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Bidirectional cross-modal fear generalization: semantic similarity in representation space as a foundational mechanism

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Abstract

Fear generalization is vital for human survival in the complex, multimodal environments. Despite extensive research on fear generalization within sensory modalities, our theoretical understanding of cross-modal generalization mechanisms remains unclear. To fill this gap, this study conducted two experiments (total *N* = 95) to investigate bidirectional cross-modality fear generalization in individuals with high and low anxiety levels: Experiment 1 used an auditory conditioned stimulus (CS) and visual generalization stimuli (GSs), while Experiment 2 used a visual CS and auditory GSs. Participants underwent fear conditioning and generalization tasks, measuring shock expectancy ratings, skin conductance responses, and prefrontal cortex activation via functional near-infrared spectroscopy. Critically, we demonstrate that fear generalized cross-modally in both directions—from auditory to visual and from visual to auditory—with auditory-to-visual generalization being significantly stronger than the reverse, indicating an asymmetric pattern. Furthermore, high-anxiety individuals exhibited elevated shock expectancy and skin conductance during generalization, alongside reduced medial prefrontal cortex activation. These findings demonstrate that semantic similarity in mental representational space fundamentally governs associative learning across sensory boundaries, and that bidirectional cross-modal fear generalization is asymmetrical. Moreover, we provide evidence of excessive cross-modality fear generalization in subclinical anxiety, enhancing understanding of anxiety mechanisms and fear-related disorders.

Keywords **fear generalization, cross-modal, anxiety, medial prefrontal cortex, semantic similarity**

Introduction

In a dynamic environment, adapting to surroundings, such as assessing whether an object is threatening based on previously learned experiences, is crucial for survival. Fear generalization, the tendency for fear responses to extend from a known threat to novel but similar contexts, is a crucial adaptive mechanism in complex environments. Extensive research on fear generalization mechanisms typically employed classical conditioning paradigms, focusing on within-modality transfer (e.g. vision or audition) and using stimuli that varied along single dimensions like size or color (Lissek *et al.* 2008, Vervliet *et al.* 2013, Dou *et al.* 2021, Fraunfelter *et al.* 2022, Sih *et al.* 2023, Zaman *et al.* 2023a, 2023b, Yu *et al.* 2025, Zhang *et al.* 2025).

However, our complex real-world environment is rich with multimodal stimuli, encompassing diverse visual, auditory, olfactory, and gustatory inputs. Consequently, individuals frequently encounter novel stimuli that differ in sensory modality from past experiences. For instance, after being bitten by a dog, one may develop fear triggered solely by barking sounds, even without visual cues. Such transfer of learned fear across sensory modalities is clearly adaptive, enabling organisms to respond to potential threats even when the available sensory information differs from that present during the original learning experience. The research on cross-modality generalization is still in its infancy. Specifically, Gerdes *et al.* (2020) pioneered the exploration of cross-modality generalization, demonstrating that conditioned fear of a visual stimulus (e.g. a picture of a telephone) could generalize to semantically related auditory stimuli (e.g. a phone

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ring). Moreover, one of our previous studies investigated whether auditory learned fear (i.e. sparrow calls) would generalize to visual stimuli and, crucially, whether the extent of this cross-modal generalization varied as a function of semantic typicality (high: pigeon, moderate: duck, low: goat), with the results revealing a graded cross-modal generalization pattern (Liu *et al.* 2025). However, there are still two unanswered questions. On the one hand, semantic representations may differ across sensory modalities rather than being fully equivalent. For example, visual and auditory concepts appear to be processed differently, with evidence suggesting that visual semantic representations are accessed more quickly and accurately than auditory ones (Palmiero *et al.* 2014). If cross-modal fear generalization depends on semantic representations, these modality-specific differences raise the possibility that generalization may not be symmetrical across directions. In other words, fear learned through auditory stimuli may generalize differently to visual stimuli than fear learned through visual stimuli generalizes to auditory stimuli. However, previous studies have typically examined only one direction of cross-modal generalization (e.g. visual-to-auditory or auditory-to-visual), leaving bidirectional cross-modal fear generalization largely unexplored. On the other hand, although prior work has demonstrated the existence of cross-modal fear generalization, the mechanisms underlying this phenomenon remain poorly understood.

Shepard (1987) proposed that generalization depends on the psychological distance between stimuli in an abstract mental space, such that conceptually closer stimuli (have a smaller distance) should evoke stronger generalized fear responses. However, evidence from conceptual fear generalization suggests that similarity-based accounts may not fully capture how humans generalize fear. Dunsmoor and Murphy (2014) showed that conceptual fear generalization is shaped by category-based induction, revealing an asymmetry effect such that fear learned for a typical category exemplar generalized to atypical exemplars, whereas fear learned for an atypical exemplar showed little or no transfer to typical exemplars. This pattern parallels the well-established reliance on category typicality in human inductive reasoning and has therefore been interpreted as a challenge to Shepard's psychological distance theory, which assumes that the distance between two objects is fixed and thus should yield symmetrical generalization (Dunsmoor and Murphy 2014). However, a recent preregistered study failed to replicate this asymmetry principle in conceptual fear generalization (Zaman *et al.* 2026). Critically, despite the central role of (conceptual) similarity in generalization theories, its role in cross-modal fear generalization has not yet been directly investigated. Importantly, the directional asymmetry investigated in the present study—whether fear generalizes more strongly from auditory to visual stimuli or from visual to auditory stimuli—is conceptually distinct from typicality-based asymmetry, as it concerns differences in representational quality across sensory modalities rather than category structure within a single modality.

To test whether similarity modulates cross-modality generalization, it is of significance to build a stimulus space based on similarity distances between stimuli before fear generalization occurs. Thus, we focused on the semantic similarity distance between visual and auditory stimuli in a semantic representation space established by the multidimensional scaling (MDS) method. The MDS, a statistical method developed by has been instrumental in quantifying psychological concepts. This technique creates a multidimensional mental space based on similarity ratings between different stimuli. In recent years, MDS has been widely adopted for quantifying semantic representation across various fields (Dalton *et al.* 2008, Jiang *et al.* 2022, van der Klis and Tellings 2022). Although previous fear generalization studies emphasized the importance of semantic similarity (Gerdes *et al.* 2020, Liu *et al.* 2025), the quantitative relationships between semantic similarity in a representation space and bidirectional cross-modality generalization have not yet been examined.

Although adaptive fear generalization helps handle potential dangers, excessive fear generalization to safe situations can lead to unnecessary avoidance and may contribute to clinical anxiety (Kessler *et al.* 2005, Baxter *et al.* 2014). A wealth of clinical research indicates that overgeneralization is a core feature of various anxiety disorders, including generalized anxiety disorder (GAD), posttraumatic stress disorder, and panic disorder (Lissek *et al.* 2010, 2014, Lis *et al.* 2020). Anxiety patients exhibit impaired safety discrimination, leading to greater fear generalization from dangerous to once-safe stimuli, thereby blurring fear response boundaries (Lissek *et al.* 2014, Lissek *et al.* 2014, Dymond *et al.* 2015, Ahrens *et al.* 2016). This pattern is consistent with contemporary theories of anxiety, which propose that pathological anxiety is characterized by excessive anticipatory responding under uncertain threat and by difficulty tolerating ambiguity (Grupe and Nitschke 2013, Carleton 2016). Importantly, such ambiguity may be especially relevant in cross-modal contexts, because visual and auditory stimuli differ in the nature of their semantic representations. Compared with visual representations, which are generally clearer and more stable, auditory representations tend to be more transient, context dependent, and therefore more ambiguous (Palmiero *et al.* 2014). From this perspective, impaired safety discrimination may increase the likelihood that semantically related cues (particularly those carried by relatively ambiguous auditory representations) are interpreted as potentially threatening, thereby promoting fear overgeneralization. Therefore, investigating the impact of subclinical anxiety levels on cross-modality fear generalization is crucial for understanding anxiety disorders, as are the neural correlates in this context.

