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Potentiation of the startle reflex is in line with contingency reversal instructions rather than the conditioning history

Gaëtan Mertens*, Jan De Houwer

Department of Experimental Clinical and Health Psychology, Ghent University, Henri Dunantlaan 2, 9000 Ghent, Belgium

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ABSTRACT

In the context of fear conditioning, different psychophysiological measures have been related to different learning processes. Specifically, skin conductance responses (SCRs) have been related to cognitive expectancy learning, while fear potentiated startle (FPS) has been proposed to reflect affective learning that operates according to simple associative learning principles. On the basis of this two level account of fear conditioning we predicted that FPS should be less affected by verbal instructions and more affected by direct experience than SCRs. We tested this hypothesis by informing participants that contingencies would be reversed after a differential conditioning phase. Our results indicate that contingency reversal instructions led to an immediate and complete reversal of FPS regardless of the previous conditioning history. This change was accompanied by similar changes on US expectancy ratings and SCRs. These results conform with an expectancy model of fear conditioning but argue against a two level account of fear conditioning.

1. Introduction

Fear conditioning is an adaptive process through which organisms learn to fear and avoid a conditioned stimulus (CS) that has been paired with an aversive event (unconditioned stimulus, US). This is usually modeled in the lab by pairing neutral stimuli (lights, geometric shapes) with an unpleasant but harmless electric stimulus. For humans, fear conditioning is often believed to be mediated by the generation of cognitive expectancies about the occurrence of the US in the presence of the CS (e.g., Lovibond & Shanks, 2002; Mitchell, De Houwer, & Lovibond, 2009; Reiss, 1980). However, according to the two level account of human fear conditioning (e.g., Hamm & Weike, 2005; Öhman & Mineka, 2001; Sevenster, Beckers, & Kindt, 2012a), this cognitive contingency learning between the CS and the US is supplemented with affective learning. Affective learning is proposed to be a highly automatic process, taking place independent of cognitive contingency learning (Baeyens, Eelen, & Crombez, 1995; Hamm & Weike, 2005; Mineka & Öhman, 2002; Öhman & Mineka, 2001) and mediated by a specifically dedicated neural system centered on the amygdala (Mineka & Öhman, 2002; Öhman & Mineka, 2001).

These two forms of learning have been mapped onto different physiological responses (Hamm & Weike, 2005). Conditioned skin conductance responses (SCRs) are usually considered to reflect cognitive contingency learning about the occurrence of the aversive US in the presence of the CS (e.g., Dawson & Furedy, 1976; Lovibond & Shanks, 2002). This hypothesis is supported by studies showing that conditioning of the SCRs only occurs when participants are aware of the CS–US contingencies (e.g., Dawson, 1970; Dawson & Furedy, 1976; Sevenster, Beckers, & Kindt, 2014; Singh, Dawson, Schell, Courtney, & Payne, 2013) and that conditioned SCRs are very sensitive to verbal instructions (Hugdahl, 1978; Luck & Lipp, 2015b; Sevenster et al., 2012a). Conditioned potentiation of the startle reflex (or fear potentiated startle, FPS), on the other hand, is believed to primarily reflect affective learning. Evidence for this idea was provided by studies suggesting that conditioning of the startle reflex does not require awareness of the CS–US contingency (Hamm & Weike, 2005; Hamm & Vaitl, 1996; Sevenster et al., 2014) and that FPS is less sensitive to verbal instructions (Dawson, Rissling, Schell, & Wilcox, 2007; Sevenster et al., 2012a). Furthermore, in a number of recent psychopharmacological studies, FPS was abolished by the administration of propranolol during a reconsolidation period while leaving expectancy of the US and SCRs intact, demonstrating a strong dissociation between FPS and cognitive measures of conditioned fear (Kindt, Soeter, & Vervliet, 2009; Soeter & Kindt, 2010). However, the evidence is not unequiv-

* Corresponding author. Fax: +32 9 264 64 89.
E-mail address: Gaetan.Mertens@UGent.be (G. Mertens).

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ocal. For instance, in a number of other studies, conditioning of the startle reflex was obtained only for participants who became aware of the CS–US contingencies (Dawson, Rissling et al., 2007; Grillon, 2002; Jovanovic et al., 2006; Purkis & Lipp, 2001).

In the current study, we tested a different prediction that follows from the proposal that FPS reflect automatic affective learning. That is, if FPS primarily reflects simple associative learning, it should primarily be a function of the past stimulus pairings (i.e., conditioning history; Lipp & Purkis, 2005) and should be relatively insensitive to verbal instructions about future stimulus pairings (Mineka & Öhman, 2002; Sevenster et al., 2012a). To test this hypothesis, we made use of the contingency reversal procedure (Grings, Schell, & Carey, 1973; McNally, 1981; Wilson, 1968). In this procedure, participants are informed after a differential conditioning phase that the contingencies of the first phase will be reversed in a second phase. Consequently, in this second phase, cognitive contingency information as provided by the verbal instructions is directly opposed to what has been learned through CS–US pairings in the first phase. If learning is a function of experienced stimulus pairings, conditioned responses in the second phase should be in line with the conditioning history of the first phase. However, if learning is the result of cognitive beliefs regarding the CS–US contingency, conditioned responses should be in line with the verbal instructions, regardless of the conditioning history. In previous studies employing this procedure with SCRs as the measure of conditioning (Grings et al., 1973; McNally, 1981; Wilson, 1968), conditioning in the second phase of the experiment was in line with the verbal instructions and no evidence for effects of past stimulus pairings was obtained.

