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The assessment of gender differences in perceptual fear generalization and related processes

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ABSTRACT

In this study we aimed to investigate gender differences in fear generalization tendencies in humans and, inspired by recent findings in animal research, examine whether any such differences could stem from differences in memory precision. Forty men and forty women underwent a differential fear conditioning procedure using geometric shapes as cues. Subsequently, generalized fear responses were assessed across a spectrum of perceptually similar shapes. Throughout generalization testing, perceptual memory accuracy was repeatedly probed using a stimulus recreation task. Using statistical and computational modeling, we found strong evidence for the absence of gender differences in fear learning and generalization behavior. The evidence for gender differences in related processes such as perception and memory was inconclusive. Although some of our findings hinted at the possibility that women may be more perceptive of physical differences between stimuli and have more accurate memory than men, those observations were not consistently replicated across experimental conditions and analytical approaches. Our results contribute to the emerging literature on gender differences in perceptual fear generalization in humans and underscore the need for further systematic research to explore the interplay between gender and mechanisms associated with fear generalization across different experimental contexts.

1. Introduction

By studying sex or gender-specific behavioral differences within experimental fear learning models, researchers seek to unveil the mechanisms contributing to the unfavorable odds for women regarding trauma and anxiety-related disorders. Women are markedly more likely than men to meet the diagnostic criteria for a diverse array of anxiety disorders (Bekker & Van Mens-Verhulst, 2007; McLean, Asnaani, Litz, & Hofmann, 2011). Moreover, women commonly manifest more severe symptoms, experience worse outcomes, have a higher disease burden, and exhibit higher rates of comorbidity with depression and other anxiety disorder subtypes (Bekker & Van Mens-Verhulst, 2007; McLean et al., 2011). Unraveling the underpinnings of these clinical gender differences is vital to developing more effective and potentially gender-specific interventions and treatments.

Sex or gender differences in fear conditioning are increasingly reported – with the bulk of findings originating from animal research. They include differences in contextual fear learning, cued fear learning, fear extinction, and spontaneous recovery (for a review, see Day, Reed, & Stevenson, 2016). However, there is a manifest gap in the investigation of sex and gender differences within the literature of fear generalization (i.e., the extension of acquired fears to perceptually or conceptually related stimuli or situations) (Dymond, Dunsmoor, Vervliet, Roche, & Hermans, 2015), despite the fact that fear generalization is considered to be a crucial aspect of trauma and anxiety-related psychopathologies (Cooper et al., 2022b; Fraunfelter, Gerdes, & Alpers, 2022).

The picture emerging from the few human studies reporting gender differences in generalized fear is unclear. Cooper, Hunt, Ross, Hartnell, and Lissek (2022a) found heightened generalization tendencies in women compared to men, while other studies reported no difference between genders (Tinoco-González et al., 2015; Torrents-Rodas et al., 2013; Xu, Xie, Yan, Li, & Zheng, 2018). Although Xu et al. (2018) found no difference in the overall generalization response pattern based on gender, they did observe a difference in the extinction of generalized responses. Specifically, their findings indicated a distinction in the

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extinction of generalized responses, highlighting that women displayed a prolonged duration in extinguishing the generalization response compared to men. Given the conflicting evidence, the first aim of the study is to investigate gender differences in perceptual fear generalization further. Here, we distinguish between sex, referring to biological and physiological characteristics that differentiate females and males, and gender, which encompasses the psychological features associated with these biological states as assigned by individuals (Deaux, 1985). When discussing gender, we use the terms 'women' and 'men' in place of 'females' and 'males'.

Findings regarding sex differences in animals can potentially help to clarify gender differences observed in humans. Animal literature suggests that females, more than males, demonstrate increasing context generalization as the interval between learning and testing increases (Keiser et al., 2017; Lynch, Cullen, Jasnow, & Riccio, 2013). A prevailing hypothesis assumes that hormonal-neural sex differences lead to the recruitment of different brain regions during memory encoding or decoding processes, thereby affecting the precision of fear memories (Lynch et al., 2013). Females are thought to rely more on the amygdala during recall, resulting in a loss of precision-encoded context memories and more generalization behavior (Keiser et al., 2017). Impaired safety learning has also been suggested to contribute to sex differences in generalized fear responding (Day et al., 2016). Yet, whether similar memory mechanisms hold and lead to possible sex-based gender differences in human fear generalization behavior remains unclear as various methodological differences exist between human and animal research. For instance, compared to the animal work that often relies on context generalization, human studies typically operationalize fear generalization as the extent to which perceptually similar stimuli (e.g., differently sized circles) start to elicit fear after a cued fear conditioning procedure. Additionally, in human research, generalization testing typically occurs immediately after fear acquisition, while several hours or days separate phases in animal research. Therefore, the second aim of the present study is to assess gender differences in the precision of memory immediately after fear learning and throughout generalization testing.

Recent advances in research on fear generalization suggest that a multitude of mechanisms can contribute to generalization behavior; an exclusive focus on fear responses renders researchers unable to scrutinize these mechanisms (Struyf, Zaman, Vervliet, & Van Diest, 2015; Yu, Tuerlinckx, Vanpaemel, & Zaman, 2023; Zaman et al., 2020a; Zaman, Yu, & Verheyen, 2023). Congruently assessing (variations in) stimulus perception, fear and safety learning, and generalized fear responses enables to account for inter- and intra-individual differences regarding the latter (Struyf, Zaman, Hermans, & Vervliet, 2017; Zaman, Ceulemans, Hermans, & Beckers, 2019a; Zaman, Yu, & Lee, 2022; Zaman, Struyf, Ceulemans, Beckers, & Vervliet, 2019b, Zaman, Struyf, Ceulemans, Vervliet, & Beckers, 2020b). It also yields generalization indexes that are comparable across individuals as they control for differences regarding learning, perception, and memory (Yu et al., 2023; Zaman et al., 2023). In a recent paper, Yu et al. (2023) investigated latent mechanisms in fear generalization behavior via a computational generalization model that parameterizes several key processes that contribute to generalized responding, including the speed of learning (Rescorla & Wagener, 1972) and the strength of a similarity-based generalization process (Shepard, 1987) while accounting for differences in stimulus perception. In addition, one of the model's interesting features is that it allocates participants (based on multivariate data, i.e., perception, learning, and generalization) to distinct mechanistically and clinically relevant subgroups (Yu et al., 2023).