The neural basis of fear generalization has been studied for several years (Dunsmoor *et al.* 2011, Onat and Büchel 2015, Huggins *et al.* 2021, Zhu *et al.* 2022). The main findings of previous studies demonstrated that the prefrontal cortex and limbic system influenced fear generalization (Webler *et al.* 2021, Wang *et al.* 2024). For instance, we demonstrated that HbO concentration in the prefrontal cortex tracked shock expectancy ratings across generalization stimuli (GSs) in a perceptual fear generalization paradigm (Dou *et al.* 2020). The medial prefrontal cortex (mPFC) is crucial for conceptual generalization, where fear transfers to stimuli within the same category as the CS, particularly in reinstating indirect threat memory across semantic categories (Cooper *et al.* 2024). Lesions in the mPFC have been shown to impair performance on both category and schema tasks (Giuliano *et al.* 2021). Furthermore, the encoding of objects in a conceptual space is linked to the function of the ventromedial prefrontal cortex (vmPFC) and orbitofrontal cortex (Wilson *et al.* 2014, Constantinescu *et al.* 2016). Liu *et al.* (2025) found that mPFC played an important role in cross-modal fear generalization. The prefrontal cortex is involved in copying subjective anxious feelings (Kenwood *et al.* 2022). Research involving anxiety disorder patients further highlights the significance of the mPFC in fear generalization (Greenberg *et al.* 2013, Cha *et al.* 2014).

Taken together, this research explores the cognitive and neural basis of cross-modality fear generalization in high and low subclinical anxiety groups. Specifically, we aim to first examine differences

between generalization from a learned visual threat to semantically related auditory stimuli and vice versa. Second, to explore the relationship between semantic similarity distances in the representation space and cross-modality fear generalization. Third, to assess how individuals with high anxiety (compared to low anxiety) behave during cross-modality fear generalization. Finally, to determine whether both cross-modality fear generalization and individual differences in anxiety levels modulate prefrontal cortex activity. Based on our aims and prior findings (Dou *et al.* 2020, Liu *et al.* 2025), we formulated four hypotheses. First, cross-modal fear generalization would differ by direction, such that visual-to-auditory and auditory-to-visual transfer would be asymmetrical. Second, semantic similarity would modulate cross-modal fear generalization, with semantically closer stimuli evoking stronger threat expectancy and fear responses. Third, high (compared to low) subclinical anxiety would be associated with stronger and broader cross-modal fear generalization. Finally, prefrontal cortex activity would vary as a function of both generalization strength and anxiety level.

Materials and methods

Reproducibility and open science

Although this study was not preregistered, the experimental data, materials, and study procedures are publicly available on OSF (https://osf.io/cxt26/).

Participants

Utilizing G-power, the required sample size for the experiment was estimated (Faul *et al.* 2007). Based on a previous study (Klein *et al.* 2020), with an effect size of 0.27, a statistical power of 0.95, and a significance level of 0.05, each of the two anxiety level groups required 18 participants. In Experiment 1, 120 university students were recruited via posters to complete the State-Trait Anxiety Inventory (STAI-trait). Following previous literature (Chen *et al.* 2020), we recruited the top and bottom 27% of trait anxiety scores to form the high and low anxiety groups, respectively. After careful screening, we finalized a group of 27 participants for the high-anxiety group and 28 for the low-anxiety group (see Table 1, Supplementary Material 3). For Experiment 2, a new group of 120 university students was recruited via posters to complete the STAI-trait (Shek 1993). After careful screening as the Experiment 1, we finalized a group of 20 participants for the high-anxiety group and 20 for the low-anxiety group (see Table 2). All participants were right-handed with normal or corrected-to-normal vision, had no hearing impairments or physical or mental disorders, and were well-rested before the experiment. After the experiment, participants received monetary compensation (about 10 euros) based on the duration of their participation. This protocol was approved by the Ethics Committee of Sichuan Normal University (ID: NO. SCNU-230621).

Table 1 Descriptive statistics of demographic variables and scale scores ($M \pm SD$) in Experiment 1.

	HTA ($n = 27$)[a]	LTA ($n = 28$)[b]	t	P
Age	19.59 ± 1.74	19.85 ± 1.41	−0.603	.549
Gender (male/female)	5/22	4/24	—	—
STAI_trait	59.73 ± 4.66	34.34 ± 4.46	19.964	<.001
STAI_state	48.43 ± 8.45	34 .03 ± 6.51	7.313	<.001
BDI[c]	15.90 ± 8.60	4.48 ± 4.56	6.335	<.001
IUS-12[d]	40.00 ± 5.884	38.31 ± 5.670	1.123	.266

[a] high-trait anxiety
[b] low-trait anxiety
[c] Beck Depression Inventory
[d] Intolerance of Uncertainty Scale

Table 2 Descriptive statistics of demographic variables and scale scores ($M \pm SD$) in Experiment 2.

	HTA ($N = 20$)[a]	LTA ($N = 20$)[b]	t	P
Age	19.80 ± 1.75	19.31 ± 2.01	1.022	.311
Gender (male/female)	6/14	2/18	—	—
STAI_trait	58.80 ± 4.14	32.40 ± 5.56	17.014	<.001
STAI_state	49.30 ± 12.53	29.25 ± 7.20	6.203	<.001
BDI[c]	16.95 ± 9.44	3.30 ± 4.69	5.552	<.001
IUS-12[d]	39.85 ± 8.39	34.85 ± 10.00	1.713	.095

[a] high-trait anxiety
[b] low-trait anxiety
[c] Beck Depression Inventory
[d] Intolerance of Uncertainty Scale

Stimuli

In Experiment 1, during the fear acquisition phase, a single cow vocalization served as the sole conditioned stimulus (CS). The auditory stimulus was a 3-s cow sound selected from the Chinese Affective Digital Sounds system (CADS; Liu *et al.* 2006). For the fear generalization phase, stimuli were selected from the semantic relatedness database developed by Jiang *et al.* (2022). Specifically, 27 animal images and an additional three cow images were chosen as GSs. Based on semantic similarity, the GSs were initially divided into three categories: GS1, GS2, and GS3, representing high, moderate, and low similarity to the CS, respectively. The three cow images were placed into the GS1. Because semantic similarity may vary across samples, the final classification of the three GS levels was determined using the MDS results derived from the similarity-rating task conducted in the present experiment. Each GS category contained 10 animal images. Detailed stimulus names are provided in Table S2 (see online supplementary material for a color version of this table).

In Experiment 2, during the fear acquisition phase, a cow image served as the sole CS. This image was selected from the animal image database developed by Jiang *et al.* (2022). For the fear generalization phase, auditory stimuli corresponding to the animals presented in the generalization phase of Experiment 1 were selected from the database reported by Jiang *et al.* (2022) and from the CADS (Liu *et al.* 2006). All sounds were edited in Adobe Audition to ensure consistency across stimuli: each sound was adjusted to a duration of 3 s, resampled to 44 100 Hz, and normalized for sound intensity. The three cow sounds were also placed into the GS1.

