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Impact of observational and direct learning on fear conditioning and generalization in humans

Running title: social learning shapes fear generalization

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Impact of observational and direct learning on fear conditioning and generalization in humans

Abstract

Humans gain knowledge about threats not only from their own experiences but also from observing others' behavior. A neutral stimulus is associated with a threat stimulus for several times and the neutral stimulus will evoke fear responses, which is known as fear conditioning. When encountering a new event that is similar to one previously associated with a threat, one may feel afraid and produce fear responses. This is called fear generalization. Previous studies have mostly focused on fear conditioning and generalization based on direct learning, but few have explored how observational fear learning affects fear conditioning and generalization. To the best of our knowledge, no previous study has focused on the neural correlations of fear conditioning and generalization based on observational learning. In the present study, 58 participants performed a differential conditioning paradigm in which they learned the associations between neutral cues (i.e., geometric figures) and threat stimuli (i.e., electric shock). The learning occurred on their own (i.e., direct learning) and by observing other participant's responses (i.e., observational learning); the study used a within-subjects design. After each learning condition, a fear generalization paradigm was conducted by each participant independently while their behavioral responses (i.e., expectation of a shock) and electroencephalography (EEG) results were recorded. The shock expectancy ratings showed that observational learning, compared to direct learning, reduced the differentiation between the conditioned threatening stimuli and safety stimuli and the increased shock expectancy to the generalization stimuli. The EEG indicated that in fear learning, threatening conditioned stimuli in observational and direct learning increased early discrimination (P1) and late motivated attention (late positive potential [LPP]), compared with safety conditioned stimuli. In fear generalization, early discrimination, late motivated attention, and orienting attention (alpha-event-related desynchronization [alpha-ERD]) to generalization stimuli were reduced in the observational learning condition. These findings suggest that compared to direct learning, observational learning reduces differential fear learning and increases the generalization of fear, and this might be associated with reduced discrimination and attentional function related to generalization stimuli.

Keywords: observational learning, fear conditioning, fear generalization, event-related potentials, alpha-band oscillations

1. Introduction

Individuals receive multiple strands of information in society, either by learning themselves (i.e., direct learning) or by learning from others (i.e., indirect learning). The indirect learning of a threat is regarded as vicarious or observational learning. Such learning contains survival value, as dangers can be avoided without directly encountering them (Lindström et al., 2016). However, excessive exposure to indirect threats can lead to anxiety and psychological stress (Mauri et al., 2011; Vannucci et al., 2017).

The Pavlovian fear-conditioning paradigm (Pavlov, 1927) has been used extensively in recent years as an effective anxiety disorder model in both humans and animals (Lissek et al., 2005; Indovina et al., 2011). In a differential conditioning procedure, a neutral stimulus (threat conditioned stimulus [CS+], e.g., a geometric figure) is paired with an unconditioned stimulus (US) (e.g., a shock), whereas another neutral stimulus (safety conditioned stimulus [CS-]) is not paired with the US. Differential learning, which means the discrimination between threat and safety stimuli in a fear conditioning procedure, is calculated by the conditioned responses [CR] (e.g., fear responses) to CS+ minus CS- (Duits et al., 2015; Dvir et al., 2019; Lau et al., 2008). The impaired differential learning has been reported in some anxiety disorders (e.g., generalized anxiety disorder [GAD] and panic disorder) and is mainly due to the increased fear responses to the CS- (Cooper et al., 2018; Lissek et al., 2009; Lissek et al., 2014). Moreover, Duits et al. (2015) provide the view that the increased fear responses to the CS- in patients with some anxiety disorders might be associated with the excessive fear generalization. A new stimulus, perceptually resembling a previously experienced threat stimulus, can also evoke fear responses. This transfer of conditioned fear is called fear generalization. As the perceptual similarity between generalized stimuli and CS+ decreases, the fear response induced by generalized stimuli also decreases. These decreasing fear responses form a curve and are known as a generalization gradient (Dunsmoor & Murphy, 2015; Hovland 1937; Lissek et al., 2008; Pavlov, 1927). More specifically, a flatter generalization gradient indicates increased generalization. In contrast, a steeper gradient indicates less generalization (Norrholm et al., 2014). Previous studies have provided evidence that overgeneralization could be an important contributor to the development and maintenance of exaggerated fear and anxiety

(Dymond et al., 2015), particularly GAD (Lissek et al., 2014), panic disorder (Lissek et al., 2009), and post-traumatic stress disorder (Kaczkurkin et al., 2016). However, some studies have not found overgeneralization in patients with GAD (e.g., Tinoco-González et al., 2015). Understanding the association between observational fear learning and fear generalization is of significant clinical interest. To our knowledge, only one study has explored whether observational fear learning influences fear generalization using a behavioral method (Selbing & Olsson, 2019), and no previous study has investigated the neural correlates of fear generalization after direct and observational learning.

The present study explored whether the two ways of learning, observational and direct fear learning, differently affect fear learning and whether they influence subsequent fear generalization differently. To this end, we adopted a modified fear-conditioning paradigm with pairs of participants who took turns being "demonstrator" (i.e., direct learning) and "observer" (i.e., observational learning) in a counterbalanced manner in a within-subjects design. Both the demonstrator and observer independently completed the fear generalization paradigm. We also investigated the effects of empathy and empathic pain on observational learning. Brain's event-related potentials (ERPs), belonging to a high temporal resolution neural recording method, were measured to record the demonstrator's and observer's neural activities during fear learning and generalization.

The two-stage model of sensory information processing of conditioned stimuli in fear learning has been supported by previous event-related potential (ERP) studies (Ferreira et al., 2019; Schupp et al., 2006). In the first stage, the visual P1 component, peaking at approximately 100 ms post-stimulus latency at the occipital electrode sites, is relevant to early discrimination of threat and safety stimuli (Keil et al., 2012; Linton & Levita, 2021; Pizzagalli et al., 2003). The P1 results in fear learning and generalization studies are, however, mixed. A few studies have reported an enhancement of P1 amplitudes for CS+ and generalization stimuli compared with CS- (Bublatzky & Schupp, 2012; Pizzagalli et al., 2003; Roesmann et al., 2020). However, the enhancement effect of the P1 amplitudes on threat stimuli in fear learning and generalization has not been found in other studies (Lei et al., 2021; Nelson et al., 2015). In the second stage (later than 300 ms after stimulus onset), selective attention to the stimuli with motivational significance is regarded as "motivated attention" (Lang et al., 1997). The late positive potential (LPP) is regarded as an important ERP component reflecting motivated attention (Ferreira et al., 2019; Schupp et al., 2006). Conditioned fear stimuli as well as generalization stimuli have been found to evoke increased LPP amplitudes compared to safety stimuli (Keil et al., 2012; Roesmann et al., 2020). In addition to LPP, occipital alpha-event-related desynchronization (alpha-ERD, 8–12 Hz) has been reported to be associated with the ventral attention network, which consists of the temporal-parietal junction and right ventrolateral prefrontal cortex, and the alpha-ERD indicates orientation attention to the threat object (Corbetta & Shulman, 2002). In fear conditioning and generalization (Miskovic & Keil, 2012: Yin et al., 2020), ERD has been associated with the ventral attention system, reflecting orienting attention to the generalization stimuli. Until now, it remains unclear whether observational learning and direct learning differently affect preferential discrimination of threat conditioned stimuli or generalization stimuli in the first stage (as reflected by P1), and whether these stimuli attract motivated attention (i.e., LPP) and orienting attention (i.e., ERD) in the second stage.

Empathy, an ability to anticipate and share others' emotional states, may shape observational fear learning (Keum & Shin, 2019; Olsson et al., 2007; Pelligra, 2011; Rak et al., 2013). Indeed, previous studies have found connections between anxious state transmission and empathy (Janus & Goldberg, 1995; Vachon & Lynam, 2016). Similarly, findings in mice indicated that the transformation of fear and subsequent learning requires the involvement of empathy (Jeon et al., 2010; Keum et al., 2016). However, whether empathy shapes observational learning in humans remains unclear (Olsson et al., 2016; Rak et al., 2013; Williams & Conway, 2020). On the one hand, Olsson et al. (2016) manipulated the empathy levels of participants in an observational learning task by using high or low empathy instructions. They found that participants in the high empathy instruction condition showed higher conditioned responses to CS+ than those in the low empathy instruction condition in a following test. On the other hand, some other studies did not find a relationship between empathy and observational fear learning (Pärnamets, Espinosa, & Olsson, 2020; Williams & Conway, 2020).

The connections between fear learning and pain have been discussed for a long time (for reviews, see Meulders, 2020; Zaman et al., 2015). Furthermore, fear transmission from one person to another may also rely on pain (Goubert et al., 2013). It has been suggested that pain includes two different categories: empathic and nociceptive pain (Zaki et al., 2016). Empathic pain is the pain that arises from observing actual or threatened tissue damage in another person (Zaki et al., 2016). Empathic pain has also been found to be activated during observational fear learning (Jeon et al., 2010; Olsson et al., 2007). For instance, Olsson et al. (2007) reported that in an observational fear learning task, participants who observed others receiving aversive stimuli showed activation in pain-related brain areas, such as the anterior insula (AI) and anterior cingulate cortex (ACC). Although the pain-related brain areas are activated during observational learning (Jeon et al., 2010; Olsson et al., 2007), it is still unclear whether self-reported empathic pain positively correlates with observational learning.