In this study, we employ the same computational framework to explore gender differences in the latent mechanisms underlying perceptual fear generalization. In essence, the model posits the dynamic interaction of two variables at each time point. The first variable, expectancy, encapsulates the expectation of a particular outcome within a given context (stimulus). This expectancy is continually updated based on individual learning rates and experiences with the learned context. The second variable, similarity, represents the degree of difference between the newly encountered context and the learned context. As the mental distance between the two contexts increases, similarity decreases exponentially, with the rate of decrease modulated by a generalization rate parameter. The resulting generalization behavior is a consequence of the dynamic interplay between these two variables. Given existing evidence for sex or gender differences regarding many of the processes involved, including perceptual acuity (Shaqiri et al., 2016, 2018) and differential fear learning (Day et al., 2016, 2020; Lonsdorf et al., 2017), the third aim of the present study is twofold: (i) to investigate gender differences in fear learning and stimulus perception; and (ii) to explore whether potential differences in fear generalization behavior stem from gender differences in a latent similarity-based generalization process or differences in adjacent processes of learning and perception.

To explore gender differences in latent mechanisms using computational modeling, we designed the experiment to closely resemble those in Yu et al. (2023). To this end, 40 men and 40 women participants completed a differential fear learning procedure followed by several blocks of generalization testing (see Fig. 1). In between blocks, memory precision was assessed using a stimulus recreation task. Throughout learning and generalization testing, self-reported US expectancy ratings and perceptual assessments were recorded on a trial-by-trial basis. This multivariate approach enabled us to (i) assess gender differences in fear generalization behavior and (ii) explore potential gender differences in fear learning, perception, and perceptual memory and their impact on fear generalization patterns.

2. Method

2.1. Research transparency statement

The current study has been pre-registered on the Open Science Framework (https://osf.io/byq82) as an extension of an earlier registration (https://osf.io/puyg3). The primary focus of the earlier registration was to explore the dynamics of perception and perceptual memory and their impact on generalization behavior under fear contexts. Both pre-registrations were completed prior to data collection and concerned the same experimental design and dataset. In this current study, we specifically investigate gender effects (N = 80, 50% women) in this dataset. We report how we determined our sample size, all data exclusions, all manipulations, and all measures in the study. All relevant materials, including experiment scripts, data, and analysis scripts, are accessible at https://osf.io/b39xc/.

2.2. Participants

We conducted a power analysis based on the reported effect size in Cooper et al. (2022a), which investigated gender differences in generalized fear and generalized instrumental avoidance. Their study found that women exhibited steeper generalization slopes compared to men. Using G*power (version 3.1.9.7), we determined the required sample size for a repeated measures ANOVA with a within-between interaction ($f = 0.131$). The effect size (f) was derived from $\beta = 0.285$ and $t(860) = 3.94$. We set $\alpha = 0.05$ and sought a power (1-β) of 0.90. The design included gender as a between-group factor (men and women) and stimulus as a within-persons factor (S1-S10). Correlation was set at 0.35 and sphericity correction to 1 ($\varepsilon = 1$). The analysis yielded a required sample size of N = 78.

We applied the following data exclusion criteria for the current study. First, participants were excluded if they indicated that they responded non-seriously during the experiment. Second, we excluded participants whose missing data exceeded 20% for any dependent variable during any phase of the experiment. We ended up recruiting 100 participants to reach the targeted sample size (N = 80). The final dataset comprised 40 women and 40 men (mean age = 21, SD = 4.01). All

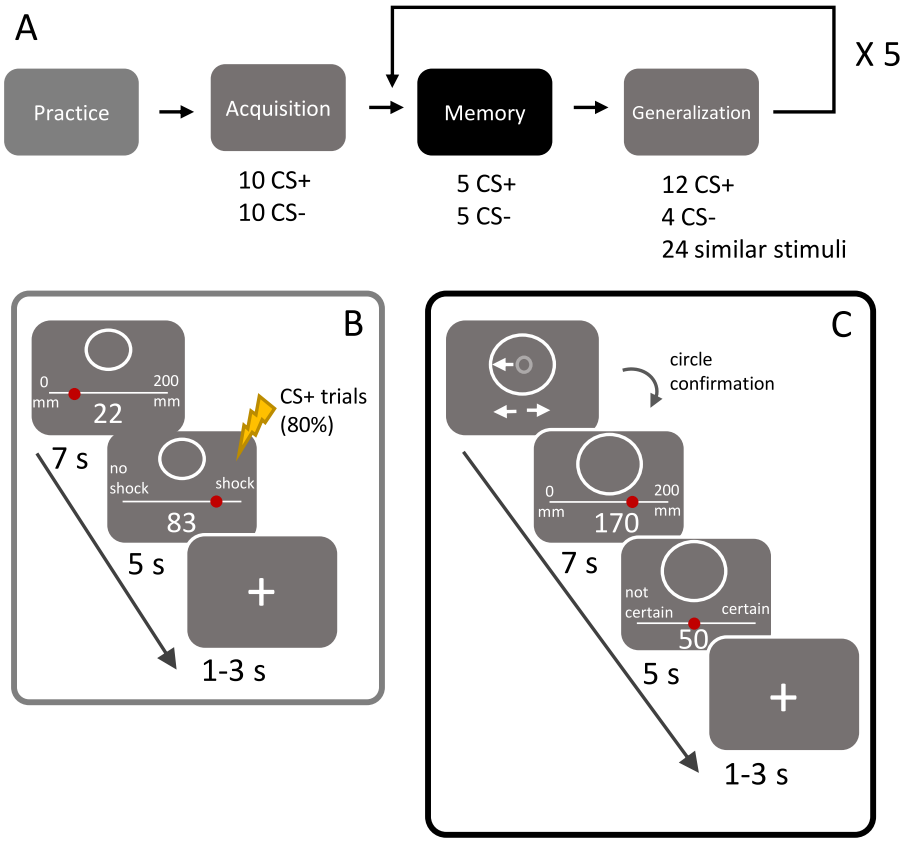

Fig. 1. Overview of the paradigm. A) The different phases. **B)** Trial structure of the practice, acquisition and generalization phase. During practice phase, no USs were presented. **C)** Trial structure of a memory trial. CS = conditioned stimulus.

