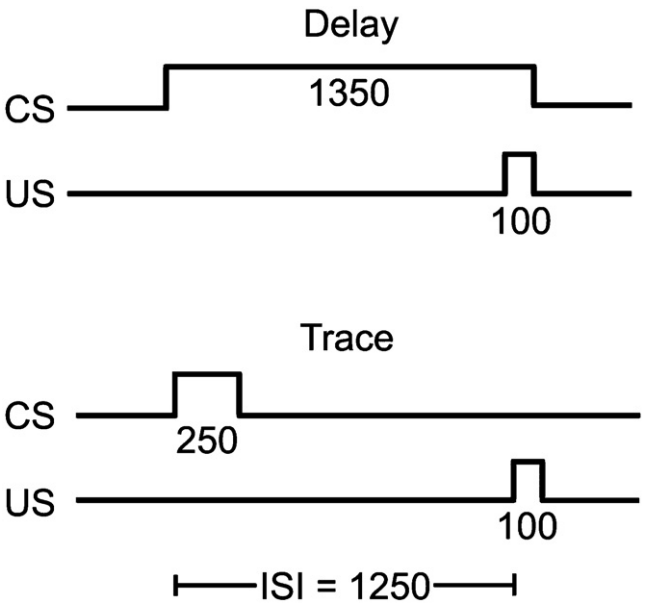

Fig. 1. Temporal parameters used for Delay conditioning (top panel; Experiments 1 and 2) and Trace conditioning (lower panel; Experiment 2). The ISI was 1250 ms for both procedures.

cized the questionnaire used to assess contingency awareness as long, confusing and insensitive. If so, the questionnaire might have wrongly classified participants who were actually aware of the differential contingency as unaware, leading to apparent unaware conditioning (see Shanks and St John, 1994, for further discussion of measurement of conscious knowledge). Lovibond and Shanks noted that other researchers had found an association between awareness and delay eyeblink conditioning (e.g., Baer and Fuhrer, 1982; Benish and Grant, 1980; Nelson and Ross, 1974; Perry et al., 1977). Two subsequent studies have also shown an association between differential delay eyeblink conditioning and contingency awareness (Bellebaum and Daum, 2004; Knuttinen et al., 2001).

In response, Squire et al. have defended their original data, and pointed out differences in the procedures used by other researchers that may account for the different outcomes they obtained. Manns et al. (2002) noted that the earlier studies had used CSs that were complex in nature, such as grammaticality (Baer and Fuhrer, 1982; Benish and Grant, 1980; Perry et al., 1977), or that were more difficult to discriminate than their own white noise and tone stimuli, such as the tones of 800 and 2100 Hz used by Nelson and Ross (1974). They suggested that in these cases CS discrimination may have required higher level analysis that would be unavailable to a low-level conditioning system. In the case of the Knuttinen et al. (2001) study, Manns et al. (2002) noted that these researchers had not excluded "voluntary" eyeblink responses. By contrast, Clark et al. had routinely excluded responses with early onset and high magnitude, on the basis of a suggestion by Spence and Ross (1959) that such a pattern is diagnostic of a strategic or voluntary source of responding. Smith et al. (2005) also pointed out that unaware participants in the Knuttinen et al. study showed little responding to either CS+ or CS−, in contrast to the usual finding that participants who fail to discriminate between CS+ and CS− show CRs to both stimuli. They noted that the auditory CSs used by Knuttinen et al. (2001) were of low amplitude (75 db), and they raised the possibility that the EEG electrodes used to record eyeblink responses may have interfered with CR production. Finally, Clark and Squire (2004) noted that Bellebaum and Daum (2004) had used a conditional discrimination procedure rather than a simple differential contingency, which they suggested may have required the involvement of forebrain systems associated with consciousness.

The question of whether there are two distinct learning/memory systems is a pivotal one in behavioral neuroscience research, with major consequences for both theoretical understanding and practical application. Accordingly, we wished to collect additional data using the differential eyeblink conditioning procedure, in an effort to resolve the inconsistencies in the available evidence. Specifically, we wished to replicate the design used by Clark et al. as closely as possible, but using a more sensitive questionnaire to assess contingency knowledge. Our hypothesis was that a shorter, more sensitive questionnaire would assess conscious knowledge more accurately, and perhaps allow an association between awareness and conditioning to be observed in delay conditioning as well as trace conditioning.

We also took advantage of the opportunity to investigate two further factors that may have contributed to the data pattern reported by Clark et al. First, we noted that they used a severe restriction on trial order such that there could be no more than two consecutive trials of the same type (CS+ or CS−). For example, after two CS− trials in a row, the next trial was always a CS+. It is possible that some participants may have learned this pattern, allowing them to predict the outcome of trials following a run of two trials. Such participants would have been able to show above-chance discrimination even if they were unaware of the differential CS-US contingency. The plausibility of such trial sequence learning has been demonstrated by Wiens et al. (2003) in autonomic fear conditioning. A second factor that may have influenced the data observed by Clark et al. is the verbal and nonverbal behavior of the experimenter at the time of questionnaire administration. If the experimenter, inadvertently or otherwise, communicated that the primary focus of the study was memory for the silent movie, then participants may not have been motivated to think carefully about the questions concerning the "distracter" stimuli, the CSs and USs (see Dulany, 1968). Experiment 1 was designed to address both of the above possibilities.

2. Experiment 1

The first experiment was modeled on the procedure used by Clark and Squire (1998) and Smith et al. (2005). We used the same silent movie that they used as a background task, the same stimuli as CSs (1000-Hz tone and white noise), and the same method for measuring eyeblink (infrared reflectance). We informed participants, as they did, that the study was concerned with the effect of distraction (sounds and airpuffs) on learning and memory (for the movie). We chose an inter-stimulus interval (ISI) of 1250 ms, as this was the ISI used in the majority of experiments reported by Clark and Squire (1998) and Smith et al. (2005). Experiment 1 employed a delay conditioning procedure (see Fig. 1, upper panel).

In order to further explore the knowledge acquired by participants, we developed a new shorter questionnaire to assess contingency knowledge as well as trial sequence knowledge. All participants completed both the new questionnaire and the original questionnaire used by Clark and Squire, in counterbalanced order. Finally, we divided participants into two groups that differed in the instructions given at the end of the experiment, just before administration of the two questionnaires. Participants in the Movie group received instructions that emphasized the importance of the questions pertaining to the silent movie, consistent with the original experimental instructions. Participants in the Contingency group, by contrast, were told that the experiment was actually about the "distracter" stimuli (sounds and airpuffs), and were asked to think carefully about those stimuli when completing the questionnaires.