This experiment had four hypotheses. First, we hypothesized that compared with direct learning, observational learning reduces the differentiation between shock expectancy ratings of CS+ and CS-. Second, based on previous findings (Egorova et al., 2015), we hypothesized that fear generalization is greater for observational learning than for direct learning. Specifically, for the behavioral results, we anticipated that the shock expectancy ratings in response to the generalization stimuli would increase because of the decreased discrimination between CS+ and CS- in differential observational fear learning. Third, based on a previous finding (Pizzagalli et al., 2003), we expected that early discrimination of generalization stimuli (P1), late motivated attention (LPP), and late orientation attention (ERD) to generalization stimuli would weaken after observational learning compared with direct learning. Forth, based on a previous study (Rak et al., 2013), we expected that experienced empathy and empathic pain to the demonstrator would positively correlate with the differentiation between shock expectancy ratings to CS+ and CS- in observational learning.

2. Methods

2.1 Participants

Gpower (version 3.1.9.4) (Faul et al., 2009) was used to calculate the priori simple size with a within-design repeated ANOVA for behavioral and EEG data ($\eta_p^2 = 0.06$, power = 0.80, alpha-level = 0.05, number of repeated measurements = 2, correlation among the repeated measurements = 0.1). The required sample size produced from Gpower was 58.

The inclusion criteria for the study were self-reported right-handedness, normal or corrected-to-normal vision, no history of neurological or psychological disorders, and no head injury with possible neurological sequelae. All participants carefully read the safety statements and provided informed consent. The experimental protocol was approved by the Medicine Ethics Committee of Shenzhen University.

Sixty-two adults (28 male and 34 female) aged 20.3 ± 1.3 years (range 18–23 years) participated in the present study. The participants were recruited from the student body of Shenzhen University through social media and posters. None of the participants knew each other before the experiment. Participants received 80 RMB (approximately 12 € and 12 USD) as compensation for their time. 58 participants' data were included in the analysis (please see 2.3. for details).

2.2. Questionnaires

Before the laboratory experiments, participants completed the state-trait anxiety inventory investigating state anxiety and trait anxiety (STAT) (Spielberger, 2010; subscales included state anxiety inventory and trait anxiety inventory); Beck's depression inventory-II investigating depressive symptoms (BDI-II) (Beck et al., 1996); the Liebowitz social anxiety scale (LSAS) investigating social anxiety symptoms (Heimberg et al., 1999, subscales included LSAS_fear and LSAS_avoidance) and the pain sensitivity questionnaire (PSQ) investigating pain sensitivity based on self-reported pain perception of imagined painful contexts (Ruscheweyh et al., 2009).

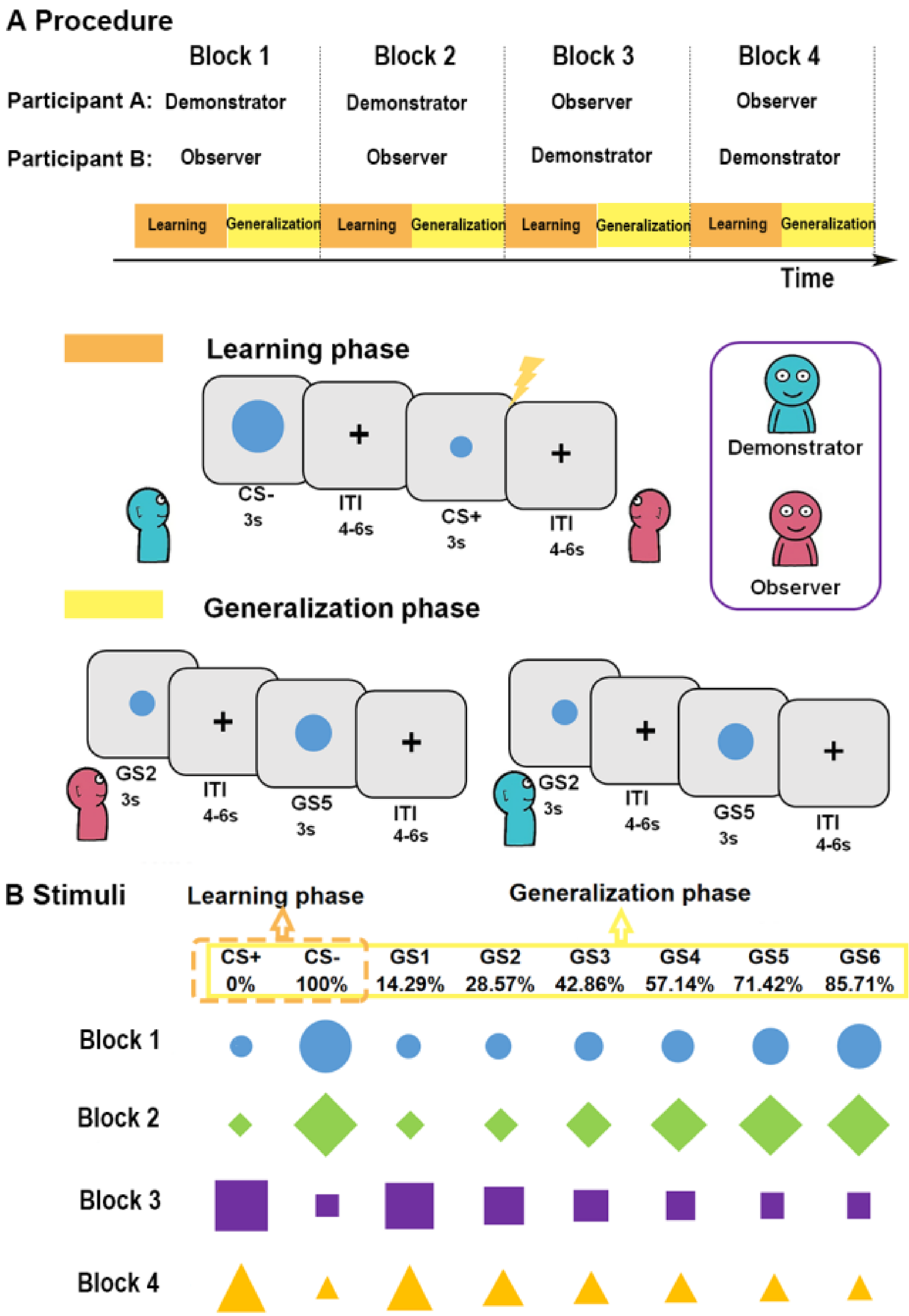

Figure 1. Schematic illustration of the experimental procedure and the visual stimuli. A Procedure. In the experimental procedure, the order of the two learning types (direct and observational) was counterbalanced between the participants. Participants A and B represent two participants in one dyad. The generalization paradigm and stimuli were the same after both learning types. There were four blocks in the experiment. Each block has a learning phase (30 trials) and a generalization phase (50 trials). A

learning phase included a differential fear learning paradigm. In block1, for example, two circles of different sizes were presented to the participants one by one for 3 seconds. One of the circles was followed by a shock (CS+) and the other was not (CS-). The demonstrator learned the CS-US association by directly receiving a shock, and the observer learned the CS-US association by perceiving the demonstrator's fear response. In each trial, both the demonstrator and observer answered how likely the conditioned stimulus was followed by a shock with a 3-point Likert scale (ranging from 1= no chance to 3= high probability). The inter-trial interval (ITI) was randomly assigned between 4 to 6 seconds. In the fear generalization procedure, the demonstrator and the observer completed the fear generalization task independently without seeing each other. The generalization stimuli were presented to the participants for 3 seconds, and the participants' task was the same as in the fear learning task. B. Stimuli. The fear learning and generalization tasks were in the four blocks. The GS1 was the most similar to CS+, and GS6 was the most similar to CS-. The percentages under each stimulus indicate the increased diameter size compared with the smallest geometric figure. Fear learning contains CS+ and CS-, and fear generalization contains CS+, GS1-6, and CS-.

2.3 Procedure

We adapted the protocols for observational learning (Pärnamets et al., 2020) and fear generalization (Lissek et al., 2010) from previous studies. The experiment was conducted in four blocks (Figure 1A). Each block included a learning phase and a generalization phase. In the learning phase, two participants (one dyad), who were the same gender, completed the learning phase together. One of the participants was the "demonstrator" and the other was the "observer". The demonstrators were asked to show their natural responses (e.g., facial expression or body movement) to CS and US without inhibiting or exaggerating their reactions. The participants then switched roles in the middle of the experiment (after two blocks).

In this experiment, US was a mild shock of 50-ms in duration delivered to the participants' left wrists (electrical stimulator, SXC-4A, Sanxia Technique Inc., China). The intensity of the shock was calibrated specifically for each participant to the degree that the participants considered the shock as "highly uncomfortable but not painful" (Dou et al., 2021). The task for all participants was to learn CS contingencies (i.e., the relationship between CS and US) by watching the demonstrator's behavioral reactions to CS or by receiving the shock on their own. At the start of the learning phase in each block, the participants were told that the CS contingencies were randomly set, and they need to learn them again without referring to any previous experience. The conditioned stimuli (i.e., the geometric figures) were presented for 3 seconds. All participants were asked to answer the question “How likely is this stimulus to be followed by a shock?” on a 3-point Likert scale (ranging from 1= no chance to 3= high probability). The response was allowed after the onset of CS and was administered before the onset of US. A random 4–6 second ITI was applied (Figure 1A). There were 30 trials in the fear-conditioning phase (15 CS+ and 15 CS-) in each block. The reinforcement rate of CS+ was set to 75%. At the end of learning phase, the observer was asked to answer three questions: 1. "Did observing the demonstrator’s behavior help you learn the rules?" (9-point Likert scale; 1 = not at all, 9 = totally agree); 2. "Did you sympathize with the demonstrator?" (1= not at all, 9 = totally sympathize); and 3. "Did you perceive the pain of the demonstrator?" (1 not at all to 9 totally perceive).