participants were recruited through the participant pool of the KU Leuven Faculty of Psychology and Educational Sciences and received either research participation credits or monetary compensation (€ 16). The experiment lasted around 90 min. Informed consent was provided by participants at the beginning of the experiment. Participants were instructed in English. They were asked to report their gender. The study was approved by the KU Leuven Social and Societal Ethics Committee (G-2022-5873-R3).

2.3. Visual stimuli

Circles of varying sizes, as white outlines against a black background, served as the stimuli for learning and testing. The dimension of circle size has been applied extensively in generalization studies with conditioned fear involving both healthy and clinical populations (Lange et al., 2017; Lissek, 2012; Lissek et al., 2008, 2014; Yu et al., 2023; Zaman et al., 2019a, 2019b). The stimulus set comprised ten circles, denoted as S1 through S10, with diameters ranging from 50.80 to 119.42 mm, spaced at intervals of 7.624 mm. To maintain a balanced design, the third-smallest circle (S3: 66 mm) and the third-largest circle (S8: 104 mm) were presented during fear learning. Either S3 was predictive of a painful electrical stimulation (CS+) and S8 of its absence (CS-) or vice versa. In 24 participants of each gender, S3 served as the CS+ and S8 as the CS-, while in the remaining participants, the reverse configuration was used.

2.4. Electrocutaneous stimulus

To induce fear, a 2-ms aversive electrocutaneous stimulus served as the unconditioned stimulus (US). These electrocutaneous stimuli were administered using a Constant Current Stimulator (DS7), delivered through a pair of Ag/AgCL electrodes (each 8 mm in diameter) positioned on the wrist of the non-dominant hand and lubricated with K-Y gel. In the calibration phase, the intensity of the US was individually tailored to each participant's pain tolerance levels. This adjustment was carried out using the Ascending Method of Limits approach (Yarnitsky, Sprecher, Zaslansky, & Hemli, 1995). The objective was to target a pain rating of 8 on a Visual Analog Scale (VAS) that ranged from 0 (no pain) to 10 (worst imaginable pain). The initial intensity of the electrical stimulus was set at 2 mA and incremented by 0.2 mA with each step. Throughout the calibration process, it was emphasized that the electrical stimulus should induce a sensation of pain that remained within tolerable limits. The average intensity of the electrical stimulus selected was 10.99 mA (SD = 5.89).

2.5. Protocol

The study employed a mixed design incorporating both experimental and quasi-experimental elements. Within the study, there were two within-participant factors: stimulus and trial repetition. Additionally, a between-participant factor was introduced, pertaining to the size of the fear-conditioned stimulus (S3 or S8). The quasi-experimental factor under investigation was gender. The experiment included five distinct phases: calibration, practice, acquisition, memory, and generalization. Before the experiment commenced, participants were provided with comprehensive instructions, both orally and in written form. These instructions not only introduced the tasks but also included visual examples of different sized lines including 5 mm, 10 mm, 50 mm, 100 mm, and 150 mm lines. Following the calibration of the unconditioned stimulus (US) intensity, participants engaged in a set of six practice trials to habituate to the task. During the practice trials, the conditioned stimuli (CSs) were presented on a computer screen for a duration of 12 s.

Concurrently, a Visual Analog Scale (VAS) indicating size, ranging from 0 to 200 mm, was displayed at the bottom of the screen. Participants were tasked with indicating their estimation of the diameter of the presented stimulus on this scale. No feedback was provided regarding their size estimations. Precisely 7 s after the initiation of the size-VAS, it was replaced by an expectancy-VAS. This second VAS, labeled from 'no shock' (0) to 'definitely a shock' (100), prompted participants to rate their expectation of receiving a shock based on the presented stimulus. The expectancy-VAS was maintained on screen for a duration of 5 s. Following the conclusion of the expectancy-VAS, a fixation cross appeared, marking the onset of the intertrial interval (ITI), lasting for a variable duration ranging from 1 to 3 s. During the practice trials, no US was presented.

After the practice phase, the acquisition phase started, encompassing a total of 10 CS+ trials and 10 CS- trials. The task structure mirrored that of the practice phase, with the sole distinction being that the US followed the CS+ 80% of the time (equating to 8 trials).

At the end of the acquisition phase, participants entered the first memory phase, wherein they were instructed to recall and recreate the CS(s). In each trial, they were presented with either the instruction "Please recall and recreate the circle that MOST often led to an electric stimulus in phase 1″ or "Please recall and recreate the circle that LEAST often led to an electric stimulus in phase 1". Upon receiving these instructions, a circle appeared with a diameter of either 160 mm or 0.1 mm. Participants were then able to adjust the circle size using button presses (in steps of 0.5 mm). Upon response confirmation, the size-VAS appeared at the bottom of the screen for 7 s, prompting participants to estimate the recreated circle's diameter. Hereafter, a confidence-VAS, ranging from 'not certain' (0) to 'certain' (100), assessed participants' confidence levels regarding the accuracy of the recreated circle (response duration 5 s). A 1-min break followed the completion of the first memory task, after which the generalization phase commenced.

