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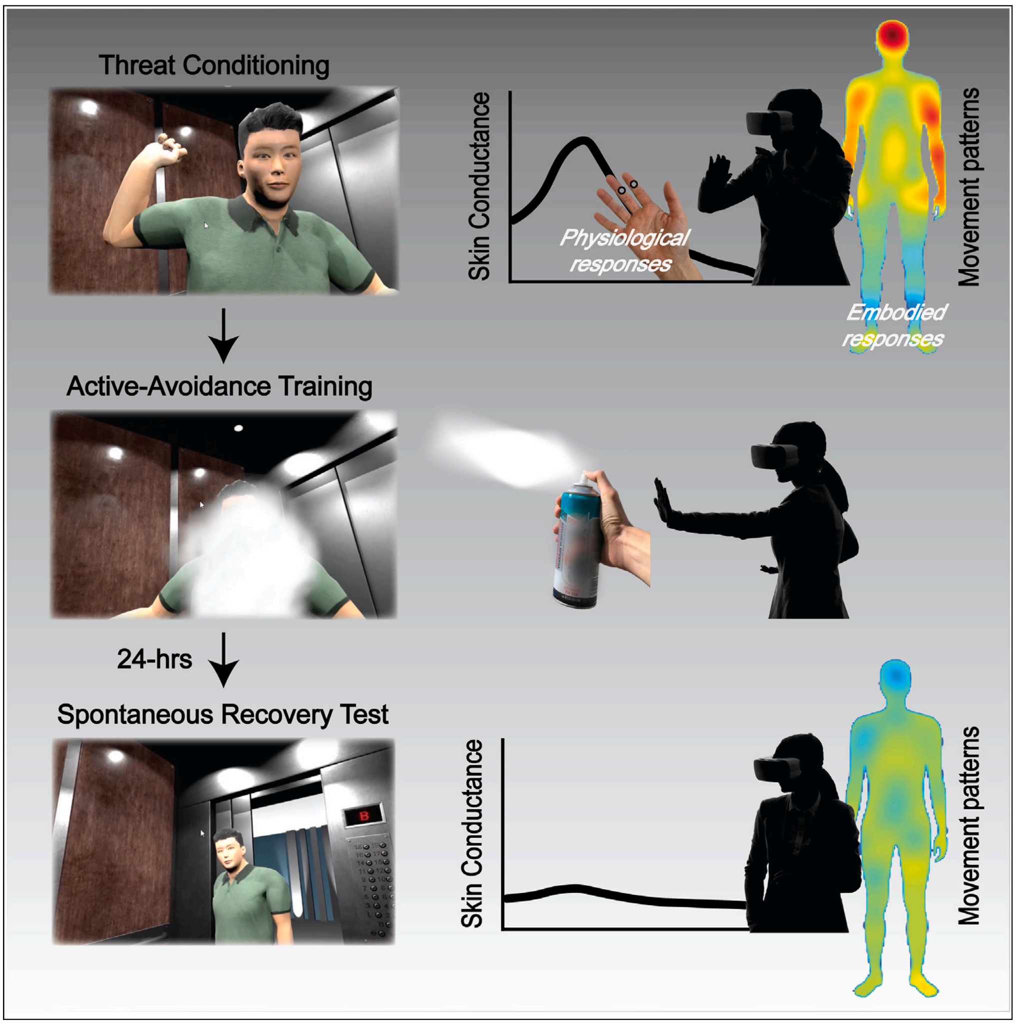

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Highlights

Body motion was tracked during virtual fear conditioning and active-avoidance training

Distinct body movement patterns emerge through fear conditioning

Training embodied avoidance action prevents the return of fear 24 h later

Interventions for traumatic memories may benefit through embodiment

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Fear in action: Fear conditioning and alleviation through body movements

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SUMMARY

Fear memories enhance survival especially when the memories guide defensive movements to minimize harm. Accordingly, fear memories and body movements have tight relationships in animals: Fear memory acquisition results in adapting reactive defense movements, while training active defense movements reduces fear memory. However, evidence in humans is scarce because their movements are typically suppressed in experiments. Here, we tracked adult participants' body motions while they underwent ecologically valid fear conditioning in a 3D virtual space. First, with body motion tracking, we revealed that distinct spatiotemporal body movement patterns emerge through fear conditioning. Second, subsequent training to actively avoid threats with naturalistic defensive actions led to a long-term (24 h) reduction of physiological and embodied conditioned responses, while extinction or vicarious training only transiently reduced the responses. Together, our results highlight the role of body movements in human fear memory and its intervention.

INTRODUCTION

Threatening experience induces associative learning between threat and its predictive cues in the environment.[1–3] This Pavlovian learning can enhance survival especially when the learned association is used to initiate defensive actions such as escaping or avoiding the threat.[4–7] In the real world, minimization of harm requires bodily defensive movements to change external situations[7,8] with rich movement repertoires.[9–13] This highlights that facilitating adaptive defensive actions might be one of the key functions of Pavlovian threat learning.[14]

Interestingly, instrumental learning to enhance active defensive movement per se can alleviate Pavlovian conditioned responses in animals.[4] For instance, conditioned passive freezing responses in rats can be reduced with instrumental training to reinforce active-avoidance, such as escaping to the other side of a chamber, by its desirable outcome to terminate a threat-conditioned cue and prevent a threatening electric shock.[15,16]

Unlike the demonstrated roles of body movements in both acquisition and alleviation of threat-associative memories in animals, evidence in humans is scarce because their body movements are often overlooked in research.[17,18] First, acquisition of threat conditioning in humans is typically assessed with peripheral physiological responses such as skin conductance responses (SCR)[19] and heart rates.[20,21] Although those physiological responses may emerge as preparatory modulators of defensive bodily movements,[22–24] they imply little about overt bodily movements.

Second, although the active-avoidance procedure in animals[15,16] has been translated to humans in seminal works,[25–30] procedures in humans are generally less embodied than in animals. For example, participants avoid aversive shocks through button-pressing to control icons on a monitor that are unrelated to ecologically valid bodily defensive actions.[25,29] Those procedures successfully alleviated fear[30] with a

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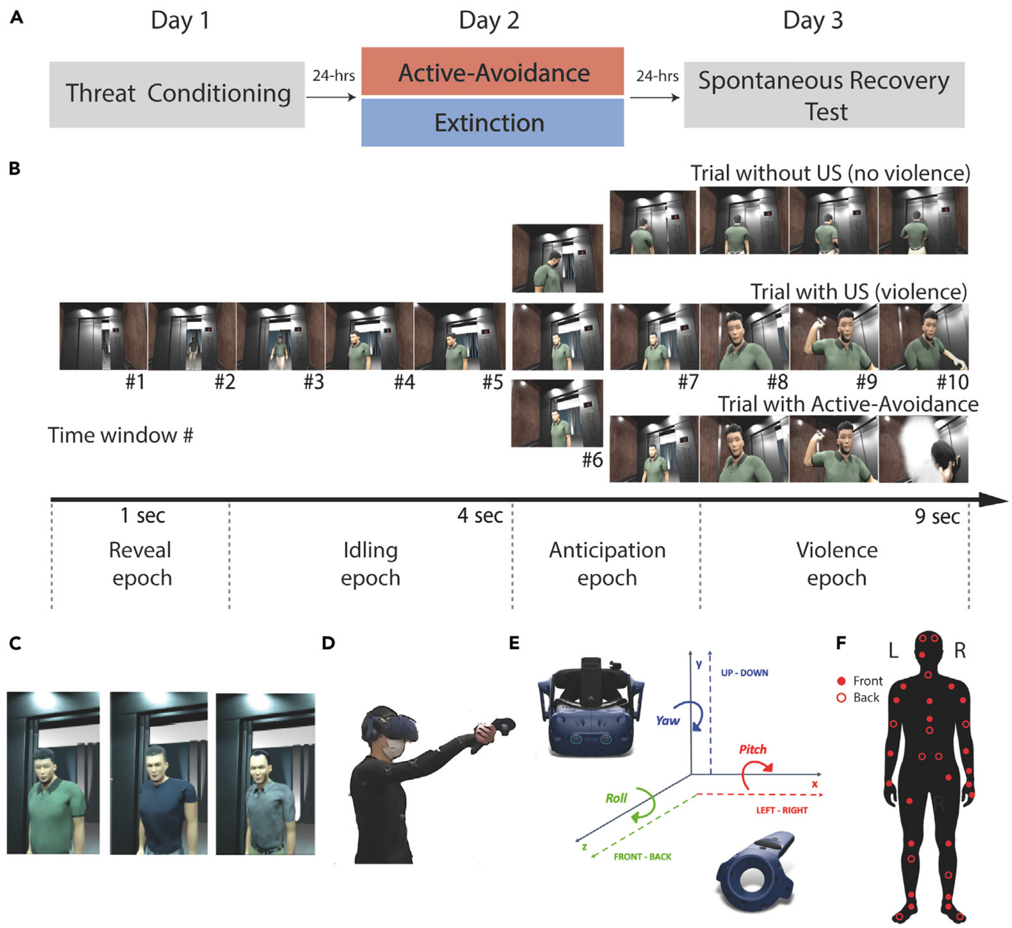

Figure 1. Schematics of the experimental design

(A) Experimental sessions across three consecutive days: Threat Conditioning (day 1; 24 min), Extinction (EXT), and embodied Active-Avoidance (ACT) training sessions (day 2; 15 min each), and Spontaneous Recovery test (day 3; 11 min). The task of participants in the Threat Conditioning session and test sessions was simply to observe the avatars throughout the session.