After the learning phase, the two participants in each pair completed the fear generalization task independently in a way that they could not see each other. Visual stimuli in the generalization phase included those applied as CS+ and CS- in the learning phase of that block; additionally, generalization stimuli modified from CS+ and CS- (GS1-6) were presented (Figure 1A). Each stimulus was presented for 3 seconds. The ITI was randomized to be 4-6 seconds. In the generalization phase, there were a total of 30 trials for GSs (GS1-6), 10 trials for CS+, and 10 trials for CS- per block. In the fear generalization phase, for the both demonstrator and observer, CS+ was paired with a shock only in the last trial of each block.

At the end of the whole experiment, the participants were asked to answer whether they had learned the rules by observing others. Only data for the participants who answered “yes” to this question were included in the final data analysis. One dyad’s data were removed because of technical errors in EEG recording. Another dyad’s data were removed because they reported that they could not learn the rules of CS-US connections by observation learning. Thus, data of two dyads (four participants) were excluded from data analysis. Ultimately, 58 participants were included in the final data analysis.

2.4 Stimuli

CS+ and CS- were geometric figures of different sizes. Four different types of shapes (i.e., circle, square, triangle, and rhombus) were used for four blocks (i.e., block 1-4), respectively (Figure 1B). For instance, the circle stimulus set was only presented in block 1. We chose to use different types of shapes in different blocks rather than one in all blocks because this can reduce the habituation effect and help to separate different stimulus blocks (De Blasio et al., 2013). CS+ was the smallest geometric figure at 5.08 cm in diameter. Each set of generalization stimuli was presented on a visual continuum from CS+ to CS- with a stepwise increase of 14.29% of the size of the smallest stimulus (i.e., GS1, GS2, GS3, GS4, GS5, and GS6). CS+ and CS- stimuli were used in the learning phase, and CS+, CS-, and GS1-6 were used in the generalization phase. The reinforcement contingencies were switched after the first two blocks. Namely, in the first two blocks (blocks 1-2) of the learning phase, the smallest geometric figure was paired with a mild electrical shock (CS+), and the largest geometric figure was never paired with the shock. In the last two blocks (blocks 3-4) of the fear learning phase, the smallest geometric figure was never paired with a shock, and the largest geometric figure was paired with a shock (Figure 1B).

2.5 EEG recording and analysis

EEG activity was recorded using a 64-channel wireless EEG amplifier (NeuSen.W64; Neuracle, Changzhou, China). The sampling frequency was 500 Hz. Online, the data were referenced to the left mastoid. Offline, the data were re-referenced to the average activity of all sensors. The EEG data were collected with electrode impedances below 5 kΩ. Next, a 30-Hz low-pass filter and a 0.1 Hz high-pass filter (Basic FIR filter, EEGLAB) were used in the pre-processing of the EEG data. Additionally, independent component analysis (ICA), as implemented in the EEGLAB toolbox (Delorme and Makeig, 2004), was used to detect and reduce ocular artifacts. The number of accepted trials for each condition is reported in the supplementary materials. Each epoch began with a 500-ms baseline before stimulus onset and lasted for 1500 ms after it. A baseline correction, where each epoch subtracted the activities from -500 ms to 0 ms stimulus onset, was adopted. To remove residual artifacts, we excluded the extreme values ±150 μV of each trial from fear learning (Astikainen et al., 2004; Hammerschmidt et al., 2017) and ±120 μV of each trial from fear generalization (Bruchmann et al., 2021; Niefind & Dimigen et al., 2016; Schindler et al., 2022); 3.7% of the total trials were excluded. EEG data were pre-processed using EEGLAB toolboxes in MATLAB (R2013a; Mathworks, Inc.).

For the time-frequency analysis, a windowed Fourier transform (WFT) with a fixed 500-ms Hanning window was used to obtain the time-frequency distribution (TFD) of the

EEG time course. For each time-frequency, there was a complex time frequency to estimate F(t,f), starting from -500 to 1500 ms (in a 2-ms interval) for latency and from 1 to 30 Hz (in a 1-Hz interval) for frequency. A baseline correction, where each epoch subtracted the activities from -400 ms to -100 ms of the stimulus onset (Lei et al., 2019), was adopted.

For event-related EEG data analyses, we focused on the parietal-occipital (POz, PO3, and PO4) and occipital (Oz, O1, and O2) areas for the P1 component, with a time window of 100 ms to 150 ms after stimulus onset (Luo et al., 2013). For the LPP, we focused on the parietal (Pz, P1, and P2) and parietal-occipital areas as in previous studies (Auerbach et al., 2015; Carolan et al., 2014), with a time window of 300-750 ms after stimulus onset. For the time-frequency analyses, we analyzed the activity in the alpha band (8–12 Hz) with a time window of 250–750 ms after stimulus onset over the occipital and parietal-occipital areas (Haigh et al., 2018).

2.6 Statistics

We adopted two-factor repeated-measures ANOVA test to examine the behavioral, ERP, and time-frequency effects in the learning and generalization phases. In fear learning, within-subjects factors were Stimulus Type (CS+ and CS-) and Learning Type (direct learning or observational learning). In fear generalization, within-subjects factors were Stimulus Type (CS+, GS1, GS2, GS3, GS4, GS6, GS6, and CS-) and Learning Type (direct learning or observational learning). To analyze the learning trajectories between direct learning and observational learning, a linear mixed model was adopted (Zenses et al., 2021). The fixed effects of the linear mixed model included Trial (1-15), Learning Type (direct learning and observational learning), Stimulus Type (CS+ and CS-), Trial × Learning Type, Trial × Stimulus Type, Learning Type × Stimulus Type, Learning Type × Stimulus Type × Trial, and the random effect included subject-dependent intercept.

For all tests, an alpha level of 0.05 was set. We adopted Greenhouse-Geisser corrections if the assumption of sphericity was violated, and Bonferroni corrections were used for compensate multiple comparisons. Partial eta-squared (η_p^2) values were reported for the effect size estimates for significant results. All ANOVA analyses were conducted using IBM SPSS Statistics 22.0.

To extract the generalization gradients, a linear mixed model using the lme4 package (Bates, 2010) in R was adopted for the behavioral and EEG data. Specifically, the dependent variables were the shock expectancy ratings, P1, LPP, and ERD (respectively); the fixed effect was the generalization stimulus, and the random effect was the subject-dependent intercept. We defined CS+, GS1–GS6, and CS- as 0%, 14.29%, 28.57%, 42.86%, 57.14%, 71.42%, 85.71%, and 100% (the percentage of the increased diameter size compared with the smallest geometric figure), respectively, to match the size of each generalization stimuli. We compared the slopes of the generalization gradient after two learning types by using a paired samples t-test (two-tailed) (Dou et al., 2020).

The relationships between self-reported empathy (9-point Likert questionnaire after observational learning), self-reported empathic pain (9-point Likert questionnaire after observational learning), and observational learning (shock expectancy ratings) were tested using Spearman correlation tests.

3. Results

3.1 Shock expectancy ratings

3.1.1 Shock expectancy ratings in fear learning

The main effect of the Stimulus Type was significant ($F_{(1, 57)} = 562.73$, $p < 0.001$, $\eta_p^2 = 0.908$). CS+ evoked a larger shock expectancy than CS- ($p < 0.001$). The main effect of the Learning Type was non-significant ($F_{(1, 57)} = 1.845$, $p = 0.180$, $\eta_p^2 = 0.031$). The interaction effect between Stimulus Type and Learning Type was significant ($F_{(1, 57)} = 12.704$, $p = 0.001$, $\eta_p^2 = 0.182$). Follow-up pairwise comparisons showed that the shock expectancy of CS+ in the direct learning condition was significantly larger than that in the observational learning condition ($p = 0.001$), whereas the shock expectancy of CS- in the direct learning condition was significantly smaller than that in the observational learning condition ($p = 0.001$) (Figure 2A). Furthermore, we found that the conditioned responses (CR) (CS+ minus CS-) in shock expectancy ratings in observational learning (M ± SD = 1.21 ± 0.72) were significantly smaller than those in direct learning (1.54 ± 0.35) ($t(57) = -3.570$, $p = 0.001$) (Figure 2B).