Within the generalization phase, participants were again tasked with estimating circle sizes and indicating their expectations of receiving a shock, mirroring the procedures employed in the practice and acquisition phases. During this phase, participants were presented not only with the CS(s) but also with an additional set of 8 circles varying in size. Notably, CS+ stimuli were consistently paired with shocks, while CS- and the other test stimuli were never paired with shocks in this phase. This sequence was repeated three times after the initial generalization phase, with each repetition involving a 1-min break, followed by the memory phase, and then the generalization phase. Upon completion of the final memory block, participants were instructed to fill out the State-Trait Anxiety Inventory (STAI). Subsequently, a debriefing session concluded the experiment.

In total, five memory blocks were administered, each consisting of 5 CS+ and 5 CS- recall instructions presented in random order. Similarly, there were five generalization blocks in total, with each block comprising 12 CS+, 4 CS-, and 3 instances of each of the other 8 circles, also presented in random order.

2.6. Analysis

We conducted analyses using both statistical and computational models, all performed within the statistical computing language R (R Core Team, 2021). For the statistical models, we employed linear mixed models using several R packages: lme4 (Bates, Mächler, Bolker, & Walker, 2015), lmerTest (Kuznetsova, Brockhoff, & Christensen, 2017), rstatix (Kassambara, 2023), and effectsize (Ben-Shachar, Lüdecke, & Makowski, 2020). Data handling and visualizations were carried out using the Tidyverse (Wickham et al., 2019) and GGpubr packages (Kassambara, 2022). These models were fitted with the function lmer in the lme4 (Bates et al., 2015) package, using maximum likelihood estimation, and hypothesis testing was performed using the Wald chi-square test (asymptotically equivalent to Type III sum of squares for fixed effects). Satterthwaite's approximation (Satterthwaite, 1946) was used to compute the degrees of freedom for the t-tests. For our analyses, we considered various predictors and their interactions, as detailed below, accounting for random effects where necessary. We present standardized coefficients along with their 95% credible intervals (CIs), and the results of Wald t-tests (see Supplementary Note 2 for a complete ANOVA report).

Regarding the acquisition data, we performed two sets of analyses: (I) Trial-by-trial US expectancies were analyzed with the predictors: Repetition (continuous, 1–10), Gender (Men vs. Women) and CS (CS+ vs. CS-) and their interactions. The random part included a person-dependent effect on the intercept and the predictor Repetition (this was preferred compared to a model without the random effect on Repetition, $\chi^2_{(2)} = 20.86$, $p < 0.001$). (II) Size estimations for the CSs were analyzed with the following model: Stimulus (S3 vs. S8), Gender and their interaction.

The data of the generalization phase were analyzed as follows. For the US expectancy data, the predictor Stimulus was categorical (due to the non-linear pattern and was preferred compared to a second-order polynomial of Stimulus) and was recoded so that a value of 3 always reflected the CS+ and a value of 8 the CS-. Furthermore, the variable Trial (continuous, 1–160) was included.[1] For the size estimation data, we employed a model consisting of Stimulus (continuous, 1–10), Gender and their interaction with person-dependent effects on Stimulus and the intercept. Based on the analysis conducted, non-registered exploratory analyses were performed to examine segments of the stimulus dimension for generalization response. Estimated marginal means with false discovery rate (FDR) corrections for pairwise comparisons were used to highlight stimulus-specific patterns within the data (see Supplementary Note 6 for a full presentation of the non-registered analysis). The memory data (size recreation, size estimation, and confidence ratings) were analyzed with a model comprising of: CS, Gender, Counterbalancing (S3 as CS+ vs. S8 as CS+), and Block (continuous, 1–5). All mixed models, unless otherwise specified, only included a random intercept.

In addition to analyses with linear mixed models, we employed computational modeling to explore the latent mechanisms of similarity-based generalization and perceptual scaling. Bayesian parameter estimation was employed for statistical inference in the computational models, allowing us to represent data uncertainty through principled probability distributions when inferring parameter values. The multilevel structure (Lee, 2011; Okada & Lee, 2016) of the model facilitated the integration of information from gender and individual levels.

Statistical inference was performed using Markov Chain Monte Carlo (MCMC) with Gibbs sampling in JAGS (Plummer, 2003). R (R Core Team, 2021), along with the jagsUI package (Kellner, 2024), was employed for analysis. To ensure robustness, both generalization and perceptual models underwent four MCMC chains, each running 100,000 iterations. A burn-in period of 75,000 iterations discarded initial samples, with a thinning factor of 10 applied, resulting in 10,000 retained samples per parameter (see Supplementary Note 3 for the estimated MCMC samples of important parameters). Gelman and Rubin diagnostics, specifically the Rhat statistic (Brooks & Gelman, 1998; Gelman & Rubin, 1992), assessed MCMC chain convergence. A stabilized state and attainment of the target distribution were confirmed when the Rhat value approached or closely reached 1.

For generalization, we employed a recently introduced model (Yu et al., 2023) that dynamically integrates error-driven learning and similarity-based generalization processes to effectively capture generalization behavior (see Supplementary Note 1 for mathematical details). The model posits that individuals continually update their CS(s)-US expectation at each time point, driven by the discrepancy between the current expectation and the new outcome (i.e., the prediction error) according to a Rescorla-Wagner learning rule (Rescorla & Wagener,

[1] We omitted the predictor trial (pre-registered) when not significant.

1972). The rate at which this updating occurs is determined by a learning rate parameter. When encountering a new stimulus, individuals transfer their current CS(s)-US expectation to the new stimulus based on either physical (variation in physical size) or perceptual (variation in perceptual size derived from the perceptual data) distance between the current stimulus and the CS(s). The extent of this transfer is modulated by a generalization rate parameter with an adjusted Shepard's exponential generalization rule (Shepard, 1957, 1987). The group-level learning rate and generalization rate parameters provide insights into the differences between genders in terms of the updating speed of CS-US expectations and the generalization tendency of learning.