The unconditioned stimulus (US) was an electric shock applied to the left wrist of participants using electrode pads (approximately 1 cm^2 in contact area) connected to a multi-channel electric stimulator (SXC-4A, Beijing Sanxia Technology Co., Ltd.). More details of US are presented in the Supplementary Material.

Procedure

The experiment was programmed in E-Prime (version 2.0), with stimuli and fixation points presented against a black background. Upon

arrival at the laboratory, participants completed a series of questionnaires, followed by rating the semantic similarity between all stimulus materials on a 1–5 scale. Thirty-one stimuli including 30 animal images and one sound were included in the semantic similarity task. The semantic similarity ratings between each stimulus pair were collected in random order with a total of 465 trials. Before the fear acquisition task, participants underwent a test to determine their shock intensity threshold.

During the habituation phase, participants passively viewed stimuli presented on the screen for 6 s for one picture and 3 s for sound stimuli, each presented once. This phase aimed to familiarize participants with the stimuli, during which they rated the valence and arousal of the stimuli (see Supplementary Material S1). The fear acquisition phase employed a fear conditioning paradigm. After a 1-s fixation point, the CS was presented for 3 s at a uniform volume of 70. After CS+ offset, participants predicted the likelihood of an electric shock occurring following the sound (from 1 to 9, where 1 = very unlikely, 9 = very likely) and pressed the corresponding number key on the keyboard. A shock was administered after the rating. Unconditioned stimuli were presented pseudo-randomly, with a 50% contingency rate. Inter-trial intervals (ITIs) ranged from 10 to 12 s.

In the generalization phase, participants were told that the task was similar to the preceding acquisition phase and that they should use their previous learning experience to judge the likelihood of shock. This phase specifically aimed to assess generalization from an auditory threat cue to semantically related visual stimuli. After fear had been acquired to the auditory CS, participants were presented with a series of animal images and asked to rate the likelihood that each image would be followed by an electric shock on a 1–9 scale. No shocks were delivered during this phase. Therefore, participants' expectancy ratings served as an index of whether conditioned fear to the auditory stimulus generalized to the visual modality. The ITIs were randomly from 10 to 12 s. Following the generalization task, participants completed the semantic similarity rating task again, in which they rated the similarity among all stimulus materials on a 1–5 scale (see Figure 1).

Experiment 2 followed the same procedure as Experiment 1, except that the modalities of the stimuli used in the fear acquisition and generalization phases were reversed. This experiment specifically aimed to investigate visual-to-auditory cross-modal fear generalization. During the fear acquisition phase, participants were presented with a visual CS, namely an image of a cow, which was paired with an electric shock. After acquiring the visual threat association, participants entered the generalization phase, in which they were presented with auditory stimuli rather than visual stimuli (see Fig. 2). These auditory stimuli differed in their semantic similarity to the conditioned visual stimulus (see Fig. 4).

Statistical analysis

Subjective ratings

Shock expectancy ratings

Shock expectancy ratings were collected by participants pressing number keys (1–9) and analyzed using SPSS 26.0. For the acquisition phase, a repeated measures ANOVA was conducted with factors of Group (high anxiety/low anxiety) and Time (first half of acquisition/second half of acquisition). For the generalization phase, a repeated measures ANOVA was performed with factors of Group (high anxiety/low anxiety) and Stimulus Type (GS1/GS2/GS3). Stimulus Type was the within-subjects variable and Group was the between-subjects variable. Bonferroni corrections were applied for post-hoc multiple comparisons of *P* value. If sphericity assumptions were violated, Greenhouse–Geisser corrections were applied to adjust the ANOVA results. The skin conductance response (SCR) used a similar statistical analysis.

Similarity ratings and shock expectancy ratings

These ratings were analyzed using MDS techniques (Leeuw and Mair 2009) implemented in R with the smacof package (Mair *et al.* 2022). By subtracting the original pairwise similarity ratings from 5, the ratings were transformed into semantic distance scores, resulting in scores ranging from 0 to 4 (e.g. a similarity rating of 5 would be transformed into a semantic distance score of 0). These semantic distance values for all participants were averaged to obtain a matrix of average distances, which served as input for non-metric MDS analysis (Jiang *et al.* 2022) (see Fig. 2a). In the resulting multidimensional space, closer semantic distances in the results indicate greater similarity between two stimuli (Barsalou 1983). The formula of MDS is as follows:

$$\min_{\tilde{X}_1,\ldots\tilde{X}_N}\left(\sum_{i<j}(\|\tilde{X}_i-\tilde{X}_j\|-d_{ij})^2\right)$$

To analyze the relationship between shock expectancy ratings and semantic similarity distances, we calculated the correlation between these two measures for each GS. The average shock expectancy and average similarity distance were calculated for each stimulus. Furthermore, to explore the different effects of semantic distance on fear generalization between the two modality transfer types (visual threat to auditory stimuli versus auditory threat to visual stimuli), we compared the correlation coefficients (between semantic distance and shock expectancy ratings) from Experiment 1 and Experiment 2. The dynamic changes of psychological space for GS were also calculated and discussed in the Supplementary Material.

Skin conductance ratings

SCR data were collected using the BIOPAC MP160 system with electrodermal activity (EDA), with a sampling rate set to 2000 Hz. The AcqKnowledge 5.0 software was utilized for recording and analyzing SCR data. Gel-based Ag/AgCl electrodes were placed on the hypothenar eminence of the participant's left hand. A high-pass filter of 0.05 Hz was applied during SCR recordings to eliminate artifacts. Trials lacking SCR peaks (no increase during the stimulus window) were marked as zero-response trials; specifically, if the difference between the maximum and minimum amplitude of any trial during the stimulus presentation was less than 0.02 μs, it was considered a zero-response trial (Boucsein *et al.* 2012). For each trial in each phase, SCR was calculated as the difference between the maximum and minimum values during the stimulus presentation window (Dou *et al.* 2020). If the difference between the maximum and minimum SCR values was negative, the absolute value's square root was multiplied by −1 to maintain the relationship direction post-initial subtraction (Lerner *et al.* 2017). Due to equipment issues, skin conductance data for one participant in the low anxiety group were not recorded, resulting in 27 participants in the high anxiety group and 27 participants in the low anxiety group included in the analysis in Experiment 1.