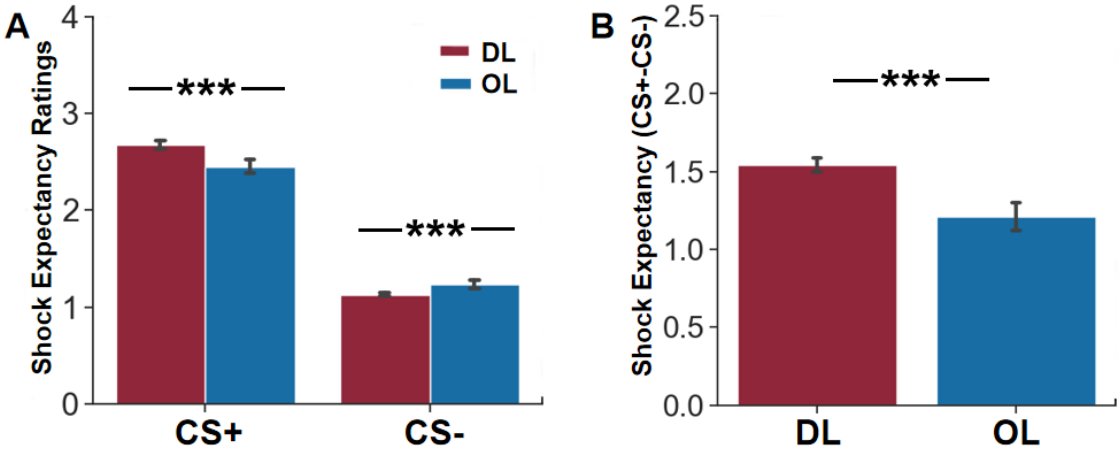

Figure 2 The bar graph of shock expectancy ratings in fear learning. A. The shock expectancy ratings of CS+ in direct learning were higher than those in observational learning, but the shock expectancy ratings of CS- in direct learning were lower than those in observational learning. B. The differential learning results of shock expectancy ratings. Direct learning showed significantly higher conditioned responses (CS+ minus CS-) compared with observational learning. DL= direct learning, OL = observational learning, * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$.

For the learning trajectory results, we found that the main effect of Learning Type was significant ($F_{(1, 6469)} = 8.03$, $p = 0.0046$), and it was modulated by a significant interaction effect between Learning Type and Stimulus Type ($F_{(1, 6453)} = 12.54$, $p < 0.001$). In the follow-up analyses, the shock expectancy ratings of CS+ in the direct learning (2.69 ± 0.021) were significantly higher than those in the observational learning (2.49 ± 0.022) ($t_{(6487)} = 9.63$, $p < 0.001$), and the shock expectancy ratings of CS- in the direct learning (1.14 ± 0.022) were significantly lower than those in the observational learning (1.21 ± 0.022) ($t_{(6487)}$= -3.68, $p < 0.001$). We did not find any significant interaction effects of Trial × Learning Type and Trial × Learning Type × Stimulus Type, indicating that the participants in both direct learning and observational learning learned the associations of CS+ and US at a similar speed (Figure 3).

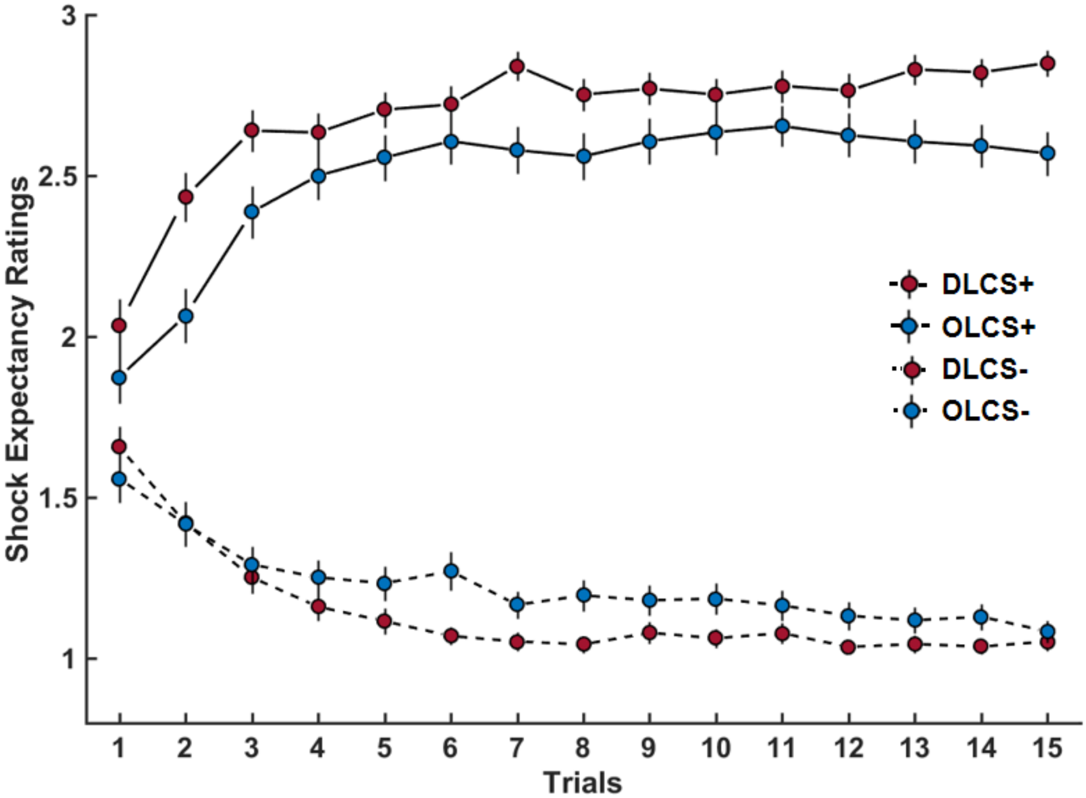

Figure 3 The shock expectancy ratings results across the fear learning trials. We found the participants in observational learning acquired the association between CS+ and CS- at a similar rate as those in direct learning (There were no significant group differences). DL= direct learning, OL= observational learning, CS+ = conditioned stimuli paired with a shock, and CS- = conditioned stimuli never paired with a shock.

3.1.2 Shock expectancy ratings in fear generalization

The repeated ANOVA results in the shock expectancy ratings showed that the main effect of Stimulus Type was significant ($F_{(7, 399)} = 130.96$, $p < 0.001$, $\eta_p^2 = 0.697$). Follow-up comparisons indicated that the shock expectancy ratings of CS+ were not significantly different from those of GS1 ($p > 0.05$) and GS2 ($p = 0.075$) but were significantly higher than those of GS3, GS4, GS5, GS6, and CS- (all *ps* < 0.001). The shock expectancy ratings of GS1 were significantly higher than those of GS2-GS6 and CS- (all *ps* < 0.001). The main effect of the Learning Type was not significant ($F_{(1, 57)} = 0.629$, $p = 0.431$, $\eta_p^2 = 0.011$), but the interaction effect between Stimulus Type and Learning Type was significant ($F_{(7, 399)} = 3.04$, $p = 0.045$, $\eta_p^2 = 0.051$). Follow-up comparisons indicated that the shock expectancy ratings of CS-, GS6, and GS5 in OL were significantly higher than those in DL (CS-, $p = 0.005$; GS6, $p = 0.001$; GS5, $p = 0.031$) (Figure 4).

The results of the generalization gradients in shock expectancy ratings revealed that the slope of the generalization gradient in DL ($M \pm SE$= -1.33 ± 0.09) was steeper than that in OL (-1.06 ± 0.11; $t_{(57)}$= -2.09, p = 0.041).

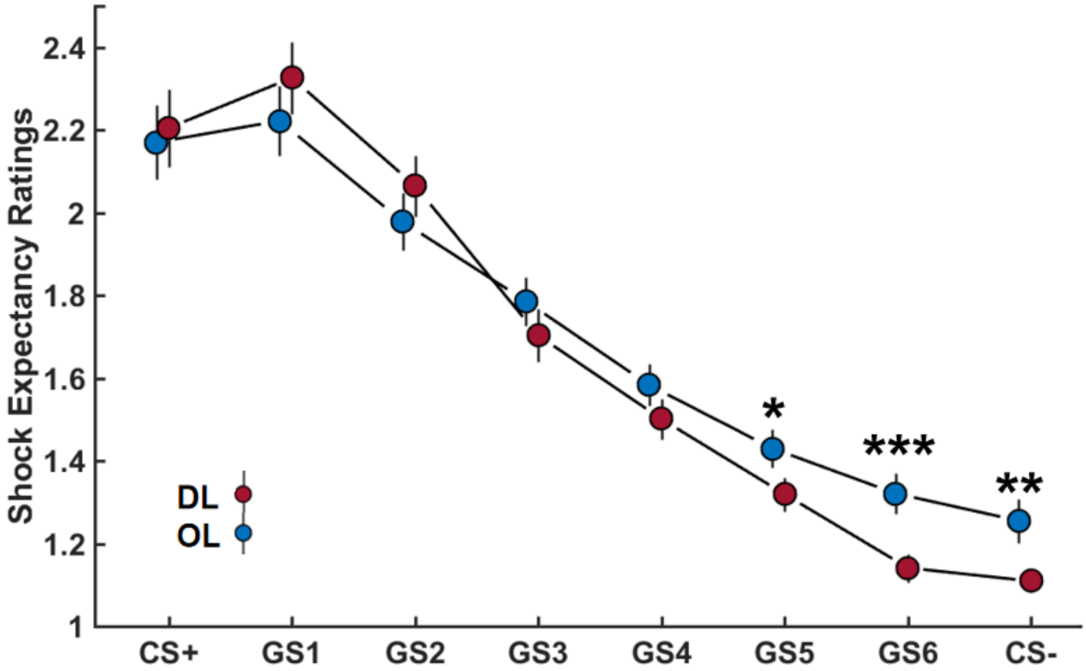

Figure 4 The line graph of the shock expectancy ratings results in fear generalization. GS5, GS6, and CS- showed significantly higher shock expectancy ratings in observational learning than in direct learning. DL= direct learning, OL= observational learning, CS+ = conditioned stimuli paired with a shock, and CS- = conditioned stimuli never paired with a shock. * = p < 0.05, ** = p < 0.01, and *** = p < 0.001.