(B) Virtual scenes for non-violent trials (upper), violent trials (middle), and embodied Active-Avoidance trials (lower) progressed across 10 representative time windows within a trial (see Videos S1–S3).

(C) Three male avatars, two of which served as CS+s and another as CS− in a counterbalanced manner across participants.

(D) Illustration of a subject performing a defense movement in the embodied Active-Avoidance training (see Video S2). The hand-held controller in his right hand appeared as a virtual security spray.

(E) Schematics of the three-dimensional spaces capture the participant's body movements as tracked in the head-mount display and a hand-held controller.

(F) Marker distribution on the full-body motion tracking system.

long-term effect (24 h),[25,28,29,31] which outperformed the effects of extinction procedures to simply repeat conditioned cues without further reinforcement with threats.[25] Examining the efficacy of embodied active-avoidance procedures in alleviating fear memory is a critical step forward in their clinical applications. This is because post-traumatic psychopathologies emerge from various threatful experiences that require bodily actions for avoidance—such as interpersonal violence, looming vehicles, and natural disasters.[32]

The scarcity of body movement measures in studying human emotions[18,33] partly owes to a common technical limitation. That is, experimental control is typically achieved by constraining participants in a seated or laid-down posture. This limits the available actions to peripheral movements such as fingers and gaze, hindering the measurements of threat-conditioned movements and the implementations of bodily defensive actions.

To overcome these limitations, we developed a spatiotemporally dynamic threat conditioning paradigm with virtual reality (VR).[18,34–37] With the paradigm, we monitored participants' naturalistic movements in standing posture with a motion-tracking system.

For threat conditioning, participants experienced a simulated traumatic scenario of interpersonal violence (Video S1), which is one of the most common traumatic events[38,39] leading to post-traumatic stress disorders (PTSD).[40] Specifically, an avatar (CS+) inflicted threatening violence (US; unconditioned stimulus) in a 3D virtual space. For Active-Avoidance training, participants underwent the training to avoid violence through naturalistic bodily defensive movements using a virtual security spray against the CS+ avatar (Figure 1, Video S2).

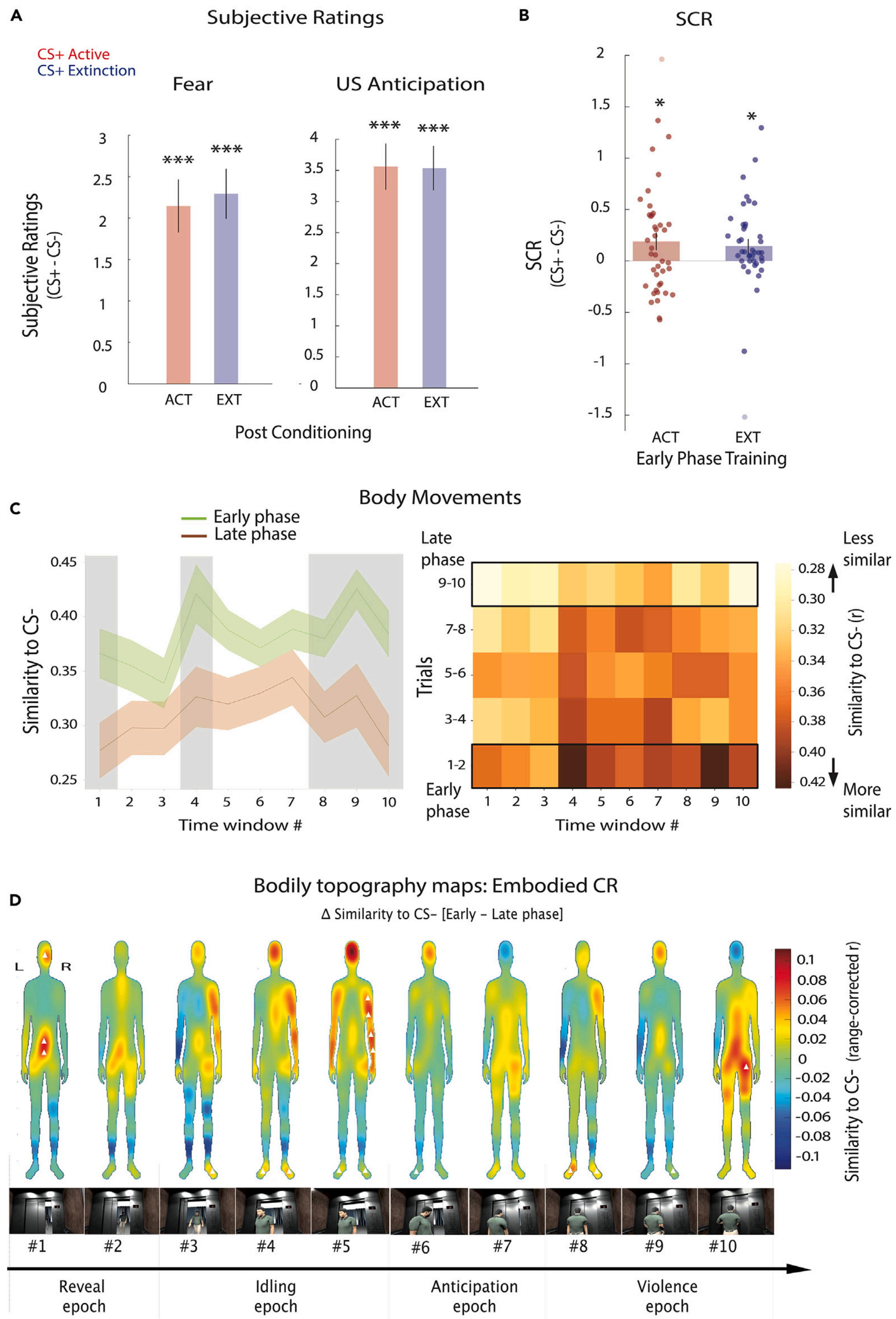

Figure 2. Threat conditioning in subjective ratings, SCR, and body movements

(A) Conditioned responses [CR: CS+ versus CS−] in subjective ratings of fear and US anticipation on day 1. Values are baseline-corrected with pre-conditioning ratings.

(B) CR in SCR during the early phase (trials 1–2) of the training on day 2.

(C) Embodied CRs captured as a decrease of similarity in body movement patterns toward the CS+s versus the CS− avatars from the early (trials 1–2) to late phase (trials 9–10) of the Threat Conditioning session. The shaded areas in the left panel indicate embodied CRs with moderate and strong evidence (BF > 3). The RSA

Figure 2. *Continued*

matrix in the right panel represents the embodied CRs (i) across 5 bins (2 trials per bin) of the Threat Conditioning session vertically (from bottom/earlier bin to top/later bin) as well as (ii) across 10 time windows (1 s each) of each trial (from left/earlier window to right/later window). Lighter colors (e.g., yellow-white) in the later phase of the Conditioning session represent stronger embodied CRs (i.e., more distinct body movements with CS+ relative to CS−). Black boxes in the RSA matrix highlight early and late phases.

(D) Maps depicting embodied CRs as threat conditioning progressed from the early (trials 1–2) to late phase (trials 9–10). In maps, the position of each bodily ROI was approximated with one of its constituent markers. Warmer colors indicate larger embodied CRs, i.e., greater CS+/CS− discrimination. For the demonstrative purpose, values (similarity to CS−, r) were corrected to restore the original min-max range after spatial smoothing per time window. Triangles (▲) in the maps indicate the ROIs with anecdotal or moderate evidence based on Bayes factors (BF). ROIs with only positive conditioning effects are shown with one-tailed Bayesian analysis for interpretation. For both SCR and body movements analysis, only the trials without violence (US) were analyzed. Error bars represent the SEM. Data are represented as mean ± between-subjects SEM. $^{*}p < 0.05$ $^{***}p < 0.001$.

First, we tested whether the acquisition of fear memory results in the adaptation of body movement patterns toward threat-predictive cues. Second, we tested whether training to actively avoid threats with naturalistic defensive movements leads to alleviation of acquired fear memories.

RESULTS

We conducted experiments across three consecutive days (Figure 1A). Two male avatars (CS+s), but not a third male avatar (CS−), intimidated and hit the participants virtually (US) on proportions of the trials, i.e., partial reinforcement (60%) (Figures 1B and 1C). In the Active-Avoidance training, participants defended themselves with a security spray to prevent violence (US) from one of the CS+ avatars (Figure 1D). Along with physiological defensive reactions as measured with SCR and subjective ratings of fear and US anticipation, the body movements of the participants were tracked with the VR head-mount-display and hand-held controller (Figure 1E) or with a full-body motion system (Figure 1F) (see STAR Methods).