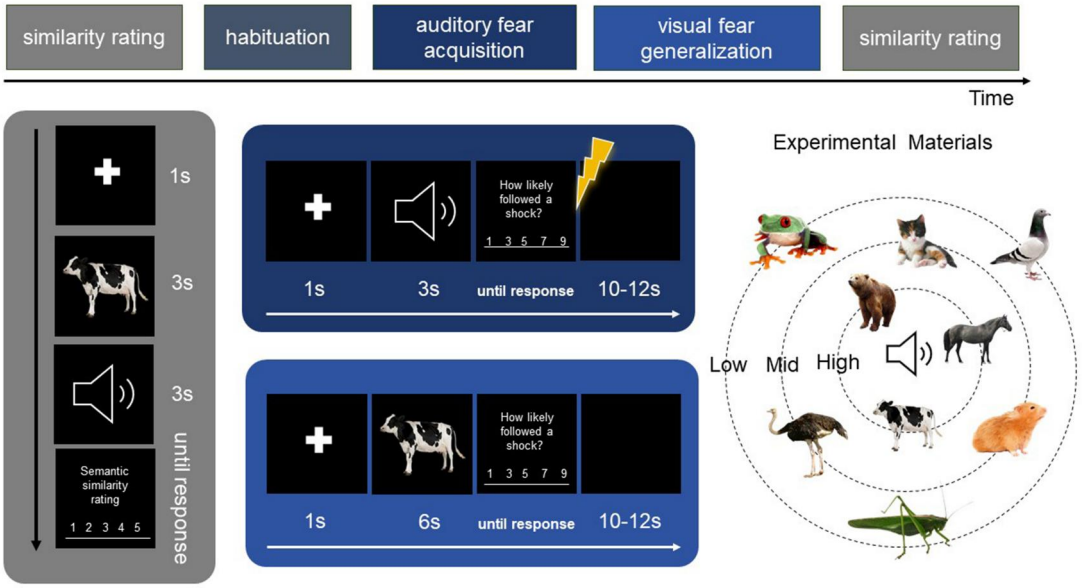

Figure 1 Procedure of Experiment 1. The experiment included similarity rating tests administered before and after the cross-modal generalization task. In the similarity rating test, pairs of stimuli were randomly presented, and participants rated their semantic similarity. The cross-modal generalization task consisted of habituation, acquisition, and generalization stages. All stimuli (sounds and pictures) were presented during habituation, the cow sound was paired with shock during acquisition, and all visual stimuli were presented during generalization. Based on their similarity to the conditioned stimulus (CS), the generalization stimuli were classified into three categories: low, medium, and high similarity.

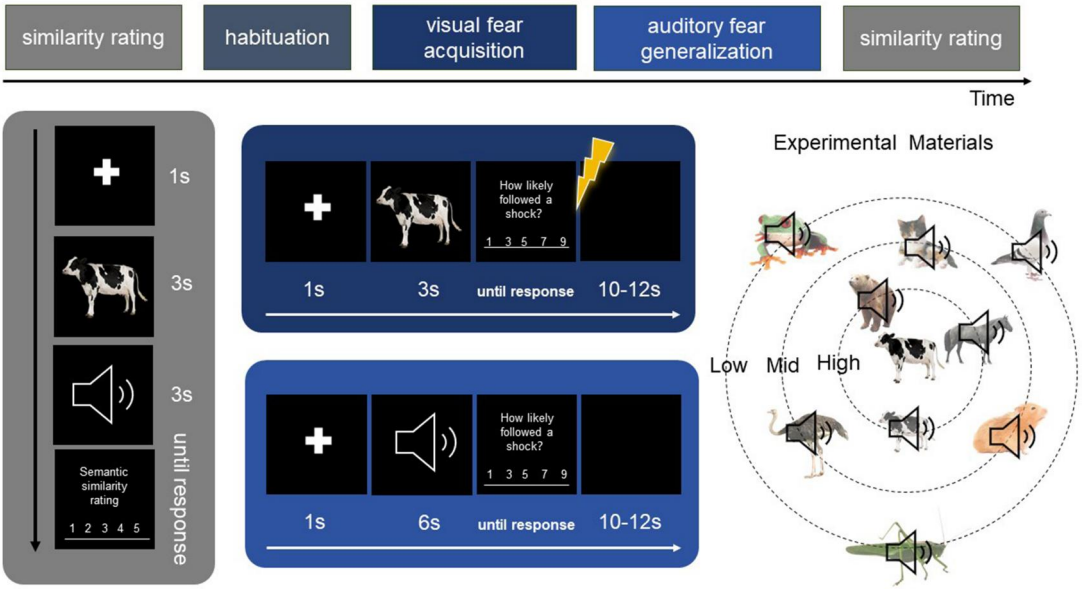

Figure 2 Procedure in Experiment 2. Experiment 2 was similar to Experiment 1 expect the materials. In Experiment 2, the CS was a picture of cow in the fear acquisition stage, and GS were the sounds in the fear generalization stage. Similarly, the auditory GS were also divided into three types including low, mid, and high similarity with the CS.

Functional near-infrared spectroscopy

The study utilized a multi-channel functional near-infrared spectroscopy (fNIRS) device (NirSmart, HuiChuang, China) to record changes in concentrations of oxyhemoglobin (HbO) and deoxyhemoglobin (HbR) during tasks, using near-infrared light with wavelengths of 730 nm and 850 nm. The sampling rate was 11 Hz. The cap included 15 light source probes and 16 detector probes, forming a total of 48 channels, with an average spacing of 3 cm between probes. The positioning followed the international 10/20 system, covering the frontal and temporoparietal regions, with the Fpz probe positioned at the center of the lower edge of the cap. Data preprocessing was conducted using the Homer2 (Huppert *et al.* 2009) plugin running on Matlab R2017b, which included steps such as intensity detection, conversion to optical density, motion artifact removal (Scholkmann *et al.*

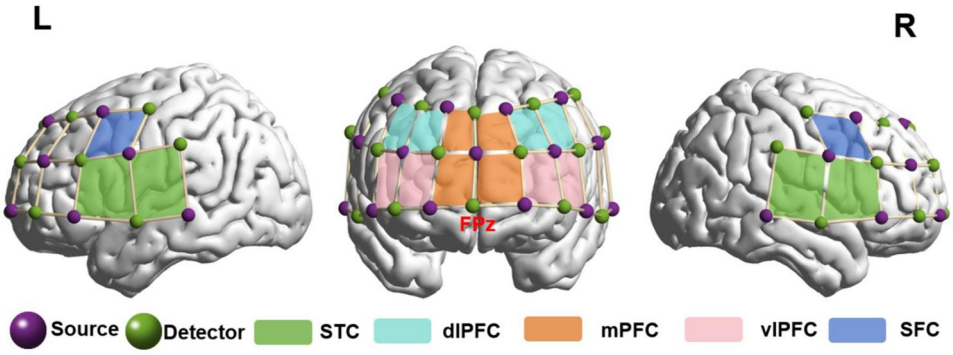

Figure 3 The location of channels.

2010), bandpass filtering (0.01 Hz to 0.5 Hz; Pinti *et al.* 2018, Li *et al.* 2026), conversion to hemoglobin concentration (Cope et al. 2012), and averaging. The period from −2 to 0 s before stimulus onset was used as the baseline, and the average change in oxyhemoglobin within the stimulus window (6 s) was calculated for each channel for further analysis (Dou *et al.* 2020, Wang *et al.* 2024, Liu *et al.* 2025, Zhang *et al.* 2025).

Our channels covering several prefrontal cortices are presented in Fig. 3 according to their MNI coordinates, including mPFC, dorsolateral prefrontal cortex (dlPFC), ventral lateral prefrontal cortex (vlPFC), superior frontal gyrus (SFG), and superior temporal gyrus (STG). Data analysis was performed using SPSS 26.0 software, with detailed analysis of oxygen data from selected channels. During the fear generalization phase, repeated measures ANOVA was conducted for stimulus type (GS1/GS2/GS3) and group (high anxiety/low anxiety) for each channel. We added a permutation test to increase the reliability of the results (Nastase *et al.* 2019). The data from the different participants and different trials were shuffled for each channel 5000 times. The F-distributions for the main effects and interaction effects of the ANOVA for the shuffled data were calculated. Only the F-values in the channel that were larger than the 95% percentile of the F-distributions were seen as activated channels. The activated channels in the same brain regions were averaged for further analysis.