To test the effect of differences in responding to CS+ and CS- in fear learning on the subsequent fear generalization test, we added the difference of CR (CS+ vs. CS-) in fear learning as a covariable in the two-way (Learning Type × Stimulus Type) repeated ANOVA test. The ANOVA results showed that the interaction effect of the Stimulus Type and Learning Type was non-significant ($F_{(2.3, 128)}$= 1.325, p = 0.270, η_p^2= 0.023) after adding the difference of CR as a covariable.

3.2 EEG results

3.2.1 P1 component

In fear learning, for the P1 component, the main effect of Stimulus Type was significant ($F_{(1, 57)}$ = 5.88, p = 0.019, η_p^2 = 0.094). CS+ evoked a significantly larger P1 amplitude than CS- (p = 0.019). The main effect of Learning Type was not significant ($F_{(1, 57)}$ = 0.058, p = 0.811). Moreover, the interaction effect of Stimulus Type and Learning Type was non-significant ($F_{(1, 57)} = 0.013$, $p = 0.908$) (Figure 5).

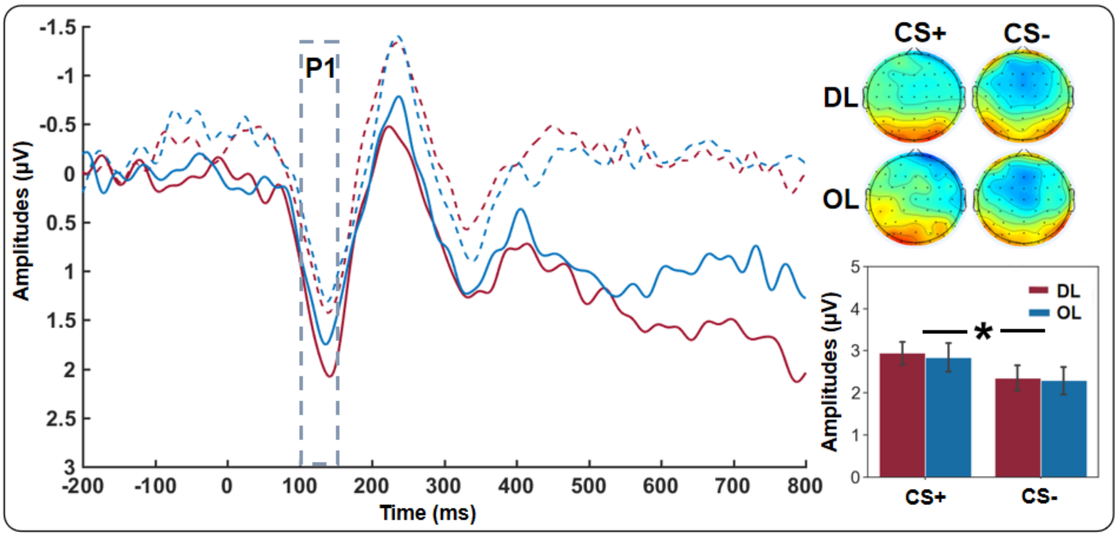

Figure 5 The P1 results in fear learning: ERP waveforms (left), brain activity topographies (right-top), and bar graph (right-bottom). CS+ evokes larger P1 amplitudes compared with CS- in both learning types. There was no significant difference between observational learning and direct learning. * = $p < 0.05$. DL= direct learning, OL = observational learning.

In fear generalization, we found the main effect of Stimulus Type ($F_{(6, 343)} = 2.806$, $p = 0.011$ $\eta_p^2 = 0.047$). Follow-up comparisons showed that GS1 (3.46 ± 0.31 μV) and GS3 (3.46 ± 0.28 μV) evoked larger P1 amplitudes compared with CS- (2.69 ± 0.27 μV), $p = 0.027$ and $p = 0.041$, respectively. The main effect of Learning Type was not significant $F_{(1, 57)} = 1.499$, $p = 0.226$, $\eta_p^2 = 0.026$). We found a significant interaction between the Stimulus Type and Learning Type ($F_{(5.5, 312)} = 3.367$, $p = 0.004$, $\eta_p^2 = 0.056$). Follow-up comparisons showed that CS+ (3.35 ± 0.31 μV) and GS2 (3.86 ± 0.37 μV) in the DL condition evoked larger P1 amplitudes than CS+ (2.49 ± 0.31 μV; $p = 0.015$) and GS2 (2.67 ± 0.38 μV; $p = 0.020$) in the OL condition. Only in the DL condition did we find that the P1 amplitudes of GS1 (3.60 ± 0.31 μV), GS2 (3.90 ± 0.38 μV), and GS3 (3.94 ± 0.36 μV) were significantly larger than those of CS- (2.69 ± 0.29 μV; GS1, p = 0.015, GS2, $p = 0.010$, GS3, $p = 0.005$) (Figure 6A, B). Moreover, the results of generalization gradients in the P1 component revealed that the slope was significantly steeper in the DL condition (M ± SD = −0.869 ± 0.327) than in the OL condition (0.119 ± 0.343; $t_{(57)} = -13.11$, $p < 0.001$) (Figure 6C).

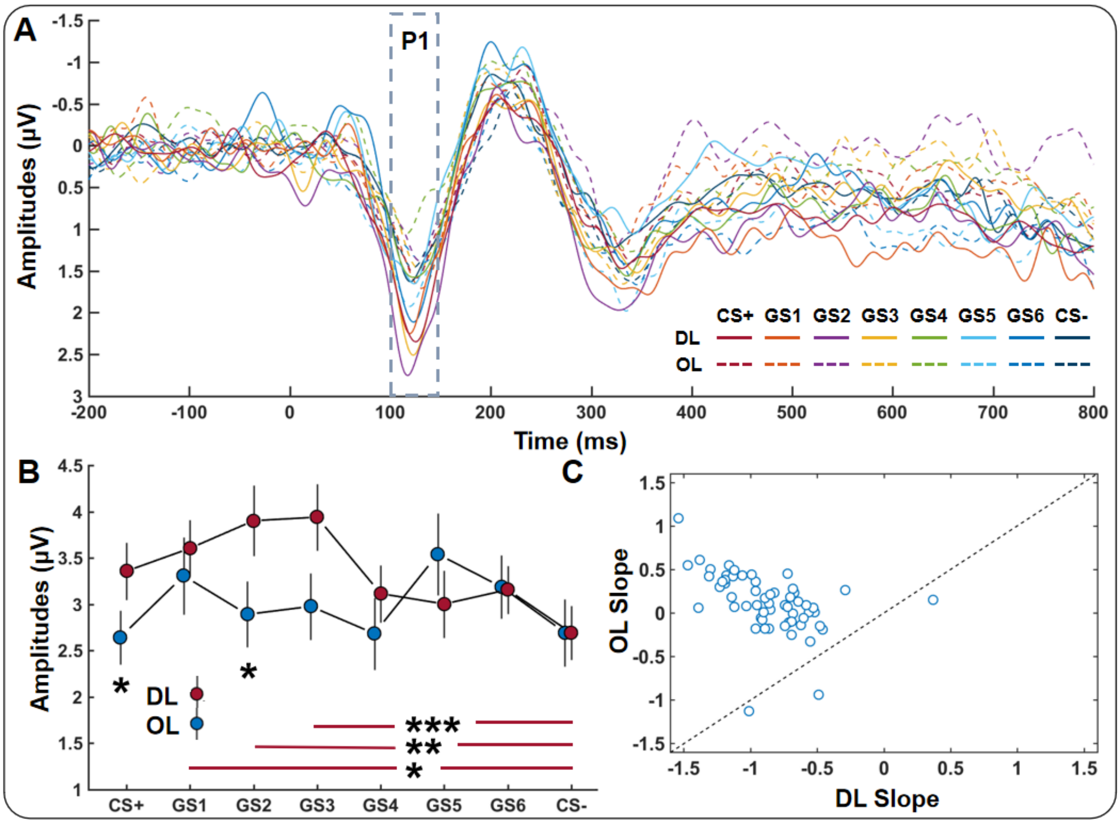

Figure 6 Results of the P1 component in fear generalization. A. The ERP plots in fear generalization for the P1 component. B. The line plots in fear generalization. CS+ and GS2 after direct learning evoked larger P1 amplitudes compared with those evoked after the observational learning. Only in direct learning did GS1, GS2, and GS3 evoke larger P1 amplitudes than CS- did. C. The scatter plots of fear generalization slope. The fear generalization slope in direct learning was more negative compared with that in observational learning. DL= direct learning, OL = observational learning.