Threat conditioning in subjective and physiological measures

With VR threat-conditioning, participants (N = 41) successfully acquired conditioned responses (CR; larger responses with CS+ than CS−), as evidenced by their subjective ratings of fear and US anticipation (Figure 2A).[41] After the Conditioning session, participants reported higher feelings of fear as well as higher anticipation of US (violence) with both $CS+_{active}$ and $CS+_{extinction}$ relative to CS− (Fear: $CS+_{active}$ $t[40] = 6.44$ $p < 0.001$; Bayes factors, $BF_{+0} > 100$; $CS+_{extinction}$ $t[40] = 8.00$ $p < 0.001$; $BF_{+0} > 100$; US anticipation: $CS+_{active}$ $t[40] = 9.97$, $p < 0.001$; $BF_{+0} > 100$; $CS+_{extinction}$ $t[40] = 11.72$, $p < 0.001$; $BF_{+0} > 100$; all one-tailed for predicted positive CR). Subjective ratings were statistically similar between CS+s ($CS+_{extinction}$ Vs. $CS+_{active}$; Fear: $t[40] = -0.601$, $p = 0.55$; $BF_{01} = 5.003$; US anticipation: $t[40] = 0.07$, $p = 0.93$; $BF_{01} = 5.91$).

Participants also displayed physiological CR in SCR measures 24 h following the Threat Conditioning session (Figure 2B). Specifically, CRs to both $CS+_{active}$ and $CS+_{extinction}$ were significant during the early phase (first 2 trials) of the training sessions on day 2 ($CS+_{active}$ $t[40] = 2.23$ $p = 0.016$; $BF_{+0} = 3.05$; $CS+_{extinction}$ $t[40] = 2.05$ $p = 0.02$; $BF_{+0} = 2.18$; all one-tailed), with no statistical difference between the two CS+s ($t[40] = 0.35$ $p = 0.72$; $BF_{01} = 5.58$). During the Conditioning session on day 1, SCR with both $CS+_{active}$ (M = 0.24 ± s.e. 0.02) and $CS+_{extinction}$ (0.24 ± 0.02) were higher than CS− (0.23 ± 0.02) on trials without US, indicating numerical yet non-significant CRs ($CS+_{active}$ $t[40] = 0.91$, $p = 0.18$; $BF_{+0} = 0.403$; $CS+_{extinction}$ $t[40] = 0.71$, $p = 0.23$; $BF_{+0} = 0.32$; all one-tailed) with no statistical difference between the two CS+s ($t[40] = 0.13$ $p = 0.89$; $BF_{01} = 5.88$) (Figure S1A). This overnight enhancement of CR from day 1 to day 2 likely reflects fear memory consolidation.[42–45]

Threat conditioning of human body movements

Next, we asked whether the participants also developed threat-conditioned body movement patterns. Using representational similarity analysis (RSA),[46–49] we examined whether the body movement similarity between the encounterance with CS+ versus CS− avatars decreased from the early (trials 1–2) to late phase (trials 9–10) of the Threat Conditioning session. A decrease in the similarity indicates the acquisition of distinctive body movement patterns for CS+ relative to CS−, representing embodied CRs. As in the analyses with SCR, to assess the anticipatory conditioned responses, only the trials without US were analyzed where both CS+ and CS− avatars displayed identical motion trajectories.

For RSA, body movement patterns were first quantified with the position and rotation on the 3D axes of the head and right hand (12 dimensions), which were tracked with the VR head-mount-display and hand-held controller (Figure 1E). To obtain a measure that is independent of coordinate values and unbiased by previous positions during a trial, we then calculated the absolute difference between two consecutive recorded samples (|Position[t2]-Position[t1]|) within trials, reflecting the magnitudes of movement per sample frame. To reduce the number of comparisons while retaining enough temporal resolution to examine unique epochs of the scene (e.g., anticipation of violence), the spatial pattern similarity was evaluated for 10 unique time windows within each trial (9 s in total); These captured *reveal (*Time windows *#1,2)*, *idling (#3–5)*, *anticipation (#6,7)*, *and violence epochs (#8–10)* (Figure 1B, see Videos S1–S3).

The embodied CRs were captured with strong evidence in four threat-relevant time windows (Figure 2C), as indicated by Bayes factors (BF). These included the period of the initial encounter with the CS avatars (*reveal-epoch*) and the last time windows, which correspond to the period of potential violence occurrence (*violence-epoch*; time windows #1, 8, 9, & 10: *t*-values[40] > 3.26, p values <0.001 FDR-corrected <0.05, Cohen's d > 0.51; all $BF_{+0} > 29.46$, all one-tailed given predicted embodied CRs with decreasing similarity, see Figure 2C for the results in other time windows). For time window #4, we observed a moderate effect ($BF_{+0} = 5.85$) which did not survive the multiple comparison corrections with frequentist statistics ($t[40] = 2.56$, $p = 0.007$ FDR corrected >0.05, Cohen's $d = 0.39$). These findings show that movement patterns in response to CS+ and CS− became increasingly dissimilar when fear conditioning was established. The results were qualitatively similar between the two CS+ avatars examined separately (Figure S1B).

Critically, the results were specific to threat conditioning effects as they were not replicated when examining the deviation of movement patterns between the two CS+s (see supplemental information). To unpack the spatial specificity of embodied CRs, we ran RSAs for the head and right hand separately. The results suggested that embodied CRs were more pronounced in the hand than in the head (Figure S1C).

To further elucidate the spatio-temporal dynamics of embodied CRs across the entire body, a supplementary group (N = 54; see procedures for the supplementary group in STAR Methods) completed the same Threat Conditioning session with an additional whole-body motion tracking system composed by 39 markers distributed across the body (Figure 1F) (see movement representational similarity analysis in STAR Methods). The markers were converted into 31 bodily regions-of-interests (ROIs) composed of the nearest three markers. We conducted RSAs with the ROIs. The bodily topographical maps, inspired by a previous study,[50] capture the gradients of CRs (i.e., decreased similarity in body movements between CS+ and CS− encounters) across the whole body and time windows (Figure 2D). While the maps serve demonstration purposes, we calculated Bayes factors for each ROI and time window. Of note, moderate embodied CRs were captured in the right arm toward the end of *idling-epoch* (time window #5: 1 ROI $BF_{+0} = 3.64$; one-tailed), consistent with Figure S1C. This CR was spatially distributed over the contiguous ROIs in the right arms with anecdotal evidence (time window #5: 3 ROIs $BF_{+0} > 1.24$; one-tailed).

Fear reduction effects through embodied active-avoidance

Next, we asked if the CRs can be alleviated through the embodied procedure to actively avoid harm (violence) inflicted by the CS+ avatar. For this, participants physically defended against one of the two CS+s avatars ($CS+_{active}$) in the embodied Active-Avoidance training (ACT training) while they merely observed the other CS+ avatar ($CS+_{extinction}$) without being reinforced by violence in the conventional Extinction training (EXT training) on day 2 (Figure 1B). The long-term (24 h) effects of training were tested in the early phase (trials 1–2) of the Spontaneous Recovery test on day 3 (Figure 1A) because the spontaneous return of CRs typically emerge only in the first few trials and quickly fade through additional extinction in subsequent unreinforced trials.[51,52]

Though preliminary, we found that the long-term effect of reducing embodied CRs may be more pronounced with ACT than with EXT training, as indicated by moderate evidence. In the early phase of the test, body movement patterns during CS+ encounters became more similar to CS− encounters after ACT training than EXT training (Figure 3A). This long-term effect to neutralize the body movements was observed within the threat-relevant *anticipation-epoch*, as indicated by moderate evidence when using Bayesian statistics. We did not observe an effect after FDR correction when using frequentist statistics (time windows #6 & 7: $t[40] = 2.53$, $p = 0.008$ FDR corrected >0.05, Cohen's $d = 0.40$, $BF_{+0} = 5.46$; $t[40] = 2.26$, $p = 0.015$ FDR corrected >0.05, Cohen's $d = 0.35$, $BF_{+0} = 3.20$; for all other times windows $BF_{+0} < 1.01$; all one-tailed for predicted advantage of ACT training).[25]

Similarly to the body movement results, the analyses of long-term effects with SCR in the early phase of the test revealed that only $CS+_{extinction}$ induced a significant CR ($t[40] = 2.21$, $p = 0.016$; $BF_{+0} = 2.21$) while $CS+_{active}$ did not ($t[40] = 0.76$, $p = 0.22$; $BF_{+0} = 0.34$; all one-tailed) (Figure 3B). CR to $CS+_{active}$ was not significantly different from CR to $CS+_{extinction}$ ($t[40] = -1.33$, $p = 0.09$; $BF_{+0} = 0.68$).

We next asked if any difference in fear alleviation effects of ACT versus EXT training already emerged during the training sessions on day 2. To capture this interim fear alleviation effect, we examined SCR in the late phase (trials 9–10) of each training (Figure 3D left). We did not assess the interim effects on embodied CRs because the task instruction for specific defensive actions itself altered the body movement patterns, hindering access to the embodied CRs during the training (see Figure S2).