With a mixture structure that incorporates the two processes mentioned above, the model distinguishes four clinically relevant qualitative paths that characterize the generation of the final generalization behavior. (1) Non-Learners: This occurs when the updating process is absent, and the response is not driven by the specified processes but by response noises. In such cases, there is nothing to be generalized. (2) Overgeneralizers: This occurs when individuals transfer at least 70% of learning to even the most physically distant stimulus from the CS. (3) Physical Generalizers: This occurs when the similarity generalization process happens more along the physical rather than perceptual distance. (4) Perceptual Generalizers: This occurs when the similarity generalization process happens along the perceptual rather than physical distance. The population-level group allocation parameter would indicate, for each category, the extent to which the data support describing the generalization behavior for women and men.

To model gender differences in perception, we explored the physical-perceptual mapping with another computational model that assumed the mapping to occur either in a non-linear or linear manner, both with a baseline and a slope parameter. The perceptual response is then assumed to be determined by the physical quantities and these two parameters, along with perceptual response noises. The population-level group allocation parameter serves to determine whether the perceptual mappings align more closely with a linear or a non-linear mapping function. The group-level intercept and slope parameters offer insights into whether there is variation in the baseline perception and perceptual sensitivity between genders.

To assess gender differences in both computational models, we calculated Bayes factors (BF) using the Savage-Dickey method (Dickey, 1971; Wagenmakers, Lodewyckx, Kuriyal, & Grasman, 2010), in comparison to a null hypothesis of no difference (i.e., difference = 0). Following the scale proposed by Kass and Raftery (1995), BF values between 10^{-1} and $10^{-0.5}$, and between 10^{-2} and 10^{-1}, provide substantial and strong evidence supporting the indifference of gender difference from 0. Conversely, BF values between $10^{0.5}$ and 10^{1}, and between 10^{1} and 10^{2}, offer substantial and strong evidence supporting a gender difference from 0.

3. Results

3.1. Acquisition data – US expectancy

When examining the effects of stimulus type (CS+ and CS-) on conditioned response, it became clear that repetition, representing the frequency of stimulus presentations, significantly influenced responses across both stimuli as shown in Fig. 2A [Repetition × CS: F (1,1414) = 162.99, $p < 0.001$, $\omega_p^2 = 0.10$]. Specifically, in the CS+ trials, each additional repetition was associated with a substantial increase in the conditioned response (β = 0.43, 95% CI [0.34, 0.51], t (81) = 9.47, p < 0.001). Conversely, in the CS- trials, the relationship was negative, indicating a decrement in response with more occurrences (β = −0.25, 95% CI [−0.36, −0.14], t (80) = −4.32, p < 0.001). Importantly, the interaction between stimulus and repetition was significant, suggesting that the impact of learning experiences differs between the two stimuli (β = −0.59, 95% CI [−0.72, −0.47], t (1411) = −9.32, p < 0.001). This pattern did not differ between men and women [Repetition × CS × Gender: F (1,1414) = 0.11, $p = 0.744$, $\omega_p^2 = 0.00$]. Both the overall effect of gender (β = −0.13, 95% CI [−0.67, 0.41], t (143) = −0.47, p = 0.09) and the interaction effect between gender and stimulus type did not reach statistical significance (β = 0.02, 95% CI [−0.12, 0.17], t (1414) = −0.15, p = 0.88). A similar conclusion came from the fitted computational model where we found learning rates differing from zero (median $\alpha_{men} = 0.30$, *95% CI* = [0.23, 0.38]; median $\alpha_{women} = 0.36$, *95% CI* = [0.28, 0.44]) with substantial evidence for the hypothesis that men and women did not differ in the speed of associative learning (learning rate BF = 0.23; Non-Learner probability BF = 0.18, Fig. 3A).

3.2. Generalization data – US expectancy

As shown in Fig. 2B, expectations spread from the CS+ in a non-linear declining pattern across the test dimension [Stimulus: F (9,12534) = 1852.16, $p < 0.001$, $\omega_p^2 = 0.57$] in a similar fashion for men and women [Gender × Stimulus: F (9,12534) = 1.58, $p = 0.114$, $\omega_p^2 = 0.0004$]. The conditioned response peaked for CS+ trials (β = 0.34, 95% CI [0.31, 0.37], t (12530) = 12.85, p < 0.001) and was lowest for CS- trials (β = −0.3, 95% CI [−0.32, −0.28], t (12530) = −12.85, p < 0.001). Additionally, pairwise comparisons for stimulus segments revealed significant differences between the CS+ and nearby stimuli, indicating a sharp decline in fear response and highlighting the specificity of the conditioned response for both genders. Notably, there were no significant differences between certain stimulus pairs (e.g., S7-S8, S8-S9, S9-S10 for women; S8-S9, S9-S10 for men), suggesting that fear responses became more uniform as the stimuli became less similar to the CS+. The overall effect of gender, with men showing a slightly higher conditioned response (β = 0.15, 95% CI [−0.14, 0.44], t (185) = 1.04, p = 0.3), was not statistically significant. Furthermore, interaction effects between stimulus and gender did not reach statistical significance for any of the stimuli (all p > 0.09). In line with this, we found strong evidence for the absence of gender difference in the parameter that captures an individual's generalization proclivity (generalization rate BF = 0.04; Overgeneralizer probability BF = 0.08, Fig. 3A).