3.2.2 LPP

In fear learning, the main effect of Stimulus Type was significant for LPP ($F_{(1, 57)}$ = 23.447, $p < 0.001$, $\eta_p^2 = 0.291$). The LPP amplitudes of CS+ were significantly larger compared with CS- ($p < 0.001$). The main effect of Learning Type ($F_{(1, 57)}$ = 1.385, p = 0.244) and the interaction effect of stimulus and learning type were non-significant ($F_{(1, 57)}$ = 0.758, p = 0.388) (Figure 7).

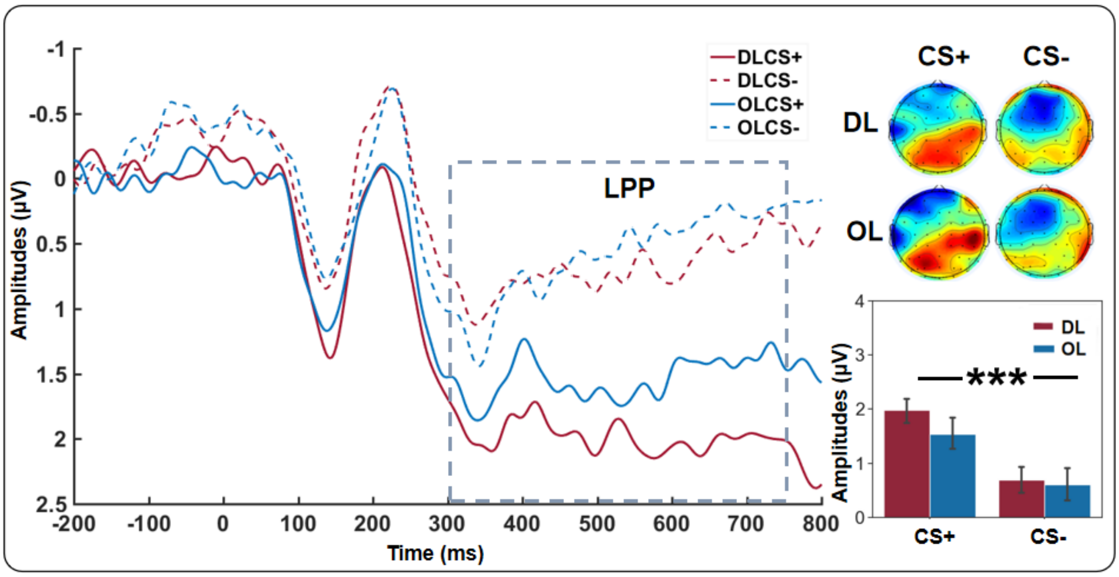

Figure 7 The LPP results in fear learning: ERP waveforms (left), brain activity topographies (right-top), and bar graph (right-bottom). CS+ evokes larger LPP amplitudes compared with CS- in both learning types. There was no significant difference between observational learning and direct learning. *** = p < 0.05, LPP = late positive potentials.

In fear generalization, we did not find any significant main effects (Learning Type: $F_{(1, 57)} = 0.950$, $p = 0.334$, Stimulus: $F_{(4.9, 279)} = 0.727$, $p = 0.601$), but we did find a marginally significant interaction effect ($F_{(5.1, 291)} = 2.036$, $p = 0.072$, $\eta_p^2 = 0.034$). The follow-up comparisons showed that CS+ (2.19 ± 0.29 μV) and the GS2 (2.06 ± 0.29 μV) in the DL condition evoked larger LPP amplitudes than CS+ (1.69 ± 0.23 μV, $p = 0.042$) and GS2 (1.01 ± 0.47 μV, $p = 0.049$) in the OL condition (Figure 8A, B). Moreover, the results of generalization gradients in the LPP component revealed that the LPP slope in the DL condition (M±SD = −0.561 ± 0.125) was steeper than that in the OL condition (0.523 ± 0.111; $t_{(57)} = -81.33$, $p < 0.001$) (Figure 8C).

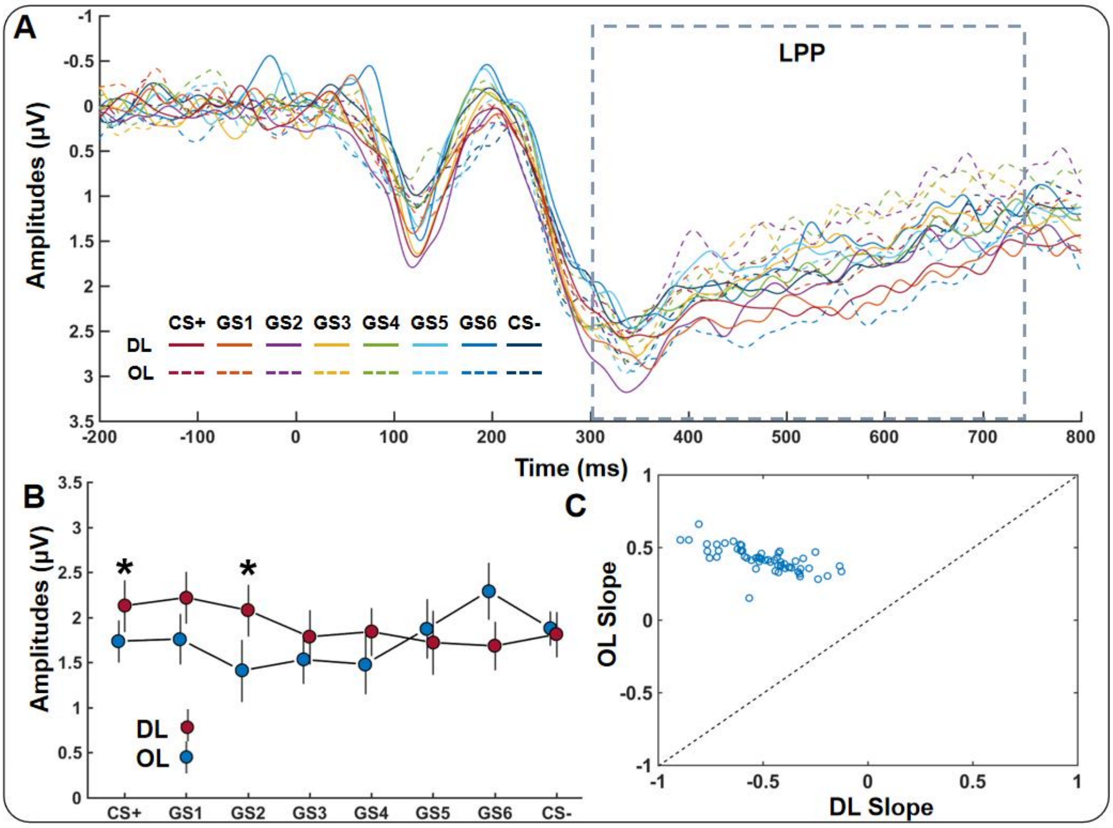

Figure 8 Results of the LPP component in fear generalization. A. ERP waveforms. B. Line plot. CS+ and GS2 after direct learning evoked larger LPP amplitudes compared with those after observational learning. C. Scatter plot of fear generalization slope. The fear generalization slope in direct learning was more negative compared with that in observational learning, which indicates that observational learning evokes more generalized fear (larger LPP amplitudes). DL= direct learning, OL = observational learning.

3.3 Alpha band oscillation

For the event-related desynchronization (ERD), in fear learning, the main effects of Stimulus Type ($F_{(1, 57)} = 0.681$, $p = 0.413$) and Learning Type ($F_{(1, 57)} = 0.001$, $p = 0.973$) were non-significant. Moreover, the interaction effect of Stimulus Type and Learning Type was non-significant ($F_{(1, 57)} = 0.490$, $p = 0.487$) (see SI Figure 1).

In fear generalization, the main effect of Stimulus Type ($F_{(4.5, 257)} = 2.933$, $p = 0.017$) was significant. Follow-up comparisons showed that CS- (-0.657 $\pm$ 0.112 μV^2) induced greater alpha-ERD compared with GS3 (-0.405 $\pm$ 0.079 μV^2). No main effect of learning type was observed (Learning Type: $F_{(1, 57)} = 1.808$, $p = 0.184$), and the interaction was also non-significant ($F_{(3.5, 201)} = 0.888$, $p = 0.462$) (Figure 9A, B). Even so, the results of generalization gradients in ERD revealed that the DL condition (0.082 ± 0.188) showed a significantly different trend compared with the OL condition (-0.141

± 0.289; $t_{(57)} = 3.793$, $p < 0.001$) (see Figure 9C).