Critically, with SCR, CRs to both $CS+_{extinction}$ and $CS+_{active}$ were no longer significant in the late training phase ($CS+_{extinction}$ $t[40] = -1.35$, $p = 0.90$; $BF_{+0} = 0.07$; $CS+_{active}$ $t[40] = 1.52$, $p = 0.06$; $BF_{+0} = 0.90$; all one-tailed), suggesting that both ACT and EXT training achieved interim effects to reduce SCR. However, CR to $CS+_{extinction}$ was lower than $CS+_{active}$ ($t[40] = 2.408$, $p = 0.02$; $BF_{10} = 4.31$) (Figure 3D left). This may not be surprising because the $CS+_{active}$ avatar continued to display precursive actions for violence (US) during the training on day 2.

These results of interim-effects, together with the results of long-term effects, suggest that ACT training resulted in a long-term reduction of SCR on day 3, although EXT training was transiently more advantageous in reducing SCR to $CS+_{extinction}$ on day 2. The differences in the effective timing were supported by an analysis of variance (ANOVA) showing a significant interaction between the training type and session (late training/early test) ($F[1,40)] = 6.65$, $p = 0.014$).

The EXT training effect may decay overnight because extinction-based procedures are prone to spontaneous recovery of once-extinguished fear responses.[53] To test this possibility, we quantified the increase of CRs from the late training on day 2 (interim effect) to the early Spontaneous Recovery test on day 3 (long-term effect) as Spontaneous Recovery Index (SRI) where interim CR is subtracted from long-term CR (long-term CR - interim CR).[25] In line with previous studies,[25,53] SRI was significant with $CS+_{extinction}$ ($t[40] = -1.97$, $p = 0.02$; $BF_{+0} = 1.90$; one-tailed) while SRI was not significant with $CS+_{active}$ ($t[40] = 0.59$, $p = 0.72$; $BF_{+0} = 0.11$; one-tailed). Critically, SRI with $CS+_{active}$ was significantly smaller than $CS+_{extinction}$ ($t[40] = -2.57$, $p = 0.007$; $BF_{+0} = 6.13$; one-tailed) (Figure 3D right).

Interestingly, the long-term effect of ACT training on SCR significantly correlated with the effect on embodied CRs (Figure 3C). In the Spontaneous Recovery test, participants with weaker CR to $CS+_{active}$ also displayed more neutralized body movement patterns to $CS+_{active}$ (i.e., increased similarity to CS−) ($r = -0.37$, $p = 0.015$). This correlation was absent with $CS+_{extinction}$ ($r = -0.01$, $p = 0.92$) with a significant difference between the CS+s (r_{active} Vs. $r_{extinction}$ $z = -1.65$, $p = 0.047$). The embodied ACT training may rely on unique fear reduction mechanisms that can neutralize conditioned body movements along with the reduction of physiological CR.

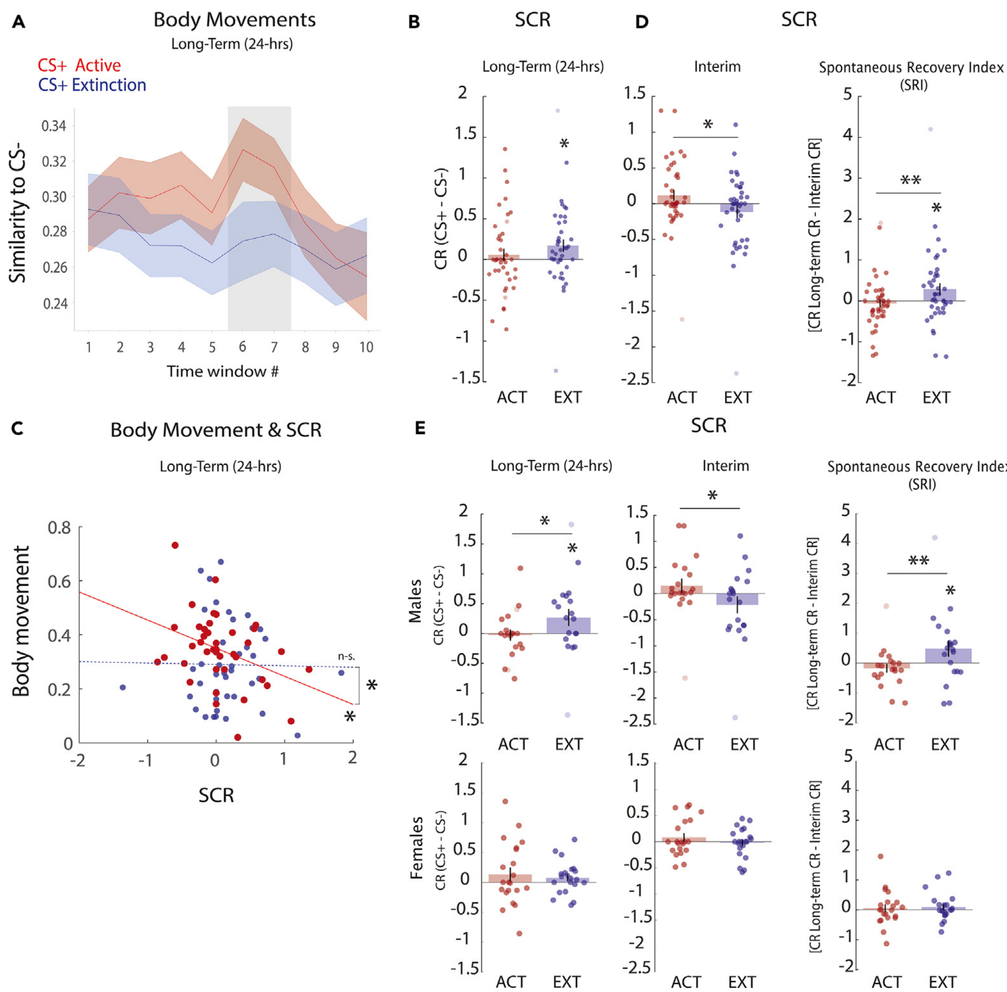

Figure 3. Comparison of fear alleviation effects between embodied Active-Avoidance (ACT) training and Extinction (EXT) training

(A) Long-term effects of ACT and EXT training on body movement patterns. Movement patterns during CS+s encounters became more similar to CS− encounters after the ACT training compared to the EXT training in *anticipation-epoch* (windows #6 & 7) as indicated by moderate evidence with Bayes factors.

(B) Long-term effects of ACT and EXT training on conditioned SCR.

(C) Correlation between CR in SCR and body movements in the Spontaneous Recovery Test 24 h after the training. Scatterplots with least-square regression lines of the intra-subject correlations between SCRs and body movements.

(D) Interim effects of ACT and EXT training on conditioned SCR (left panel) and Spontaneous Recovery Index (SRI) reflecting the difference between the interim versus the long-term conditioned SCR (right panel).

(E) The ACT and EXT training Interim and long-term effects and on SRI in female and male gender groups. All panels in Figure 3 include only the trials without US. Error bars represent the SEM. Dots superimposed on bar graphs represent individual participants' data where outliers were included in the analyses yet faded in their colors for the demonstrative purposes. Data are represented as mean ± between-subjects SEM. *p < 0.05 **p < 0.01. The shaded areas in (A) indicate moderate and strong evidence (BF > 3).

Together, although the interim effect of ACT training was transiently weaker than EXT training, the fear reduction effect of ACT training was more stable over 24 h to resist spontaneous recovery. The difference of interim effects on SCR between the training sessions could not be explained by the magnitude of body movements during the training (see supplemental information). The long-term effects of ACT training were unaffected by the training order (Figure S3A) and outliers (Figure S3B). See supplemental information for interim and long-term effects assessed with subjective ratings (Figure S4).

The ACT training may resist spontaneous recovery of CRs because it relies on a unique fear reduction mechanism than the EXT training. A conventional extinction procedure is prone to spontaneous recovery because its mechanism suppresses original fear memories.[54] In line with this, participants who showed smaller CRs to $CS+_{extinction}$ during EXT training on day 2 showed a larger return of CRs on day 3 ($R = -0.58$, $p < 0.001$; $BF_{+0} = 529.8$) (Figure S3C), suggesting that stronger suppression of CRs may result in a stronger return of CRs 24 h later. Critically, such a correlation was absent with ACT training ($r = 0.12$, $p = 0.42$; $BF_{+0} = 0.26$) with a significant difference between the training types (r ACT Vs. r EXT $z = -3.41$, $p = 0.002$), suggesting that ACT training may be more independent from the suppressive mechanisms than EXT training.

Finally, given the gender differences in treatment responses among patients with PTSD,[55] we examined potential gender differences with a conventional physiological measure of SCR (21 females, 20 males). This revealed a significant interaction between gender and training in the long-term effect (Figure 3E) (F[1,39] = 4.76, p = 0.03). Only males showed a significantly better long-term reduction of CR through ACT than EXT training (t[19] = −2.51, p = 0.02; BF_{+0} = 2.77) when females did not (t[20] = 0.53, p = 0.601; BF_{+0} = 0.25) (Figure 3E left). The analysis of SRI also revealed a significant interaction between gender and training type (F[1,39] = 5.94, p = 0.01) (Figure 3E right), suggesting how the interim effect of EXT training was outperformed by ACT training in long-term (24 h) among males. Only with males, SRI was significantly higher with $CS+_{extinction}$ than $CS+_{active}$ (t[19] = −3.27, p = 0.004; BF_{+0} = 11.18; t[19] = −3.61, *p tukey* = 0.004) while not with females (t[19] = −0.25, *p tukey* = 0.99). Gender did not interact with the interim effects alone (Figure 3E middle). These results suggest that the embodied ACT training may potentially benefit males more than females.