Results

Results in Experiment 1

Shock expectancy rating

During the acquisition phase, the US expectancy ratings were significantly lower in the first half of the acquisition phase compared to those in the second half (F (1, 53) = 24.103, $P < .001$, η^2_p = 0.313). The main effect of Group was not significant, F (1, 53) = 0.465, $P = .498$, η^2_p = 0.009. The interaction between Time and Group was also not significant, F (1, 53) = 0.014, $P = .906$, η^2_p = 0.0003.

During the generalization phase, we found the main effect of Stimulus Type, F (1.4, 71.6) = 66.997, $P < .001$, η^2_p = 0.558. Participants' shock expectancy ratings for GS1 were significantly higher than those for GS2, and ratings for GS2 were significantly higher than those for GS3 (Ps <.001). The main effect of Group was not significant, F (1, 53) = 0.192, $P = .663$, η^2_p = 0.004 nor was the interaction between Stimulus Type and Group, F (1.4, 71.6) = 0.450, $P = .563$, η^2_p = 0.008.

Shock expectancy rating and semantic similarity distances

In Experiment 1, the correlation analysis revealed a negative relationship between the semantic distance of CS+ and GS pairs and the shock expectancy ratings for the GS ($r = -0.825$, $P < .001$) (see Fig. 4b). This indicates that the greater the distance between the GS and CS+, the lower the shock expectancy ratings of the GS.

In Experiment 2, the results of correlations between semantic distance and shock expectancy ratings showed that the semantic distance between CS+ and GS negatively correlated with the shock expectancy ratings of the GS ($r = -0.583$, $P = .001$; see Fig. 4c), which indicated that the greater the distance between the GS and CS+, the lower the shock expectancy ratings of the GS. Moreover, the A-V generalization (A-V= auditory to visual) showed a higher correlation between semantic distance and shock expectancy ratings compared to the V-A (visual to auditory) generalization (Fisher's $z = -2.340$, $P = .019$).

Skin conductance response

During the acquisition phase, we found a significant main effect of Time, F (1, 52) = 9.589, $P = .001$, η^2_p = 0.156. The SCR during the first half of the acquisition phase was significantly higher than that during the second half. The main effect of Group was not significant, F (1, 52) = 0.909, $P = .345$, η^2_p = 0.017, and the interaction between Time and Group was also not significant, F (1, 52) = 0.530, $P = .470$, η^2_p = 0.010 (see Fig. 5).

During the generalization phase, the results showed a significant main effect of Stimulus Type, F (2, 104) = 5.215, $P = .010$, η^2_p = 0.091, with participants showing a significantly higher SCR to GS2 compared to GS3. There were no significant SCR differences between GS1 and GS2. The main effect of the Group was not significant, F (1, 52) = 0.057, $P = .812$, η^2_p = 0.001. The interaction between Stimulus Type and Group was also not significant, F (2, 104) = 0.469, $P = .598$, η^2_p = 0.009.

Functional near-infrared spectroscopy

In the fear generalization phase, the main effect of Group was significant in several regions including mPFC (CH 8, 9, 11, 26, 27, 42, 43, 44) (F (1, 53) = 10.337, $P = .002$, η^2_p = 0.163), right dlPFC (CH 41) (F (1, 53) = 4.291, $P = .043$, η^2_p = 0.075), right superior temporal cortex SFC(CH 20, 38)(F (1, 53) = 5.333, $P = .025$, η^2_p = 0.091) after the permutation test; follow-up test showed that the HbO levels to the GS in the high anxiety group were significantly lower than those in the low anxiety group in

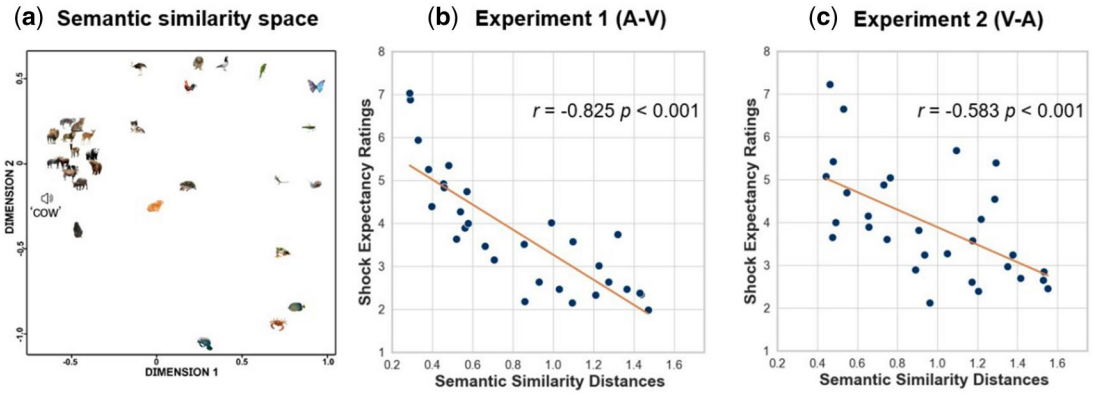

Figure 4 The relationship between shock expectancy ratings and semantic similarity distance to CS+. (a) The semantic similarity space derived from MDS method in Experiment 1, the sound icon represents the cow vocalization, while other icons represent visual stimuli. Semantic similarity distances are calculated as Euclidean distances between stimuli. (b) Correlation between the semantic similarity distance and shock expectancy ratings in Experiment 1. (c) Correlation between semantic similarity distances and shock expectancy ratings in Experiment 2.

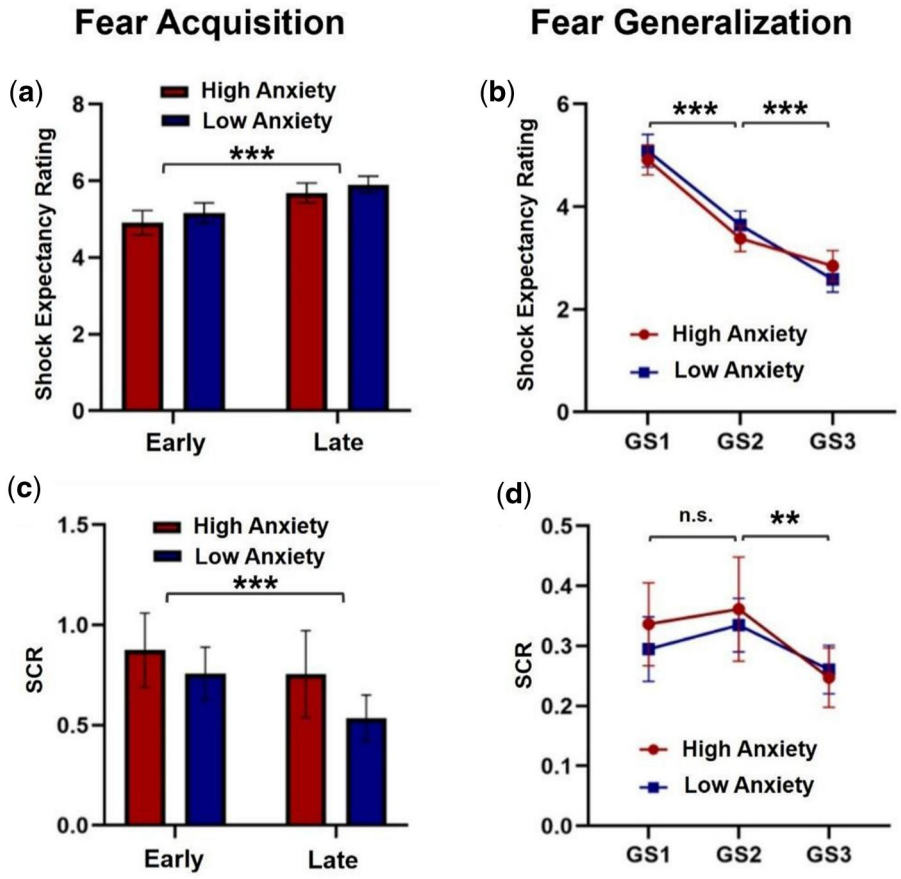

Figure 5 Shock expectancy ratings and SCRs in Experiment 1. (a, b) Shock expectancy ratings during auditory fear acquisition and visual generalization. (c, d) SCRs during auditory fear acquisition and visual generalization. n.s. not significant, * $P < .05$, ** $P < .01$, *** $P < .001$.