3.3. Size estimation

During the acquisition phase (Fig. 2C, top panel), the effect of gender on perceived size was not significant [Gender × Stimulus: F (1,1476) = 19.16, $p < 0.001$, $\omega_p^2 = 0.01$] (β = 0.02, 95% CI [−0.22, 0.27], t (83) = 0.19, p = 0.85). However, we found smaller size perceptions for the large circle (S8) in men compared to women (β = −0.08, 95% CI [−0.12, −0.05], t (1476) = −4.38, p < 0.001). Likewise, in the generalization phase (Fig. 2C, bottom panel), the effect of gender on perceived size was non-significant [Gender × Stimulus: F (1, 78) = 5.94, $p = 0.017$, $\omega_p^2 = 0.06$] (β = 0.12, 95% CI [−0.09, −0.32], t (86) = 1.12, p = 0.27). When exploring this physical-to-perceptual mapping using computational modeling, we found that a non-linear rather than a linear function best described this relationship (the model selection parameter was estimated with a median of 0.28 [0.15, 0.42], where a value smaller than 0.5 indicates a preference for the non-linear function) with only substantial evidence for a gender difference in the perceptual intercept parameter (BF = 4.15, Fig. 3B) and strong evidence in favor of the absence of gender differences for the perceptual slope (BF = 0.05, Fig. 3B).

3.4. Memory data – size recreations

To unpack the significant 4-way interaction [Gender × Block × CS × Counterbalancing: F (1, 708) = 3.91, $p = 0.049$, $\omega_p^2 = 0.004$], we reran the analyses per Counterbalancing and CS type. In the participants where S3 served as the CS+, the effect of gender was not significant

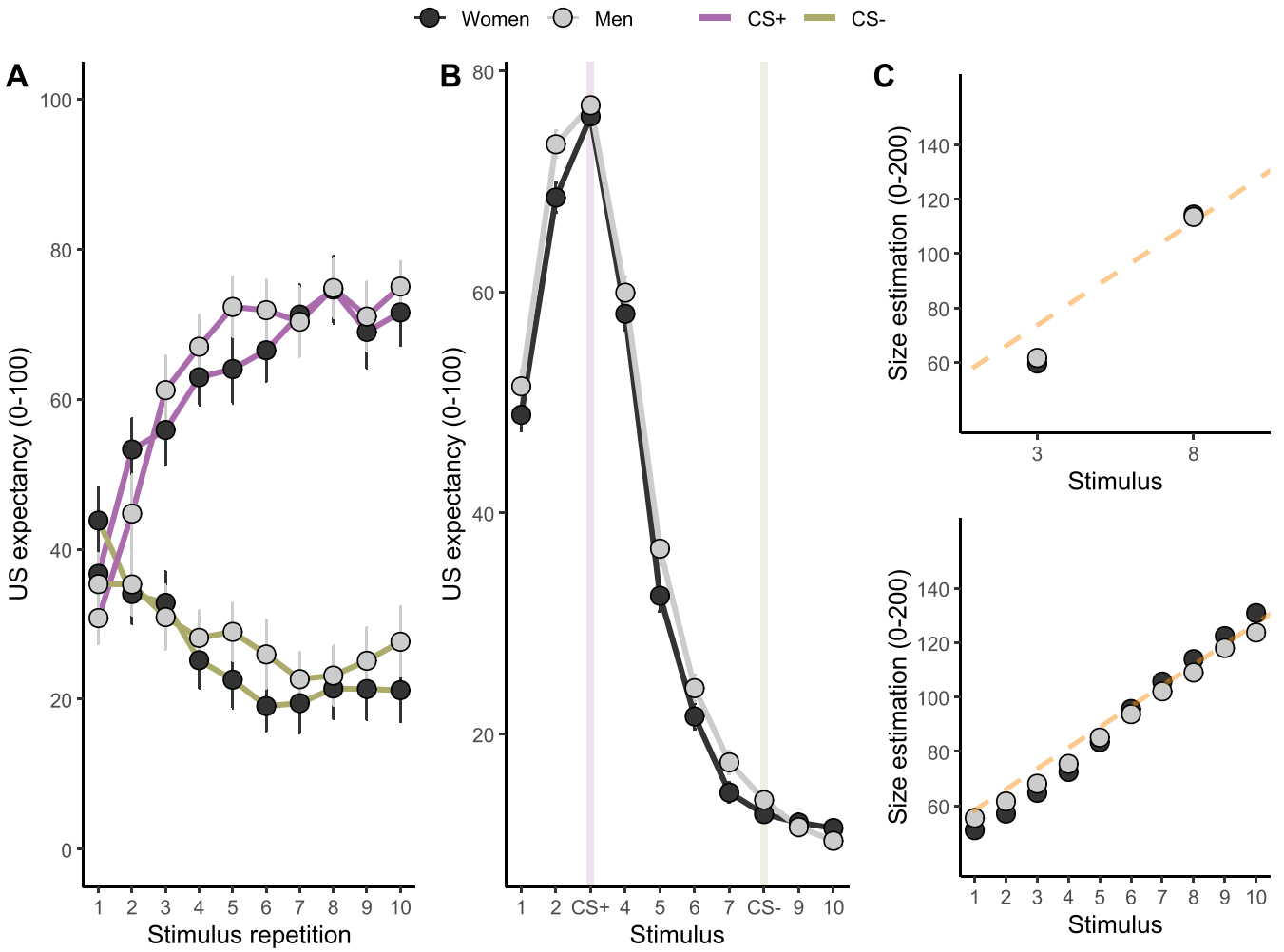

Fig. 2. Group averages for women and men. A) US expectancy ratings per CS during the acquisition phase across CS repetitions. **B)** US expectancy ratings during the generalization phase. **C)** Size estimations during the acquisition (top) and generalization (bottom) phases. Error bars denote standard errors.