In a recent study by Costa, Bradley, and Lang (2015), fear was installed in a first phase by providing threat information to participants. In a second phase, one of the threatened CSs was instructed to be safe, while the other threatened CS remained a threatening stimulus. Similarly, for the initially safe CSs, one of these was threatened, while the other CS remained safe. This adapted reversal procedure allowed them to compare reversed and non-reversed CSs after the reversal instructions and thus controlled for time-related changes (e.g., habituation, sensitization) that could explain the reversal effect. Costa et al. (2015) found that fear reactions, including FPS, completely reversed on the basis of verbal contingency instructions, which demonstrates that FPS is very sensitive to cognitive information (see also: Grillon, Ameli, Woods, Merikangas, & Davis, 1991). However, conditioned responses in their study were instantiated only via verbal threat instructions and not by direct conditioning. Therefore, pairings of the CS in close proximity to the US were absent in the study of Costa et al. (2015), possibly excluding simple associative learning as the result of actual stimulus pairings (Blair, Schafe, Bauer, Rodrigues, & LeDoux, 2001). Hence, it is possible that affective learning did not take place in the study of Costa et al. (2015) due to the absence of CS–US pairings (see also: Olsson & Phelps, 2007, 2004). Therefore, in the current study, we set out to investigate whether FPS to a threatened CS can be reversed on the basis of verbal instructions, even when this CS has actually been paired with the US. Furthermore, we included threatened, but not actually conditioned CSs in our experiment to conceptually replicate the results of Costa et al. (2015) and to compare reversal on these CSs to reversal of threatened CSs that have been actually paired with the US. In line with the hypothesis that FPS reflects affective learning, we predicted that reversal of conditioned responses would be less pronounced for FPS than for SCR and ratings of US expectancy when threat instructions are combined with direct CS–US pairings.

Table 1
Overview of the different CS types.

CS	Relationship with the US	Contingency reversal?
CS+T/P	Threatened + paired	No
R-CS+T/P	Threatened + paired	Yes
CS+T	Threatened	No
R-CS+T	Threatened	Yes
CS-	Safe	No
R-CS-	Safe	Yes

2. Method

2.1. Participants

Thirty-six right-handed students (11 men, 25 women) at Ghent University participated in the experiment in exchange for €8. Age ranged between 18 and 32 years (M = 21.44, SD = 2.66). Psychophysiological data from one participant was lost due to a recording error. All participants completed an informed consent form and were instructed that they could discontinue the experiment at any point without any negative consequences. This study was approved by the ethics committee of the Faculty of Psychology and Educational Sciences of Ghent University.

2.2. Material

2.2.1. Conditioned stimuli

CSs were six white geometric shapes (circle, square, triangle, pentagon, trapezium and diamond) with a maximal radius, longitude and/or latitude of 300 pixels presented in the middle of a 17 in. Dell computer screen (resolution: 1024 by 768 pixels) with a black background. Assignment of these shapes to the different CS types (see Table 1) was randomized over participants.

2.2.2. Unconditioned stimulus

The US was an electric stimulus that consisted of 10 rectangular pulses of 2 ms with and inter pulse interval of 8 ms, creating an electric stimulus of 100 ms. This stimulus was administered by two lubricated Fukuda standard Ag/AgCl electrodes (1-cm diameter; inter-electrode distance: ~2-cm) to the left leg over the retromalleolar course of the sural nerve. The stimulus was generated by a constant current stimulator (DS7A, Digitimer, Hertfordshire, UK). The intensity of the electric stimulus was determined for each participant individually to be unpleasant but not painful using a stepwise work-up procedure (see Section 2.6 for details concerning this work-up procedure).

2.3. Psychophysiology

2.3.1. Skin conductance responses (SCRs)

SCRs were collected using a Coulbourn V71-23 skin conductance coupler (Coulbourn Instruments, Allentown, PA) and disposable Ag/AgCl electrodes (3 M Red Dot 2259–50, 17 mm diameter) attached to the thenar and hypothenar eminences of the non-dominant hand. The signal was measured using a constant voltage coupler (0.5 V) and digitized at 10 Hz. The collected data were smoothed and further analyzed offline with Psychophysiological Analysis (PSPHA) (De Clercq, Verschuere, De Vlieger, & Crombez, 2006). SCRs were calculated by subtracting the mean value of a baseline period (2 s before CS onset) from the highest amplitude within a 1–7 s interval after CS onset (Milad, Orr, Pitman, & Rauch, 2005; Pineles, Orr, & Orr, 2009; Raes, De Houwer, De Schryver, Brass, & Kalisch, 2014; Soeter & Kindt, 2012). In this scoring method, negative values and values smaller than 0.02 μS were scored as zero. Finally, collected SCRs were range corrected with the highest recorded amplitude for that participant to account for individual differences in responsivity (Lykken & Venables, 1971) and square