mPFC, dlPFC, and SFC. The main effect of Stimulus Type was significant in mPFC (CH 28, 42)(F (2, 106) = 4.732, P = .011, η_p^2 = 0.082). The follow-up test showed that the HbO level of the GS1 was significantly higher than that of the GS3 (P = .009) (see Fig. 6). However, the interaction effect between Stimulus Type and Group was not significant.

Results in Experiment 2

Shock expectancy ratings

Results showed a significant main effect of Time, F (1, 38) = 16.792, $P < .001$, η_p^2 = 0.306, indicating that the shock expectancy ratings were

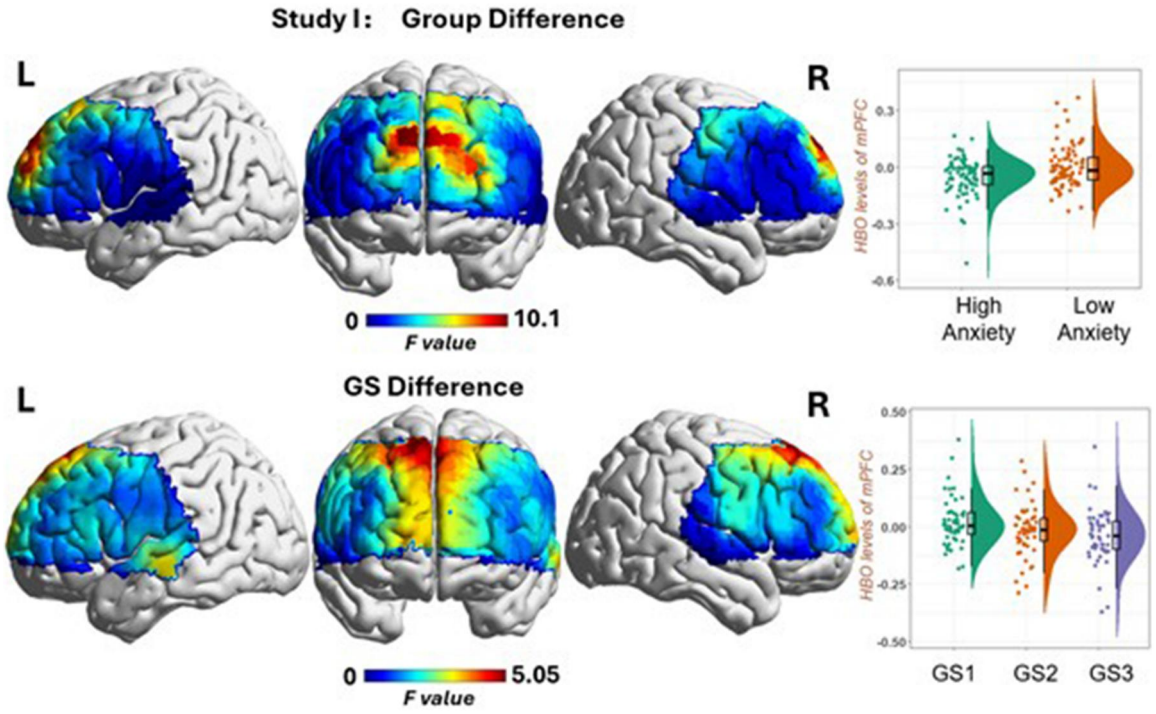

Figure 6 fNIRS results for Experiment 1. The HbO levels in the mPFC during the generalization stage. Compared with the low anxiety group, the high anxiety group showed lower HbO levels in the mPFC. In addition, the GS1 evoked higher HbO levels in the mPFC than the GS3.

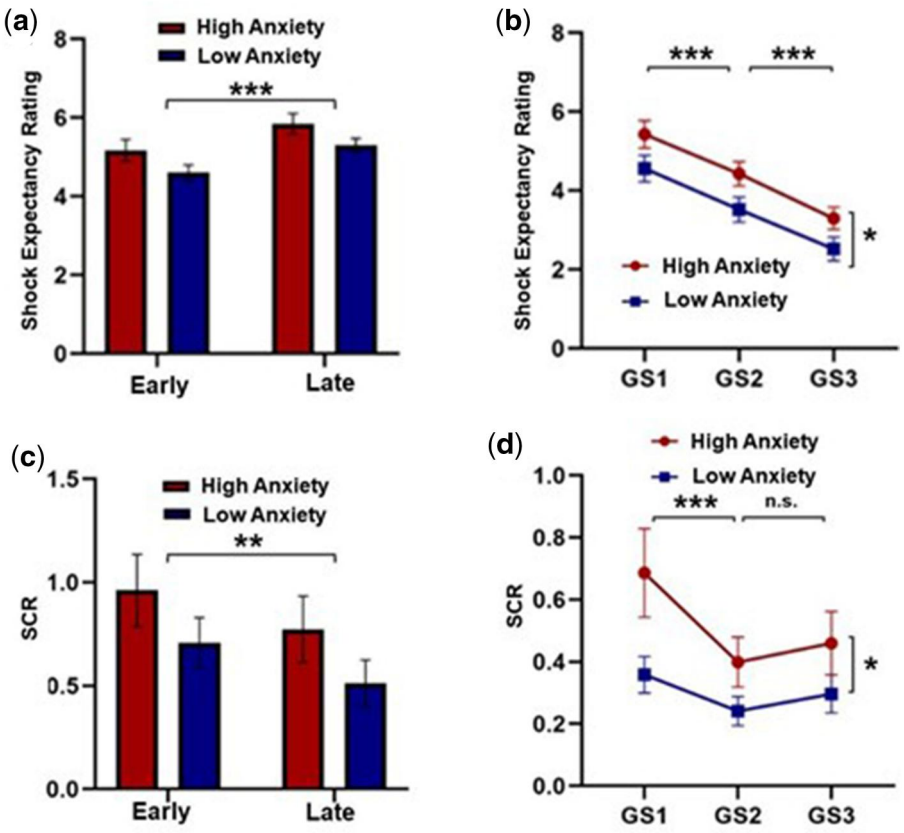

Figure 7 The results of US ratings and SCR in Experiment 2. (a, b) Shock expectancy ratings during the visual fear acquisition and auditory generalization phases. (c, d) SCR in the visual fear acquisition and auditory generalization phases. n.s. not significant., *$P < .05$, **$P < .01$, ***$P < .001$.

significantly lower during the early learning phase compared to the late learning phase. The main effect of Group was non-significant, F (1, 38) = 1.486, P = .230, η_p^2 = 0.038, as well as the interaction between Time and Group, F (1, 38) = 0.003, P = .955, $\eta_p^2 < 0.001$.