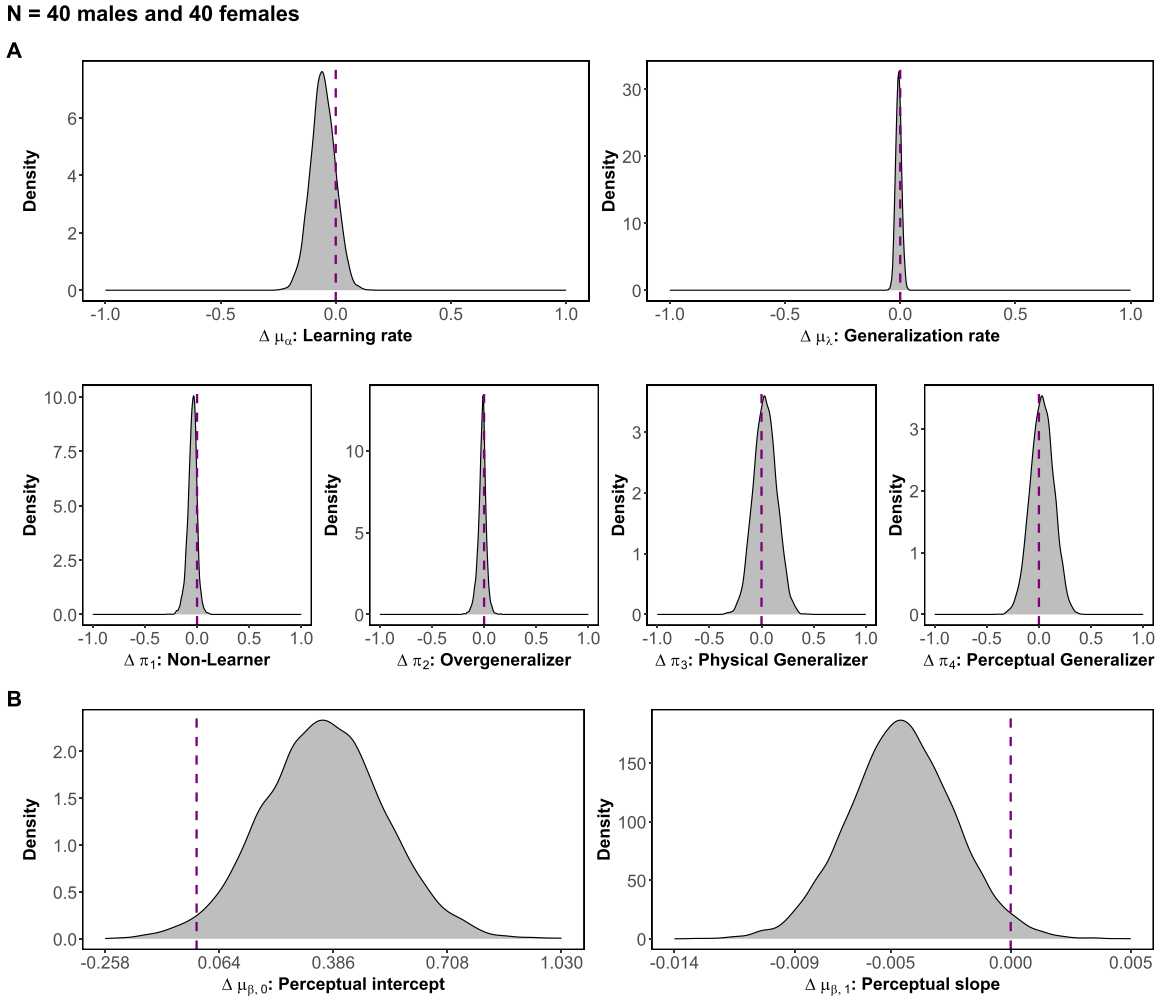

Fig. 3. Gender differences in parameter estimates for the computational models in perception and generalization. A) Concerning perception, the examined parameters include the differences in the gender-specific group-level perceptual intercept, defining the baseline of sensory mapping, the group-level perceptual slope regulating sensitivity to physical quantity variations (with a non-linear logistic mapping function). **B)** Regarding generalization, the parameters under investigation encompass gender differences in group-level generalization rate, learning rate, and the probabilities associated with four paths of generalization patterns. The dashed line indicates no gender difference.

when recalling CS+ or CS- (CS+: $\beta = 0.01$, 95% CI [−0.43, 0.45], t (135) = 0.05, p = 0.96; CS-: $\beta = -0.11$, 95% CI [−0.53, 0.31], t (127) = −0.52, p = 0.61). Similarly, the effect of memory block was also not significant for neither stimulus recall (CS+: $\beta = -0.13$, 95% CI [−0.31, 0.05], t (190) = −1.38, p = 0.17; CS-: $\beta = 0.07$, 95% CI [−0.10, 0.25], t (190) = 0.84, p = 0.40), indicating that reconstructed size did not significantly vary across different memory blocks. However, there was a significant interaction between gender and memory block when recalling CS- ($\beta = 0.40$, 95% CI [0.09, 0.71], t (190) = 2.56, p = 0.01), suggesting that the effect of memory block on reconstructed size differed between men and women, but not when recalling CS+ ($\beta = 0.08$, 95% CI [−0.24, 0.41], t (190) = 0.50, p = 0.62). Specifically, men demonstrated a greater increase in reconstructed size across memory blocks compared to women, as shown in Fig. 4A. No differences emerged between men and women when S8 served as the CS+ (all p's > 0.19). In the majority of conditions, the gender-specific distributions of the recreated size were found to be significantly divergent from the corresponding physical values (p's < 0.001) (see Supplementary Table 9). However, there were two exceptions to this trend. Specifically, in the case of the memory distribution for CS- when S3 served as the CS+ among women, the results did not reach statistical significance (t = −1.41, p = 0.16). Similarly, for the memory distribution of CS+ when S8 served as the CS+ among men, there was no significant difference observed (t = −1.53, p = 0.27).

3.5. Memory data – size estimations

For comparison purposes to the findings from the circle reconstruction data, we followed up the three-way interaction between Gender × Block × Counterbalancing for the size estimation analyses [F (1,651) = 4.69, $p = 0.031$, $\omega_p^2 = .006$] per Subgroup and CS type. Paralleling the pattern in the reconstruction data, only men had an increased size estimation throughout blocks when S3 served as the CS+ ($\beta = 0.48$, 95% CI [0.15, 0.81], t (176) = 2.84, p = 0.005, Fig. 4B). No other gender differences emerged across memory blocks (all p's > 0.3). A one-sample t-test revealed that the distributions of perceived size reproduction consistently differed from the corresponding physical values across all conditions (p's < 0.001) (see Supplementary Table 11).