Fear reduction effects depend on embodiment of active-avoidance

Do fear reduction effects of ACT training depend on whether participants defend against threats through their own body movements? To test this, the supplementary group with full-body motion tracking (N = 54) (Figure 1F) underwent the ACT training either with or without their own movements in two subgroups (Figure 4A): Self-group (N = 27) physically defended themselves with a virtual security spray to prevent violence (Figure 1D), whereas Vicarious-group (N = 27) merely observed a third avatar defending with a security spray on their behalf (Figure 4B). Both groups underwent the ACT training with one of the two CS+s ($CS+_{active}$) while they underwent no training with the other CS+ ($CS+_{untrained}$). The training effect was compared between the two subgroups in the Spontaneous Recovery test 24 h later.

Critically, we found the superiority of the Self-group relative to the Vicarious-group in neutralizing the conditioned body movements (Figure 4C). Specifically, in the Spontaneous Recovery test, Self-group showed training effects to neutralize body movements (i.e., increase in movement similarity to CS− relative to no-training) in several ROIs in bilateral arms during *violence-epoch* as indicated by moderate evidence (time window #8: 6 ROIs BF_{+0} > 3.10; one-tailed) and by anecdotal evidence (3 ROIs BF > 1.25). Additionally, Self-group showed effects in *reveal-epoch* in the left arm and feet as indicated by moderate and strong evidence, respectively (Left arm: time window #1: 1 ROI BF_{+0} = 5.12; Left feet: #2: 1 ROI BF_{+0} = 63.25; all one-tailed) (see supplemental information).

On the contrary, Vicarious-group did not show any apparent training effect in any body part during *violence-epoch*. A single moderate training effect was observed only in the right leg in *idling-epoch* (time window #5: 1 ROI BF_{+0} = 4.66), with additional anecdotal effects in a few spatially sparse ROIs during *anticipation-epoch* (see supplemental information).

Moreover, long-term reduction of SCR was more robust in Self- than in Vicarious-groups (Figure 4D left). In the early phase of the Spontaneous Recovery test, only Vicarious-group showed a significant CR to $CS+_{active}$ when Self-group did not (Vicarious: t[25] = 1.96, p = 0.03; BF_{+0} = 2.08; Self: t[25] = −1.02, p = 0.84; BF_{+0} = 0.11; all one-tailed). Only Self training significantly reduced CR toward $CS+_{active}$ relative to $CS+_{untrained}$ (t[25] = −1.91, p = 0.03; BF_{10} = 1.91) when Vicarious training did not (t[25] = 1.25, p = 0.22; BF_{10} = 0.47) (Figure 4D). SRI was only significant in the Vicarious-group (t[25] = −2.36, p = 0.02; BF_{+0} = 3.90; one-tailed) while not significant in the Self-group (t[25] = 1.42, p = 0.16; BF_{+0} = 0.21; one-tailed). The long-term advantage of Self-group was also captured by a lower SRI to $CS+_{active}$ (return of CR from day 2 to day 3) than Vicarious-group (t[52] = −2.20, p = 0.03; BF_{10} = 1.97), with a significant interaction between group and CS+ type (F[1,50] = 4.68, p = 0.03) (see Figures S6 and S7 for SCR results in Renewal test and Reconditioning sessions and subjective rating results).

Together, these results suggest that long-term fear reduction effect is more pronounced with the embodied Active-Avoidance training, as the less-embodied control training with Vicarious defense training (Figure 4B) as well as Extinction training (Figure 1B) only led to a transient reduction of fear which returned 24 h later.

DISCUSSION

By tracking naturalistic body movements of participants in original ecologically valid VR paradigms, we demonstrate that adapting body movements correlates with both acquisition and modification of fear memory among humans.

Fear acquisition in body movements

First, we demonstrate that human participants acquire distinct body movement patterns through threat conditioning. In human studies, body movements have been generally overlooked compared with other common measures such as physiological, subjective, or neural responses.[17,56] Adapting body movements may thus serve as one important function of fear memories in humans.

Fear alleviation through avoidance actions

Second, we show that embodied training to actively defend against a threat achieves long-term (24 h) fear alleviation effects, reducing conditioned responses (Figure 3C). Crucially, the embodied Active-Avoidance training was resistant to a spontaneous return of physiological defensive responses (i.e., SCR), which is one of the major constraints of conventional extinction training.[53,57] Moreover, the long-term fear reduction effect of Active-Avoidance training[25,28–31] is improved through the embodiment of avoidance actions relative to the less-embodied procedures (Figures 3D and 4D).

The differences in the critical time windows for fear acquisition (window 8–10; Figure 2C) versus alleviation effects (window 6–7; Figure 3A) on body movements could suggest that the ACT training effect may not be a mere diminishment of the original embodied conditioned responses. Although speculative, ACT training effect may be more pronounced in dampening of proactive preparatory body movements prior

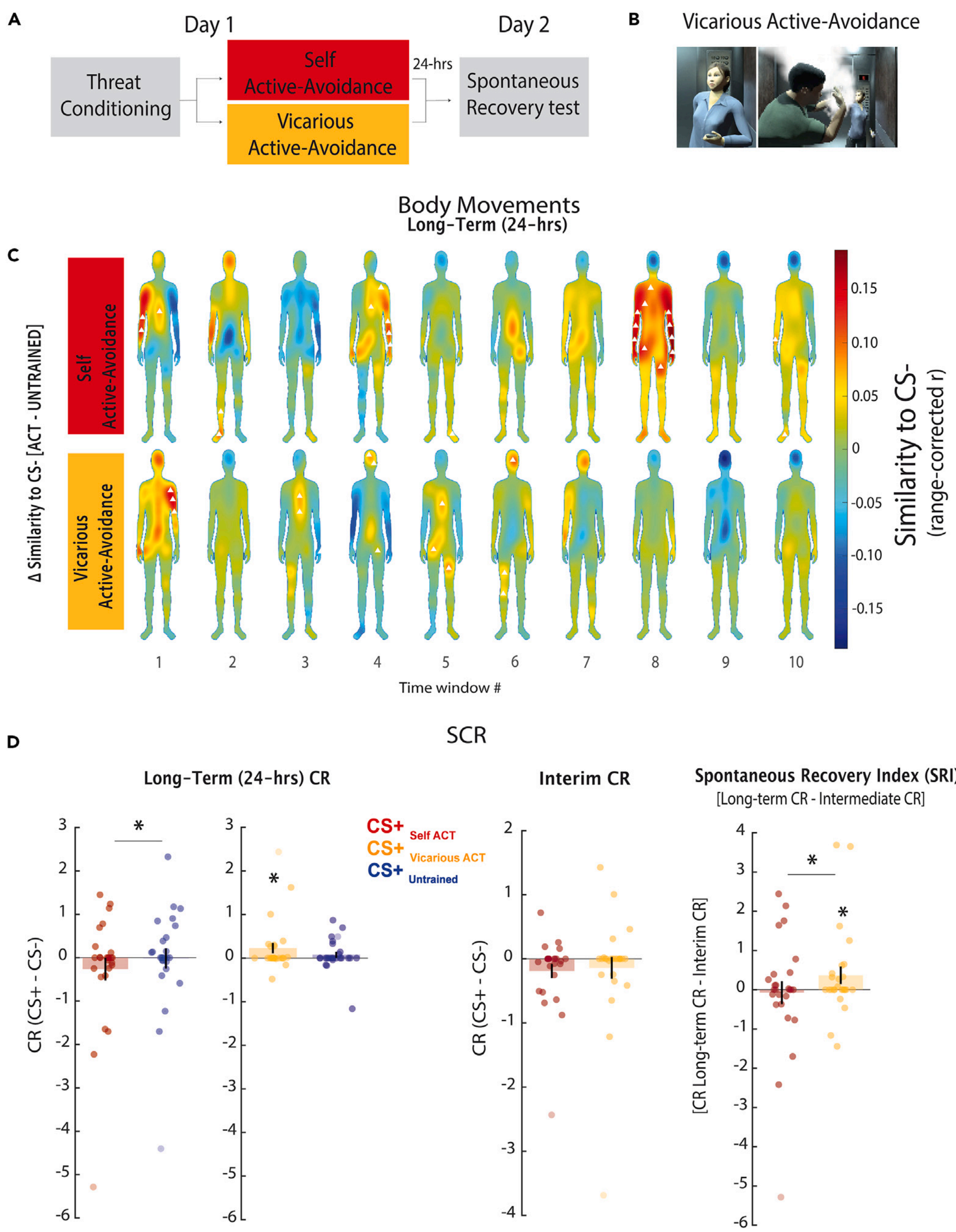

Figure 4. Comparison of fear alleviation effects between Self and Vicarious ACT training

(A) The flow of the experiment for the supplementary group across two consecutive days.