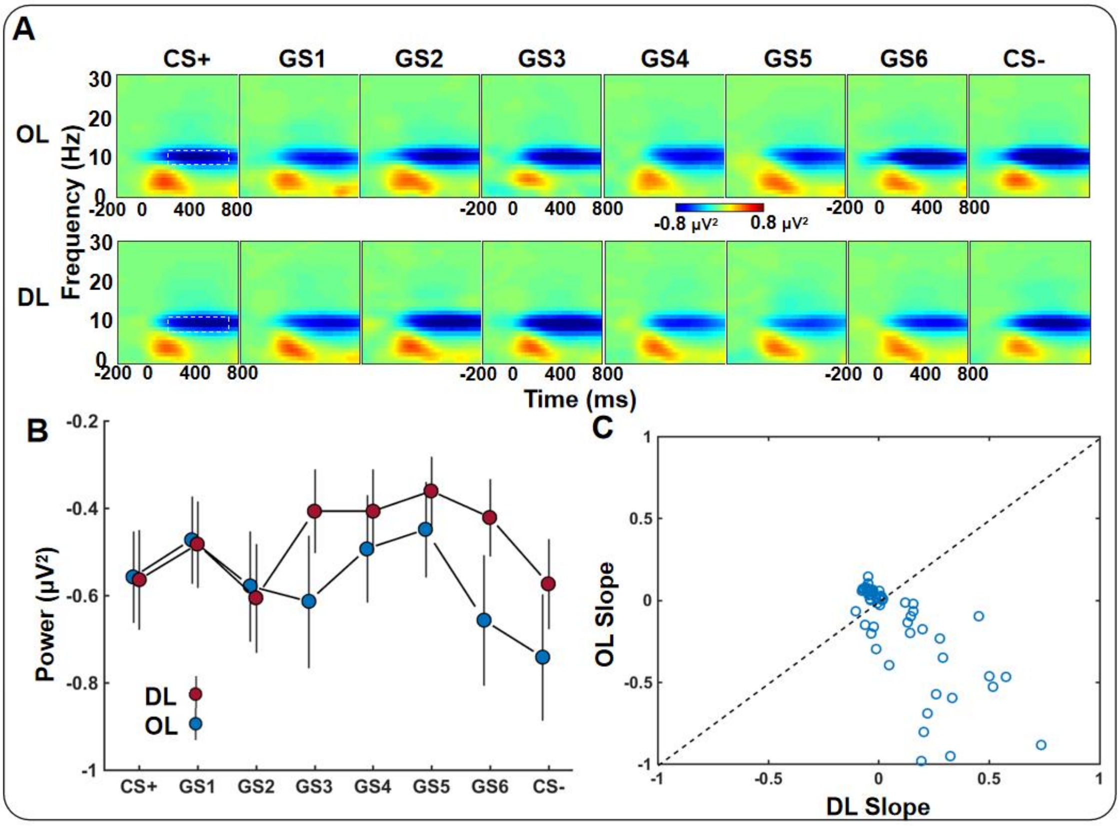

Figure 9 The alpha-ERD results in fear generalization. A. The time-frequency information. B. The line figure of alpha-ERD C. Scatter plot of the generalization slope in direct and observational learning, which indicates that the direct learning slope showed a steeper trend than the observational learning slope. DL= direct learning, OL = observational learning, and GS = generalization stimulus.

3.4 Self-reported empathic pain and empathy

To test the effects of self-reported empathy and empathic pain on observational learning and generalization, the correlations between the empathic pain, empathy, and observational learning (the shock expectancy differentiation of CS+ and CS-) were calculated. We found that empathic pain significantly correlated with observational learning (empathic pain, $r = 0.442$, $p = 0.001$), but the self-reported empathy did not correlate with observational learning.

4. Discussion

The present study examined the impact of observational and direct fear learning on fear generalization by recording the shock expectancy ratings and EEG results. The main results for fear learning showed that observational learning reduced the shock expectancy rating differentiation between the conditioned threatening stimuli compared to direct learning. The threatening conditioned stimuli in observational and direct learning increased the P1 and LPP amplitudes compared with safety conditioned stimuli. For the main results of fear generalization, we found observational learning increased the shock expectancy ratings to the generalization stimuli compared with direct learning. The P1, LPP, and alpha-ERD generalization gradients after observational learning were more gradual than those after direct learning.

In the behavioral results of fear learning, we found that observational learning reduced the differentiation between CS+ and CS- compared to direct learning. In line with previous findings (Mineka et al., 1984; Olsson et al., 2007; Olsson and Phelps, 2007), the fear learning results showed that the shock expectancy for CS+ was higher than for CS-, indicating that the fear acquired by observational learning can establish an association between CS and US. However, the shock expectancy ratings for observational learning showed a reduced differentiation between CS+ and CS- compared with direct learning. In line with our result showing reduced learning in observational learning, a previous study found that observational learning evoked a smaller skin conductance response differentiation between the objects paired with high and low pain compared with direct learning (Egorova et al., 2015).

The EEG results in fear learning showed that CS+ evoked larger P1 amplitudes compared with CS-. Our findings for the P1 component are consistent with the previous studies of fear learning (Bublatzky & Schupp, 2012; Dolan et al., 2006; Linton & Levita, 2021; Pizzagalli et al., 2003). For example, Pizzagalli et al. (2003) adopted different faces in a classical fear conditioning task and found P1 enhancements to CS+. According to previous findings (Forscher et al., 2016; Linke et al., 1999; Meynadasy et al., 2019; Sperl et al., 2021; Thorpe, 2009; Wieser & Keil, 2020), P1 reflects the early threat discrimination in fear-relevant tasks. Here, we did not find P1 amplitude differences between direct and observational learning, which may indicate that the early threat discrimination is not affected by social learning.

Regarding the results of the later ERPs, the LPP amplitude in fear learning was enhanced to CS+ compared with CS- in both direct and observational learning, which was consistent with several previous studies (Dolan et al., 2006; Panitz et al., 2015; Pizzagalli et al., 2003) in fear learning. Panitz et al. (2015) found CS+ evoked larger LPP amplitudes compared with CS- in a facial fear conditioning task. According to previous EEG results in fear learning, the LPP component reflects motivated attention (Ferreira et al., 2019; Schupp et al., 2005)—that is, selective attention to the stimuli with motivated significance. Motivated attention involves preparing defensive behaviors and elaborate processing of the significant stimuli (Ferreira et al., 2019; Lang et al., 1997; Schupp et al., 2004), and it is associated with activity in the amygdala and the visual processing area, including the parieto-occipital region (Bradley et al., 2003). Also in our study, the increased LPP amplitudes to CS+ may reflect increased motivated attention to threatening stimuli in fear learning. However, we did not find an alpha-ERD difference between CS+ and CS- in either observational or direct learning. According to previous studies, there are two attention systems (McHugo et al., 2013): the attention orienting system in the ventral attention network (i.e., the temporoparietal junction and the ventrolateral prefrontal cortex; Armony and Dolan, 2002; Corbetta and Shulman, 2002) and the motivated attention system in the brain regions involved in defensive behaviors (i.e., the amygdala as well as the parietal and temporal cortices; Amaral et al., 2003; Keil et al., 2009). One possible explanation for no enhancement of alpha-ERD to CS+ in fear learning is that the orientation attention network (Yin et al., 2020) has a competitive relationship with the motivated attention system (reflected by the LPP component). The motivated attention system, including the amygdala region, can be activated preferentially (Lang et al., 1997) compared to other attention systems. The orientation attention might be distracted because the attention system is occupied by motivated attention. Another possible explanation for the alpha-ERD result is that the index of alpha-ERD in fear learning is not as stable as other indexes, such as LPP. More evidence of alpha-ERD in fear learning is needed from future studies.

Furthermore, our findings indicate that observational learning and direct learning affect fear generalization differently and that there are also differences in the associated EEG activity. Behaviorally, and in agreement with the second hypothesis, we found that the slope of the shock expectancy across the generalization gradient was steeper after direct rather than observational learning. The shock expectancy ratings for GS5, GS6, and CS- were larger after observational learning than after direct learning. The finding that observational learning evoked higher shock expectancy ratings for the GS5 and GS6 might be interpreted by reduced differential learning in observational fear acquisition. Previous studies have reported that differential learning can modulate the shape of the subsequent fear generalization gradient (Dunsmoor and LaBar, 2013; Struyf et al., 2015), which supports our findings. Furthermore, we did not find an interaction between Learning Type and Stimulus Type in fear generalization for shock expectancy ratings when we added the differential learning (CS+ minus CS-) as a covariable. This finding might indicate that in observational learning, the increased shock expectancy ratings to GS5 and GS6 after observational learning were caused by the reduced fear discrimination of CS+ and CS-.

In fear generalization, the results regarding the P1 supported and expanded previous findings. A previous MEG study (Roesmann et al., 2020) found that facial GSs resembling CS+ evoked a larger P1 amplitude in the occipito-temporal area compared with GSs resembling CS-. As discussed in the context of P1 in the learning phase, P1 is associated with early discrimination of threat and safety stimuli in fear generalization studies (Bublatzky & Schupp, 2012; Pizzagalli et al., 2003; Roesmann et al., 2020). Furthermore, previous studies have reported that P1 amplitude could reflect the perceived fear intensity of expressions in a fear discrimination task (Frenkel & Bar-Haim, 2011; Meynadasy et al., 2019). For instance, Meynadasy et al. (2019) found that the more fearful the facial expression was, the larger P1 amplitude it evoked. Our data showed a similar result for the generalization stimuli after direct learning: the more similar to CS+ GS is, the larger P1 amplitudes it evoked. Moreover, we found that the generalization gradient of P1 after observational learning was more gradual compared to that after direct learning, indicating that early threat discrimination to generalization stimuli after observational learning decreased.