For the generalization phase, results showed a significant main effect of Stimulus Type, F (2, 76) = 42.358, $P < .001$, η_p^2 = 0.527. Participants had significantly higher shock expectancy ratings for GS1 compared to GS2 and for GS2 compared to GS3. The main effect of Group was significant, F (1, 38) = 5.499, P = .024, η_p^2 = 0.126, indicating that the high anxiety group had significantly higher shock expectancy ratings compared to the low anxiety group. The interaction between Stimulus Type and Group was non-significant, F (2, 76) = 0.047, P = .905, η_p^2 = 0.001 (see Fig. 7).

Skin-conductance responses

Results showed a significant main effect of Time on SCRs during the acquisition phase, F (1, 38) = 11.101, P = .002, η_p^2 = 0.226, indicating that SCRs were significantly higher during the early learning phase compared to the late learning phase. The main effect of Group was non-significant, F (1, 38) = 1.719, P = .198, η_p^2 = 0.043, as well as the interaction between Time and Group, F (1, 38) = 0.003, P = .957, $\eta_p^2 < 0.001$.

For the generalization phase, results indicated a significant main effect of Stimulus Type, F (2, 76) = 25.311, $P < .001$, η_p^2 = 0.399. Post hoc tests revealed that participants had significantly higher SCRs to GS1 compared to GS2. The main effect of Group was significant, F (1, 38) = 4.278, P = .045, η_p^2 = 0.101. Post hoc tests showed that the high anxiety group showed higher SCR compared to the low anxiety group. The interaction between Stimulus Type and Group was non-significant, F (2, 76) = 1.638, P = .208, η_p^2 = 0.041.

Functional near-infrared spectroscopy

In the fear generalization phase, the main effect of Group was significant in several regions including mPFC (CH 7, 8, 25, 27) (F (1, 37) = 7.240, P = .011, η_p^2 = 0.164) after the permutation test; follow-up test showed that the HbO levels to the GS in the high anxiety group were significantly lower than those in the low anxiety group in the mPFC. The interaction effect between Stimulus Type and Group was significant in the mPFC (CH 8, 42, 43) (F (2, 74) = 4.646, P = .013, η_p^2 = 0.112) and right SFC(CH 20, 38) (F (2, 74) =4.943, P = .010, η_p^2 = 0.118). The follow-up test in mPFC showed that the HbO level of the GS1 in the high anxiety group was significantly lower than that in the low anxiety group (P = .001). The HbO of the GS1 in mPFC was higher than that of the GS2 in the low anxiety group (P = .059), but this trend disappeared in the high anxiety group. The follow-up test in SFC showed that the HbO level of the GS1 in the high anxiety group was significantly lower than that in the low anxiety group (P = .024) (see Fig. 8). However, the main effect of Stimulus Type was not significant.

Discussion

We explored the relationships between cross-modality fear generalization and semantic similarity distances and examined whether anxiety levels modulated these processes. In two experiments, we focused on bidirectional cross-modality fear generalizations: visual-to-auditory (V-A) and auditory-to-visual (A-V). Our findings suggest not only that cross-modality fear generalization occurs in both directions but also that its pattern may differ depending on the direction of transfer. Specifically, we found that the bidirectional cross-modality generalization is asymmetrical. The correlation between A-V fear generalization and semantic similarity was stronger than that for V-A

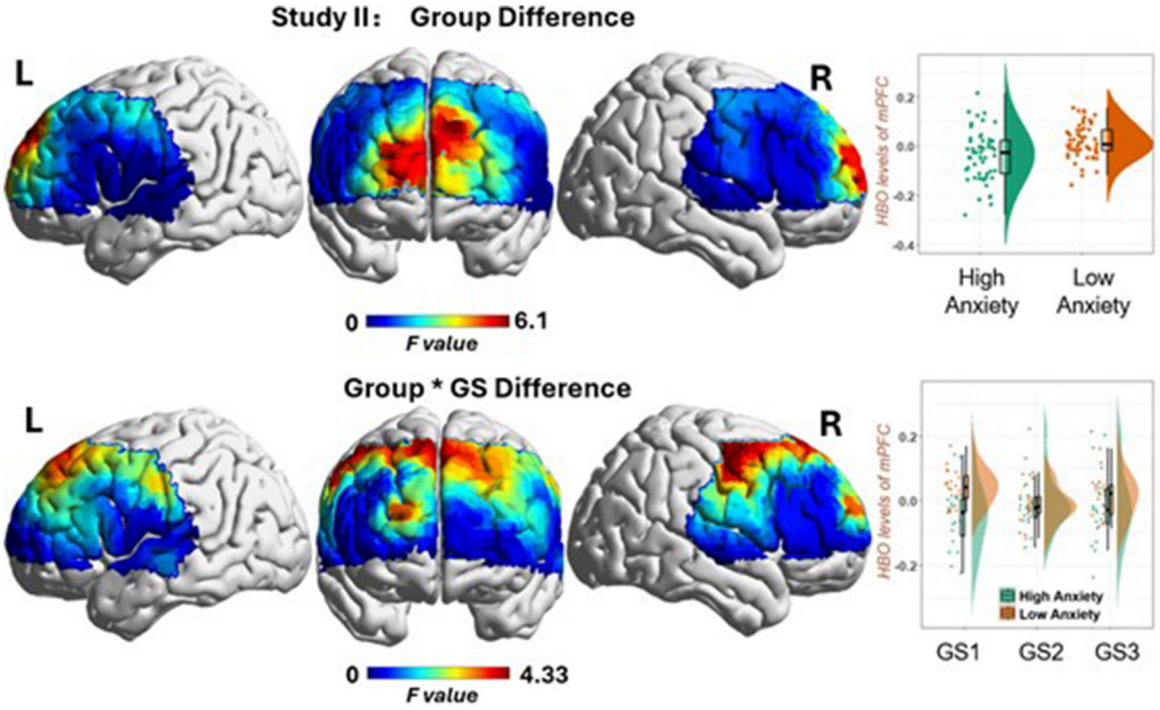

Figure 8 fNIRS results for Experiment 2. The HbO levels in the mPFC during the visual-to-auditory generalization stage. The high-anxiety group showed lower HbO levels in the mPFC than the low-anxiety group during the generalization stage. Moreover, the GS1 elicited higher HbO levels in the mPFC in the low-anxiety group than in the high-anxiety group.

fear generalization. This asymmetry may be explained by the differences in the semantic representation between visual and auditory stimuli (Palmiero *et al.* 2014). Palmiero *et al.* (2014) found that visual semantic representations are processed more quickly and accurately than auditory ones. The weaker correlation observed in our study may be attributed to auditory representations potentially carrying less conceptual information than their visual counterparts. These results corroborate and extend the work of Gerdes *et al.* (2020), broadening our understanding of multisensory fear generalization to encompass both A-V to V-A pathways. These findings also support and generalize Shepard's (1987) similarity-based generalization theory to the bidirectional cross-modality generalization. Our results indicate that fear responses can be generalized across sensory modalities based on the semantic similarity of stimuli within the fear network. It should be noted, however, that the present paradigm cannot fully distinguish between a semantic distance account and a category-based generalization account. All stimuli used in both experiments were animals, meaning that all GS shared category membership with the CS. Under Dunsmoor's category-based account (Dunsmoor and Murphy 2014), fear may have spread to GS partly because they belonged to the same broad category as the CS, rather than purely as a function of graded semantic distance. The negative correlation between semantic distance and shock expectancy is consistent with both accounts, since more typical or semantically similar category members are by definition closer in representational space. Future studies should include stimuli drawn from multiple categories to disentangle the independent contributions of semantic distance and category membership to cross-modal fear generalization.