(B) Female passenger avatar defending against the violent CS+$_{active}$ avatar with a security spray on the participant's behalf in the Vicarious training.

(C) Maps depicting ACT training effects by comparing body movements with CS+$_{active}$ and CS+$_{untrained}$ in the Spontaneous Recovery test session for Self- (upper) and Vicarious-group (lower). Warm colors indicate that the ACT training rendered body movements with CS+ encounters more similar to CS− encounters compared to no training. Triangles (▲) in the maps indicate the ROIs with anecdotal, moderate, or strong evidence based on BF, where only ROIs with increased similarity to CS− movements compared to no training are shown for interpretation.

(D) Interim and long-term effects of Self and Vicarious training on conditioned SCR (left and middle) and Spontaneous Recovery Index (SRI) (right). All panels in Figure 4 include only the trials without US. Error bars represent the SEM. Data are represented as mean ± between-subjects SEM. Dots superimposed on bar graphs represent individual participants' data where outliers were included in the analyses yet faded in their colors for the demonstrative purposes. *$p < 0.05$.

to the timing of threat whereas initial fear acquisition may be more pronounced in the reactive movements during the later timing of actual threat. However, the temporal inconsistency between fear acquisition and alleviation effects is one of the limitations of this study that needs to be directly tested in future.

Fear reduction mechanisms with embodied active-avoidance

The absence of spontaneous recovery with the Active-Avoidance training may be due to the difference in the learning mechanisms between Pavlovian extinction and instrumental Active-Avoidance training.[25] With Pavlovian extinction training where conditioned cues are repeated without US reinforcements, conditioned responses are typically suppressed.[58] Meanwhile, instrumental training to exert control over threats with active-avoidance enhances the avoidance action as a behavioral outcome alternative to passive conditioned responses.[7,12] Studies have shown that when active-avoidance behaviors emerge, fear-like responses such as freezing decrease[4] and that this shift between reactive and active responses may be moderated by higher cortical areas.[7,12,25] Thus, while Pavlovian extinction training may result in mere inhibition of the conditioned responses, instrumental learning (i.e., linking active-avoidance and its outcome of threat omission) may promote alternative active behavioral responses, thereby potentially replacing reactive responses with active-avoidance responses. These differences in learning mechanisms may account for differential outcomes between the ACT and EXT training in our study.

Nevertheless, whether avoidance training benefits or harms fear alleviation may depend on experimental conditions. Studies have demonstrated that avoidance training could interfere with subsequent fear extinction training.[59] A conventional account for this interference is that the omission of the US is attributed to the avoidance action rather than to the fact that the stimulus is no longer followed by a threat.[59] Although speculative, given that social factors such as dominance modulates fear learning,[60,61] avoidance may particularly benefit fear reduction when realistic social stimuli serves as the conditioned stimuli (Boeke et al.,[25] and our current study). That is, exercising control to gain dominance over other individuals may help reduce fear toward them compared to avoiding threats associated with non-social stimuli such as geometric shapes.[59] As there are some other methodological differences among studies, future studies may directly examine how and in which circumstances Active-Avoidance training, especially when the training is embodied with actual body movements as in our study, can facilitate the fear alleviation processes in humans.[25]

A sense of control or agency over negative events has been suggested as a critical factor on fear responses to stimuli signaling threat.[62] The fear alleviation effect of the participants' own defense movement could be due to their body movement, sense of control, or both. As the sense of control is intrinsic to bodily defense movements, the contributions of movement, and sense of control may be studied more systematically in the future.

On clinical application of embodied active-avoidance

The extinction of fear in VR settings appears slightly more effective than non-VR extinction procedures.[63] Our results suggest that the efficacy of VR interventions may further improve through embodiment. Because a third of patients with PTSD do not respond to conventional exposure therapies[64–66] which are based on extinction procedure,[67] the embodied training might benefit those non-responders in future. However, we note that avoidance training may be effective only when individuals execute active-avoidance actions under their sense of control as in our study. Such active forms of avoidance should be cautiously distinguished from more passive, less-controlled forms of avoidance which are themselves considered as symptoms of anxiety-related disorders.[68,69]

Interestingly, male participants were more likely to benefit from the embodied Active-Avoidance training relative to the Extinction training (Figure 3E). As the use of only male violent avatars limits our interpretation of the participants' gender effect, future studies should more directly test the gender effect.

Our study suggests that virtual violence could serve as a novel US to induce threat conditioning in humans. As conventional studies typically rely on a small repertoire of US such as electric shocks and noxious sounds,[20,70] virtual violence could enhance the ecological validity and clinical translatability of fear memory studies in the future.

Limitations of the study

The Active-Avoidance training involved precursive actions of violence and thus transiently led to higher SCR to CS+ than the Extinction training during the training sessions (Figure 3D). This suggests a potential limitation of the ACT training that participants could momentarily experience more physiological reactions to the threats during the training. Thus, embodied Active-Avoidance training may be applied to reduce fear among individuals who can readily tolerate those temporarily elevated reactions.

In summary, we demonstrate that body movements correlate with fear learning and alleviation in humans. The findings may benefit the field by calling to re-centralize the body in research of human fear and its disorders such as PTSD.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
  - Lead contact

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2024.109099.

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DECLARATION OF INTERESTS

Authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw data	Dryad	https://doi.org/10.5061/dryad.bcc2fqzj3
Software and algorithms		
Tobii Pro Lab software	Tobii	ver 1.145.28180 https://www.tobii.com/products/software
Unity	Unity	ver 2019.3.0 https://unity.com/
OptiTrack Motive	OptiTrack	ver 2.3 https://optitrack.com/software/motive/
MATLAB	MathWorks	ver R2019b https://www.mathworks.com/
Python	Python	ver Python 3.8.1 https://www.python.org
Other		
Shimmer3 GSR	LoAndStream, Shimmer®	ver 0.11.0 https://shimmersensing.com
HTC VIVE Pro Eye	HTC Vive	ver 2019 https://www.vive.com/eu/product/vive-pro-eye/overview/
Motive OptiTrack	OptiTrack	Flex13 https://optitrack.com/cameras/flex-13/specs.html

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Maria Alemany-González (marialemany1991@gmail.com).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- Data have been deposited at Dryad and are publicly available as of the date of publication. The DOI is listed in the key resources table.
- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Forty-one adults (20 males, Mean age = 25 $\pm$ 6 years old) without any fear of violence or a reported history of traumatic events (e.g. personal abuse), anxiety or related disorders were paid to participate in the three-day experiment (8000 yen per day including agent charge). All participants were Asian and were recruited from a general population through a temp staff agency and the experiment was conducted in an experimental room at Tobii Japan. The study was approved by an IRB committee at Sony (Tokyo). All participants provided written informed consent prior to their participation. The sample size was estimated with power analysis based on our pilot study using G*power 3.1.9.6.[71] We estimated sample size as follows. To detect a conditioning effect in our virtual Conditioning session (the difference in SCR between CS+ and CS−) with a one-tailed t-test yielding an effect size of dz = 0.54 with a power of 0.95, the required sample size was estimated to be $N = 39$. The sample size was rounded to 40 participants to ensure counterbalancing. We obtained data from an extra participant because one participant did not complete the last session of no main interest (i.e., reconditioning). The data for all 41 participants were included in the data analyses. This sample size is similar to a previous study with active-avoidance among 28 human participants.[25]

METHOD DETAILS

The instructions were given to participants verbally along printed text instructions prior to each experimental session (Figure S8).

Threat Conditioning session

Two male avatars (CS+s), but not a third male avatar (CS−), intimidated and hit the participants virtually on proportions of the trials (Figures 1B and 1C, see Video S1). Here, violence by CS+ avatars served as an unconditioned stimulus (US). The three avatars appeared on 10 trials each without showing any violence. Two of the avatars appeared on an additional 15 trials with violence, hence they both served as CS+s with partial reinforcement (60 %). One avatar never appeared with violence and thus served as a CS−. The assignment of the three avatars to each CS was counterbalanced across participants.

On each trial, a participant was virtually situated in an elevator (Figure 1B, see Videos S1–S3): After 4 sec, the door of the elevator opened and one of the three male avatars CSs entered the elevator and the door was closed. In safe trials without violence, the avatar idled with his body facing toward the participant for 2 s and then turned around to face the closed door to remain standing semi-still for the rest of the trial (8 sec). On the trials (CS+) with violence, an avatar entered the elevator and idled with identical movements as in safe trials (CS−). However, after 6 s the avatar quickly walked toward the participant and raised his right arm to hit the participant's head. The hitting action by the avatar was accompanied by a corresponding sound effect. The opening of the elevator door was also accompanied by a sound effect and the background machinery noise of the elevator was constantly played throughout each trial to enhance a realistic VR experience. Each trial lasted 15 sec and the inter-trial interval was 6 sec.