In the late ERPs, we found that observational learning modulated LPP amplitude to GSs during the fear generalization test. In generalization after direct learning, the LPP amplitudes for CS+ and GS2 were higher than those in the generalization after observation learning. Previous studies on fear generalization have found an increased

LPP amplitude to the generalization stimuli resembling CS+ (Nelson et al., 2015); they interpreted the increased LPP to GS as the activation of motivated attention (Roesmann et al., 2020). The enhancement of LPP to CS+ and GS2 in generalization after direct learning in the present study might indicate the increased motivated attention compared with observational learning. We also found that the slope of the LPP generalization gradient was steeper for direct learning than for observational learning, indicating increased generalization of the LPP component in observational learning, which is similar to the results of the shock expectancy ratings. Furthermore, the LPP amplitude differences to the generalization stimuli between learning types might also be due to the differences in the extinction effect between observational and direct learning. Indeed, the extinction effect in the generalization phase probably occurred in our study because only the last trial of CS+ in fear generalization was paired with a shock.

In the late EEG activities of fear generalization, we found that the alpha-ERD activity induced by the generalization stimuli after observational learning did not form a generalization gradient. Only in generalization after direct learning did the generalization gradient show the following trend: the more similar to CS+, the stronger alpha-ERD activity the GSs induced. In previous findings, the alpha-ERD induced by CS+ was associated with the ventral attention network and the orienting attention (Corbetta & Shulman, 2002; Yin et al., 2020). In our study, the alpha-ERD result suggests that observational learning reduced the function of the orienting attention to the generalization stimuli after observational learning relative to direct learning.

Our results generally suggested that observational learning reduced differential learning and reduced differential learning leads to a modulated generalization pattern, which supports the view that the shape of a generalization gradient is a byproduct of differential learning. Specifically, for the shock expectancy rating results, the reduced differentiation of CS+ and CS- in observational learning modulated the fear generalization gradient. However, neither P1 nor the LPP amplitudes showed differences between learning types in fear learning, only for fear generalization. The potential reason why we did not find the differential learning differences between observational and direct learning in the ERP results is that the early visual discrimination (P1) and motivated attention (LPP) to the threat stimuli in observation learning were enhanced. Previous findings have reported that early visual discrimination (P1) and motivated attention (LPP) to the threat stimuli

(CS+) is associated with the activation of amygdala (Liu et al., 2012; Rotshtein et al., 2010; Sabatinelli et al., 2013). To some extent, when the observer looks at the demonstrator's fear responses, the strength of the US is ambiguous to the observer because they did not suffer from the shock themselves. The amygdala activation to an ambiguous threat stimulus is under the "better safe than sorry principle" (Eilam et al., 2011; Flannelly et al., 2017), which leads to the enhanced activation of amygdala in the observation learning. The enhancement of amygdala finally increased the P1 and LPP amplitudes in observational learning, which leads to no differences of the P1 and LPP amplitudes between direct and observational learning. However, one interpretation we cannot deny is that the neural activities in fear generalization may not be merely byproducts of those in fear learning. Considering that shock expectancy ratings and ERPs are related to different cognition, it is not surprising that they do not show a similar result pattern. While shock expectancy ratings are associated with threat anticipation and risk assessment, which activates the prefrontal cortex (e.g., orbitofrontal cortex) (Kirlic et al., 2017; Nitschke et al. 2006), P1 and LPP are associated with the early visual and attention systems (Lang, Bradley, & Cuthbert, 1997), and these components were observed in the parietal-occipital electrode sites in our study. Considering the absence of enough experimental evidence, caution should be exercised when considering these interpretations, and more future research is warranted.

In agreement with the fourth hypothesis, we found that the observer's empathic pain for the demonstrator showed a positive correlation with observational learning in our experiment: the more observers showed empathic pain for the demonstrators, the greater was the shock expectancy discrimination of CS+ and CS- in observational learning. This finding was consistent with previous findings (Olsson et al., 2016), which showed that in the high empathy group, participants showed a higher skin conductance response to the conditioned stimuli compared to the low empathy group.

This study had some limitations. First, in our study, the participants played the roles of both the demonstrator and observer in a counterbalanced order in a within-subject design. We tested the effect of the order in our study (Supplementary materials). We found that the shock expectancy ratings and LPP were not affected by the order of the roles, which is similar to the finding of a previous studies (Pärnamets et al., 2020). However, the role effect was found for P1 and LPP, which indicates that early threat discrimination and late directing attention might be sensitive to previously learned experiences. Future studies should use a between-subjects design to examine the differences between observational and direct learning on fear generalization. Another aspect is that although the demonstrator was asked to perform as naturally as possible when they received a shock without inhibiting or exaggerating their responses in our experiment, the demonstrator's responses to the shock might have been different from their responses they had been in the situation alone. At last, the protocol of this experiment has limited ecological validity compared to observational learning in the natural environment. The conditioned stimuli are here presented as abstract and static pictures, since CSs were pictures of geometric figures, and electrical shocks were used as US. Though effective in conditioning studies, they are not common events in the real world.

5. Conclusion

The present study revealed that observational learning reduces differential learning (CS+ minus CS-) compared to direct learning. Additionally, the fear responses to generalization stimuli depend on whether the fear learning experience is direct or observational. Specifically, observational fear learning exhibited more gradual fear generalization gradients in terms of shock expectancy than direct learning, indicating that observational learning increases fear generalization. Moreover, compared with direct learning, early fear discrimination (reflected by the decreased P1), the late motivated attention (reflected by the decreased LPP), and orienting attention (reflected by the reduced alpha-ERD) to generalization stimuli were weakened after observation learning. These differences in P1 and LPP between the learning conditions were specific to the fear generalization phase and were not observed in the fear learning phase.

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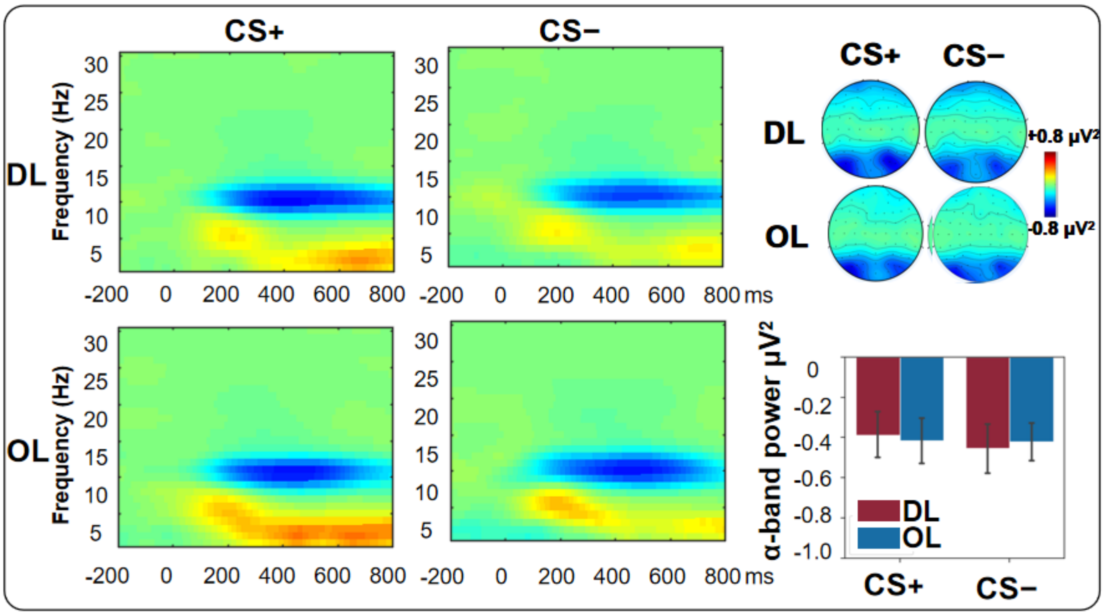
Supplementary Materials

1 The graphic of ERD results in fear learning



SI Figure 1. The graphic of alpha-band ERD results. There was no significant difference in the alpha-band ERD in fear learning. DL= direct learning, OL= observational learning.

2 The effect of role order of learning type on fear generalization

To clarify the order effect, i.e. whether observational or direct learning was first, on responses, we adopted a three-factor repeated-measures analyses of variance (ANOVAs) for the data in the fear generalization phase. The within-subjects factors were Stimulus Type (CS+, CS-, GS1-GS6), Learning Type (direct learning [DL] or observational learning [OL]), and Role Order (Before and After role switch).

2.1 Shock expectancy ratings

There were neither significant effects of Role Order nor any of its interaction effects (all ps > 0.259).

2.2 P1

The interaction effect between Role Order and Learning Type ($F_{(1, 28)} = 4.362$, $p = 0.046$, $\eta_p^2 = 0.135$) was significant. Follow-up pairwise comparisons showed that after the role switch, the generalization stimuli after the direct learning evoked larger P1 amplitudes than after the observational learning (p = 0.001). Other effects of Role Order and its interaction effects were not significant (all ps > 0.130).

2.3 Late positive potential (LPP)

The interaction effect between Role Order and Learning Type ($F_{(1, 28)} = 2.791$, $p = 0.027$, $\eta_p^2 = 0.069$) was significant. Follow-up pairwise comparisons showed that in observation learning, the generalization stimuli before role switch evoked larger P1 amplitudes than after role switch (p = 0.012). Other effects of Role Order and its interaction effects were not significant (all ps > 0.056).

2.4 Alpha ERD

There were neither significant effects of Role Order nor any of its interaction effects (all ps > 0.216).

Author statement

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Conflicts of interest

There is no actual or potential conflict of interest in relation to this article.

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