Notably, the SCR generalization gradient in Experiment 1 did not mirror the linear pattern observed in shock expectancy ratings. While expectancy ratings followed the expected gradient of GS1 > GS2 > GS3, SCR showed a non-linear pattern in which GS1 and GS2 elicited similarly elevated responses relative to GS3, with no significant difference between GS1 and GS2. This dissociation between subjective and physiological indices of generalization is consistent with prior work showing that expectancy ratings and SCR do not always converge across levels of threat similarity (Lissek *et al.* 2008) and may reflect two complementary processes. On one hand, autonomic ceiling effects may have prevented SCR from differentiating between GS1 and GS2, as both stimuli exceeded a threshold of perceived threat proximity sufficient to produce maximal sympathetic responding. On the other hand, SCR to GS1, the most threat-relevant stimulus, may have been subject to habituation across repeated generalization trials, attenuating what would otherwise have been the highest response in the gradient. Together, these patterns suggest that expectancy ratings may provide a more sensitive and graded index of semantic generalization than SCR, particularly when stimuli vary in similarity rather than along a simple perceptual continuum.

Past studies have focused on exploring the role of overgeneralization in the pathology of various anxiety disorders (Lissek *et al.* 2014, Dunsmoor and Paz 2015, Laufer *et al.* 2016). Our study extends this line of inquiry by pre-clinical data on how anxiety levels influence cross-modal fear generalization between auditory and visual contexts. Specifically, in Experiment 2 (V-A generalization), the high-anxiety group exhibited higher shock expectancy ratings and SCRs than the low-anxiety group, indicating that high-anxiety individuals are more sensitive to integrating visual fear memories with auditory stimuli. The differences in the multisensory information integration might take part in the cross-modality generalization, which finally influenced the impact of anxiety on cross-modality generalization. Previous studies have suggested that high-anxiety individuals may show stronger integration of information across sensory modalities (Ferneyhough *et al.* 2013, Heffer *et al.* 2022), which could increase the likelihood of cross-modal fear generalization. For example, the high-trait anxiety group showed more tightly visual and auditory integration in front of anger expression compared with those in the low-trait anxiety group (Heffer *et al.* 2022). In our study, this tighter cross-modal integration may explain the enhanced fear responses observed in the high-anxiety group during V-A generalization in Experiment 2. However, no similar effects were noted in the A-V generalization in Experiment 1, possibly due to differences in semantic representation between visual and auditory stimuli (Palmiero *et al.* 2014). Visual representations tend to be clearer, while auditory representations are often more ambiguous. This increased uncertainty in auditory stimuli could potentially amplify the fear response in high-trait anxiety individuals (Bensi and Giusberti 2007), leading to enhanced fear responses to auditory GS. This interpretation may be further understood in light of theoretical accounts emphasizing heightened sensitivity to ambiguity and uncertain threat in anxiety. Together, these findings suggest that high trait anxiety selectively enhances visual-to-auditory fear generalization through the joint influence of tighter cross-modal integration and increased sensitivity to the ambiguity of auditory representations.

For the neural results, both Experiment 1 and Experiment 2 revealed decreased activity in the mPFC among the high-anxiety group compared with the low-anxiety group during fear generalization. Additionally, in Experiment 2, the low-anxiety group displayed a trend where the greater semantic similarity between GS and CS, the higher mPFC of the GS evoked; however, this trend was absent in the high-anxiety group. Our findings align with previous research on perceptual fear generalization in clinical populations (Greenberg *et al.* 2013, Cha *et al.* 2014). For instance, generalization slopes of the vmPFC in patients with GAD are found to be more inhibited compared to those in healthy controls (Greenberg *et al.* 2013). Across both experiments, GSs that were more semantically similar to the CS tended to evoke stronger mPFC activation. This might indicate two potential ways to explain the function of the mPFC. On the one hand, mPFC activity might reflect the discrimination between threat and safety. For example, Likhtik *et al.* (2014) found that theta synchrony between the mPFC and amygdala in mice is associated with better discrimination between CS+ and CS−. On the other hand, the mPFC in our task might play an important role in conceptual representation. This interpretation is supported by previous findings linking mPFC function to conceptual representation (Wilson *et al.* 2014, Constantinescu *et al.* 2016).

Finally, one limitation concerns the spatial sensitivity of fNIRS. Given its limited penetration depth and sensitivity primarily to superficial cortical tissue, it remains uncertain whether the recorded signals adequately captured activity from the vmPFC (Tachtsidis and Scholkmann 2016, Pinti *et al.* 2020). Therefore, the observed reduction in mPFC activation should be interpreted with caution, as it may primarily reflect hemodynamic changes in more superficial cortical regions rather than activity specifically originating from the vmPFC. Another limitation is that, although valence and arousal were considered in stimulus selection, other potentially relevant stimulus dimensions, such as familiarity, were not explicitly assessed. As a result, the possible influence of these uncontrolled characteristics on participants' behavioral and neural responses cannot be completely ruled out. Future studies should more comprehensively evaluate and

control additional stimulus dimensions to strengthen the internal validity of the findings.

Conclusion

We revealed asymmetries between generalization directions: auditory-to-visual generalization showed stronger correlations with semantic similarity than visual-to-auditory generalization, likely reflecting that visual semantic representations carry more conceptual information and are processed more accurately than auditory ones. Moreover, anxiety disrupts prefrontal control mechanisms while amplifying fear responses through tighter cross-modal integration when processing inherently ambiguous auditory stimuli.

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Author contributions

Haoran Dou (Conceptualization [equal], Data curation [equal], Funding acquisition [equal], Methodology [equal], Software [equal], Writing—original draft [equal], Writing—review & editing [equal]), Shanhe Du (Data curation [equal], Methodology [equal], Software [equal]), Jonas Zaman (Conceptualization [equal], Writing—review & editing [equal]), Kenny Yu (Conceptualization [equal], Writing—review & editing [equal]), Ying Mei (Writing—review & editing [supporting]), Yiwen Qiu (Writing—review & editing [supporting]), and Yi Lei (Conceptualization [equal], Funding acquisition [equal], Supervision [equal], Visualization [equal], Writing—review & editing [equal])

Supplementary material

Supplementary material is available at *SCAN* online.

Conflicts of interest

None declared.

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Data availability

Experiment 1—Preregistration: No aspects of the study were preregistered. Materials: All study materials are publicly available (https://osf.io/cxt26/). Data: All primary data are publicly available (https://osf.io/cxt26/). Analysis scripts: All analysis scripts are publicly available (https://osf.io/cxt26/). Experiment 2—Preregistration: No aspects of the study were preregistered. Materials: All study materials are publicly available (https://osf.io/cxt26/). Data: All primary data are publicly available (https://osf.io/cxt26/). Analysis scripts: All analysis scripts are publicly available (https://osf.io/cxt26/).

Ethical approval

This research received approval from the Ethics Committee of Sichuan Normal University (ID: SCNU-230621).

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