The experience of being hit virtually served as threatening unconditioned stimuli (US). Three avatars were all males to reflect the relatively higher prevalence of violent incidence by males and related psychological traumas.[37]

The trial order was pseudorandomized with the restriction that no more than two consecutive trials of the same condition occur (e.g., a male avatar A with violence) to avoid habituation.[17] Each of the initial two trials was always with one of the two CS+s avatars with violence in a counterbalanced order across participants. This was to boost expectation for threat in the session[72] and to avoid inducing any difference in potential *blocking* of conditioning effects[73,74] due to unequal numbers of safe trials with the two CS+s prior to the occurrence of initial violent trials.

For movement analysis, CR (CS+>CS−) was averaged across the first 2 trials [early phase] and the last 2 trials [late phase] of the Threat Conditioning session.

Training sessions

Two training sessions, the embodied Active-Avoidance (ACT) and Extinction (EXT) sessions, were conducted in a counterbalanced order separated by a 15 min break. Only one of the CS+s appeared during the ACT session ($CS+_{active}$) and only the other CS+ appeared during the EXT session ($CS+_{extinction}$), along with the CS− in both sessions.

In the ACT session, participants positioned their bodies and pulled the lever on the controller to virtually emit the white mist against the avatar to defend themselves and prevent violence (US) from one of the CS+ avatars ($CS+_{active}$) (Video S2, Figure 1D). Upon the spraying, the avatar displayed suffering with his hands covering his face (Figure 1B, see Video S2). $CS+_{active}$ and CS− appeared 25 and 10 times, respectively. Among the trials with $CS+_{active}$, $CS+_{active}$ appeared 15 times showing the common entering and idling actions followed by preparatory actions for hitting (i.e., approaching a participant to raise an arm over the participant) as in the first 9 sec of the CS+s trials in the Conditioning session (Figure 1). Here, $CS+_{active}$ trials never ended with actual hitting (US) due to the preventative defense of spraying by participants. In a small proportion of trials (0.32 % among all participants) where participants did not execute the defense action within a time window (0.7 sec from the initiation of violent precursive movement by the $CS+_{active}$ avatar, i.e., raising arm), the $CS+_{active}$ avatar kept intimidating the participants with his lifted arm without resulting in actual hitting. Thus, none of the $CS+_{active}$ trials was followed by the US during the training. In the remaining 10 trials, $CS+_{active}$ showed no sign of violence as in the trials with CS−.

In the EXT session, participants were repetitively exposed to the other CS+ ($CS+_{extinction}$) avatar without further reinforcement by violence (Video S3). The $CS+_{extinction}$ avatar appeared 25 times with the same action as the CS− avatar (i.e., no violence) along with CS− appearing 10 times. Thus, the total number of trials (35) was identical to that of the ACT session. In the EXT session, participants were simply instructed to observe the avatars.

The context of the two training sessions was the identical elevator space as in the Threat Conditioning session. In the ACT session, the first two trials were always without precursor actions for violence to avoid the overestimation of the violence frequency in the upcoming trials[72] relative to the EXT session.

For SCR and movement analysis, CR (CS+>CS−) was averaged across the first 2 trials [early phase] and the last 2 trials [late phase] of both training sessions.

Spontaneous Recovery test session

Participants encountered both $CS+_{active}$ and $CS+_{extinction}$ avatars without violence and we tested for the return of threat-conditioned responses in the spontaneous recovery test session. $CS+_{active}$, $CS+_{extinction}$ and CS− avatars appeared 8 times each. The first trial was always with a CS− to capture an irrelevant orienting effect and its data was not included in the analysis.[25,75] For SCR and movement analysis, CR (CS+>CS−) was averaged across the first 2 trials [early phase] of the test session.

Participants underwent an additional test session with a new context (Renewal test) and a Reconditioning session. The participants did not hold the virtual security spray during the test sessions.

Participants underwent an additional test session (renewal test) with a new context (dimly lit virtual elevator) and Reconditioning session. As the conditioned responses were diminished through extinction during the unreinforced trials from the spontaneous recovery test, the results of the Renewal test and the Reconditioning session are presented in supplemental information (Figure S5).

Rating sessions

Participants provided subjective ratings on their fearful feelings and US anticipation[41] upon seeing the CS avatars in a virtual elevator. Throughout the experiment, they provided ratings 6 times in total; before and after the Conditioning session, after the Active-Avoidance, after the Extinction sessions, after the Renewal test, and after the Reconditioning session. They underwent rating sessions as separate sessions from other experimental sessions (e.g., Conditioning session). Participants provided verbal reports of their ratings on a seven-point scale, and an experimenter recorded the ratings. They were asked to rate "How fearful do you feel seeing this man?" and "How likely do you feel this man will inflict violence on you" in this order (Figure S9). Instructions were given verbally before the experiment. Specifically, they were instructed to report their ratings intuitively without thinking too hard.

Mirror sessions

Prior to each experimental session, a participant was virtually situated in the back corner of an elevator for one minute to enhance an immersive feeling.[76] The elevator was identical to the experimental sessions except that a mirror appeared toward the wall on the left side from the participant. A mirror reflected him or herself as a human-like avatar. The avatar-self was semi-personalized to match the gender of each participant. A participant was asked to move around his or her body to observe the corresponding movements of the avatar-self. Only prior to the ACT session, the avatar-self appeared with a spray in the right hand. The position of the hand-held controller was reflected as a virtual defense spray can in the hand of a participant's avatar-self, and pulling a lever on the hand-held controller resulted in triggering to emit virtual mist from the spray can. The participant practiced for one minute to position their bodies to trigger a virtual defensive spray to exert active-avoidance movements. In all sessions, the movements of the participants were constantly reflected in the movement of their avatar self.

Procedures for the supplementary group

Fifty-four adults (27 males, Mean age = 23 $\pm$ 3 years old) were enrolled as the supplementary group. They were recruited from university students through SNS and word of mouth. The experiment was conducted at the Psychology Department of the University of Tokyo. All participants provided written informed consent prior to their participation. The supplementary group was divided into two sub-groups (Self-group: N = 27, 14 males, Mean age = 24 $\pm$ 2; Vicarious-group: N = 27, 13 males, Mean age: 24 $\pm$ 3). One participant from the Self-group stopped the experiment due to a malfunction of the equipment and the data was not included.

We conducted the experiment in the supplementary group across two consecutive days. The Conditioning session was identical to the main experiment, and some modifications were introduced only during the ACT training sessions (day 1) and spontaneous recovery tests (day 2). The overall procedure for the supplementary group was similar to the main experiment with four exceptions:

(1) In the ACT training session, participants in the Self-group underwent the same procedure as in the main experiment, where they actively defended themselves with a virtual security spray to prevent violence. Participants in the Vicarious-group observed a third-passenger avatar defending against the violent avatar with a security spray on their behalf. In both groups, the third avatar accompanied the participants in the training sessions to equate the potential effect of social presence in fear responses[77] with the Vicarious-group. The third avatar was a female passenger that stood in front of the participant's standing position, facing the center of the elevator, in front of the number button on the right side of the elevator door (Figure 4B). The gender of the third avatar was fixed to be female across participants to make her clearly distinguishable from the CS male avatars so that participants would not potentially anticipate threat (violence) from the third avatar. When the male avatar CS was going to attack in the Vicarious ACT training session, the third avatar sprayed the virtual security spray toward the head of the avatar at the time when the paired Self-group participant sprayed on the same trial. When the avatar CS did not inflict violence, the third avatar operated her smartphone to reflect a common encountering scene with others in an elevator. The third avatar, however, lowered her smartphone and looked up at the male CS avatar when the participants in the Self-group initiated the spraying action, as the absence of reaction from the third avatar would otherwise appear unrealistic. Since subjects did not undergo EXT training, one CS+ was associated with ACT training ($CS+_{active}$) and the other CS+ was untrained ($CS+_{untrained}$). None of the participants in the Self-group failed to execute defense action on any of the trials of the ACT training session. Thus, none of the participants from both the Self- and Vicarious-group experienced violence during the ACT training.
(2) Since the aim with the supplementary group was to compare the alleviation of fear responses to $CS+_{active}$ between the groups, we did not include the EXT training as a reference. Instead, participants underwent the ACT training with one of the two avatars ($CS+_{active}$) while the other CS+ received no training ($CS+_{untrained}$).
(3) Both conditioning and ACT training sessions were conducted on day 1.
(4) After the test session, the supplementary group additionally underwent a second test and Reconditioning sessions. Briefly, we conducted the second test in the same context (i.e., fully lit elevator) as in the Conditioning session but with a third avatar (Figure 4B) from ACT training sessions to examine the effect of social presence on fear memory retrieval. Participants were informed that a

passenger would appear prior to the second test. As the conditioned responses were weakened through extinction during unreinforced trials from the first spontaneous recovery test, the details of those sessions are presented in Figure S6.

Equipments

The image presentation and the recording of the tracked data were controlled by a laptop (G-Gear: N1588J-710/T) with NVIDIA® GeForce RTXTM 2070, Intel® CoreTM i7-9750H processor, and Windows 10 Pro. Eye-tracking was calibrated with the Super Reality (SR) runtime implemented in the HTC VIVE Pro Eye prior to each experimental session. Their skin conductance was measured by wireless Shimmer3 GSR (LoAndStream v0.11.0, Shimmer®) with its electrodes attached to the participants' left palm. The skin conductance signal was recorded at 250 Hz with a Tobii Pro Lab software (ver 1.145.28180) installed in another laptop (Dell: Precision 7720) with Windows 10 Pro. The interactive VR images were programmed with the Unity 2019.3.0 and were presented at 60 Hz with a head mounted display, the HTC VIVE Pro Eye (2019, https://www.vive.com/eu/product/vive-pro-eye/overview/).

Equipments for body movement tracking

Positional and rotational data of head positions (x, y, z) were also enabled by the HTC VIVE Pro Eye and the tracking of hand positions (x,y,z) were obtained by the Vive Trackers bound to the right hand. Both head and hand motions of the subject in the VR were continuously tracked at 60 Hz during all experimental sessions for both the main and supplementary group. We obtained head and hand positions and rotations across the three axes (x, y and z) (Figure 1E). The sensor measurements of the trackers are provided in a head-fixed coordinate system where the x-axis points to the right, the y-axis points upward and the z-axis points forward.

Only in the supplementary group, their body movements were additionally tracked by Motive OptiTrack Flex13. Specifically, the position on the 3D axes of 39 markers were tracked. Four markers for a head were placed on the nearest surface of the VIVE headset to keep the markers visible for tracking. Eight OptiTrack Flex13 cameras captured the motion of 39 markers and were recorded with the OptiTrack Motive 2.3 software at 120 Hz.

QUANTIFICATION AND STATISTICAL ANALYSIS

Subjective ratings

Subjective ratings on fearful feelings and US anticipation were analyzed separately. Differential subjective ratings for both CS+s were calculated relative to the CS− within the same rating sessions (i.e., subjective CRs). Pre-conditioning ratings were used as baseline to correct ratings in each session.

Exceptionally for the two post-training rating sessions, subjective ratings were analyzed for CS− and only one of the CS+s which appeared during the training session immediately before the rating session. This was to avoid including the rating data for the untrained CS+ due to the counterbalanced order of the two training sessions across participants.

SCR

SCR data were low and high-pass filtered (0.015 - 0.05 Hz) with an FIR (Finite Impulse Response) filter,[78] detrended and normalized. The SCR onsets and peaks were automatically detected by Tobii Pro Lab software (Tobii Pro AB (2014). Danderyd, Sweden). The cumulative SCR was computed as the summation of all the trough to peak amplitude deflections of individual SCR(s) within each trial, to effectively quantify the responses during the relatively long trial (14s) with a naturalistic VR scene with dynamically changing CS avatars. Only when the peaks and corresponding onsets of individual SCR(s) were observed within a trial, their values were accumulated as they may otherwise reflect irrelevant responses to the start or end of a trial. The trials with US or active-avoidance actions from any session were not included in the analysis.

The cumulative SCR was log-transformed as log(SCR+1)[79,80] and scaled to the maximum cumulative SCR of the CS trials (not followed by US) of the Conditioning session. The test sessions always started with one CS− presentation to capture the orienting response and was not included in analysis.

Movement Representational Similarity Analysis

To investigate the relationship between body movement and learned threat associations we used Representational similarity analyses (RSA).[46–48] We calculated the similarity of body movements upon seeing different CS avatars based on the position and rotation of both head and hand for the three axes (12 dimensions, see Figure 1D). The trials with US in all sessions were removed from the analyses to reflect the movement pattern deviations in learned anticipation of violence.

The RSA was first conducted to assess threat conditioning by comparing the CS+s to CS− similarity between the early and the late phases of the Conditioning session (trials 1-2 versus trials 9-10, one-sided paired t-tests). We expected the CS+s to CS− similarity to decrease in the late phase of the Conditioning session due to the emergence of threat conditioning effects in body movements. Second, RSA was performed to compare the effect of embodied Active-Avoidance and Extinction training on spontaneous recovery on day 3 by comparing $CS+_{active}/CS-$ similarity versus $CS+_{extinction}/CS-$ similarity in the first two trials of the test session. We expected the ACT training to be more effective in reducing the fear response, resulting in greater $CS+_{active}/CS-$ similarity compared to $CS+_{extinction}/CS-$ similarity. For the RSA analyses, we used the NeuroRA (https://neurora.github.io/NeuroRA) toolbox.[47]

Motion tracking with VR system

To obtain a measure that is independent of coordinate values and unbiased by previous positions during a trial, we calculated the absolute difference between two consecutive recorded samples $\sum(|\text{Position}(t2)\text{-Position}(t1)|)$ within trials. This yielded a measure of sample-by-sample change in the movement for each of the 12 movement parameters. For all analyses, CS+s trials with a US (violence) were discarded, such that the remaining CS+s trials were identical to the CS− trials except for the avatar identity ($CS+_{active}$, $CS+_{extinction}$, or CS−, see Figure 1C). Next, to reduce the number of comparisons we divided the data within a trial into 10 time-windows of 833 ms (50 samples) each. We created a vector per condition (e.g., CS+ or CS−) for each participant per time window. Each vector now contained the spatial pattern of movement (12 movement parameters) within a specific time window (50 time-samples), related to a particular condition. Pairwise Pearson correlations were calculated between vectors of condition pairs, resulting in a similarity measure, depicting correlations among conditions for each participant per time window. For instance, the correlation between movement in response to the CS+s and CS− avatar was provided for each time window of the trial, and for each participant a metric of how similar the movement in (non-violent) CS+s trials was relative to CS− trials. Correlation coefficients were then Fisher-transformed and compared using classical and Bayesian paired t-tests.

Tracking of 31 ROIs with motion tracking system

A set of 39 markers were distributedly placed based on the conventional body coordinate of OptiTrack covering each participant' body surface in the supplementary group (Figure 1F). Six out of 39 markers were discarded from the analysis because data was lost in 30 - 42% of the participants, and we conducted subsequent analyses with the remaining 33 markers. Additional markers with gaps longer than 10 s were discarded from one session in five participants.

The RSA analysis in the supplementary group was based on 33 markers covering both sides of the body (Figure 1F). For each body marker, we systematically grouped 2 nearest markers (including both sides of the body) to form a ROI clustering 3 markers, to examine the local, yet spatially distributed, patterns of movement. Avoiding overlaps of clusters with identical 3 markers, this procedure yielded 4 ROIs in the head, 8 ROIs in the trunk, 11 ROIs in the arms and 8 ROIs in the legs (31 clusters in total).

The recorded motion data were preprocessed with OptiTrack Motive 2.3 to fix body-position labelings of markers when their labels were swapped between markers during recording or when their labelings were lost for some data points. Gaps in motion tracking data corresponding to the time points where marker(s) were disattached or hidden by participants' body parts from the tracking cameras during less than 10 s were linearly interpolated with Matlab.

Statistical analysis

Where Shapiro-Wilk's test indicated that normality assumptions were violated, Wilcoxon correction was applied. In addition to traditional null hypothesis significance testing (NHST), we computed Bayes factors (BF) for all analyses. BF allowed us not only to find evidence for our tested hypotheses but to quantify the evidence in favor of the null hypothesis. We based our results on BF especially when it was beneficial to infer the relative degree of evidence across multiple time windows (10) within a trial to capture the temporal dynamics in the body movement analyses. For the Bayesian analyses, a Cauchy prior distribution centered around zero was used with an interquartile range of r = 0.707. All analyses were performed using JASP (Version 0.16).

We used paired one-tailed t-tests and directional Bayesian t-tests (BF_{+0}) in examining the predicted general conditioned effect (i.e., larger responses to CS+s than to CS−), general spontaneous recovery after both trainings (i.e., larger CR on day 2 [early phase test] than on day 1 [late phase training]), and the advantage of the ACT training than EXT or no-training. Specifically, we predicted more robust long-term (24 hrs) fear reduction effect (e.g., weaker CR in the long-term test) as well as the reduced spontaneous recovery after the ACT training than the EXT or no training, based on previous literature.[25] Otherwise, we used two-tailed t-tests and non-directional Bayesian t-tests (BF_{10}). To test for evidence supporting the null hypothesis, we performed Bayesian paired samples t-tests (BF_{01}). We used a common interpretation of the Bayes factors (BF 1-3: anecdotal evidence, BF 3-10: moderate evidence, BF>10: strong evidence).[81] For the classical t-tests of body movement similarity conducted across 10 time windows, we corrected for multiple comparisons by fixing the false discovery rate (FDR) at 0.05.[82]

We did not exclude any participants based on the absence of differential SCR to CS+s relative to CS− during the conditioning because those with less differential CR could be more prone to anxiety and thus represent a relevant cohort in fear memory research.[20,83] In addition, we did not use SCR as exclusion criteria given that we aimed to evaluate the degree of threat-conditioning multidimensionally, not only with SCR but with additional measures of bodily movements and subjective ratings. However, we shared how results remain quantitatively similar after removing SCR-based outliers across sessions. The changes in SCR and movement data within or across sessions were analyzed by examining responses in the early and late phases (two trials each) within a session. As the subjective ratings were collected only once after each session type, the data were not divided into smaller phases.

To examine the effects of participants' gender and training order on fear attenuation and the effects of ACT training type (Self- versus Vicarious-group) on fear attenuation in the supplementary group we used Repeated Measures ANOVA and Tukey test for multiple comparisons.