3.6. Memory data – confidence ratings

As shown in Fig. 4C, there were different patterns in the evolution of memory confidence between genders with repeated memory testing [Gender × Block: F (1,612) = 9.90, p = 0.001, $\omega_p^2 = 0.01$; Gender × Block × Subgroup: F (1,612) = 11.95, p = 0.001, $\omega_p^2 = 0.02$]. When S3 served as the CS+, the analysis revealed that gender did not significantly impact memory confidence ratings for either CS+ recall ($\beta = 0.18$, 95%

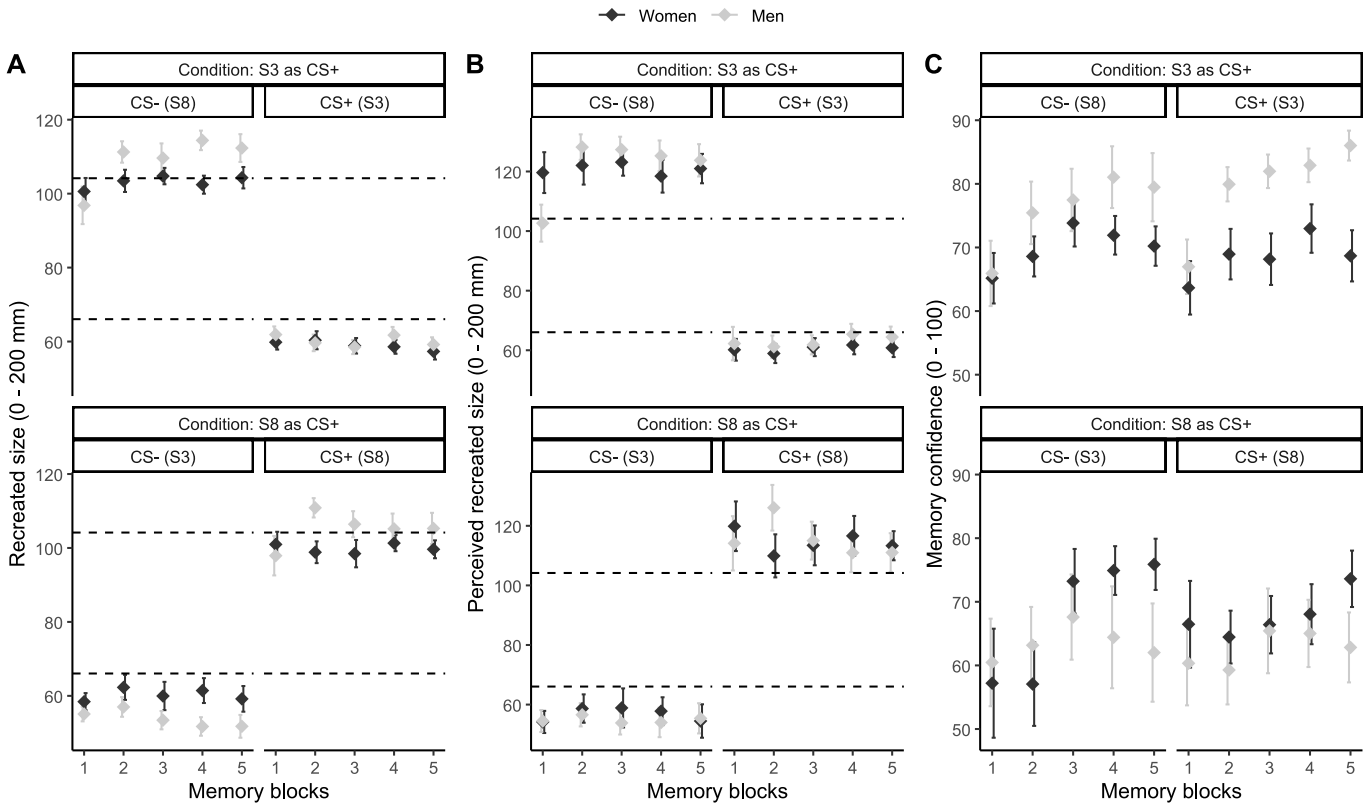

Fig. 4. Group averaged data for women and men of the memory phase. A) Recreated circle diameter. **B)** Estimated size of the recreated circle. **C)** Confidence rating of memory correctness. Error bars denote standard errors.

CI [−0.18, 0.54], t (106) = 0.98, p = 0.33) or CS- recall (β = 0.003, 95% CI [−0.35, 0.36], t (82) = 0.02, p = 0.99). However, confidence ratings increased over blocks in both CS+ recall (β = 0.20, 95% CI [0.03, 0.38], t (168) = 2.33, p = 0.02) and CS- recall (β = 0.23, 95% CI [0.05, 0.40], t (159) = 2.59, p = 0.01). Furthermore, for CS- recall, it increased more for men than for women (β = 0.35, 95% CI [0.02, 0.68], t (169) = 1.97, p = 0.05). Similarly, when S8 served as the CS+, gender did not significantly influence memory confidence ratings for either CS+ recall (β = 0.09, 95% CI [−0.58, 0.76], t (111) = 0.28, p = 0.78) or CS- recall (β = 0.42, 95% CI [−0.12, 0.96], t (81) = 1.524, p = 0.13). However, confidence ratings for the CS- increased across memory blocks (β = 0.50, 95% CI [0.27, 0.72], t (103) = 4.39, p < 0.001), but more profoundly in men than women (β = −0.58, 95% CI [−1.00, −0.16], t (104) = −2.74, p = 0.007).

4. Discussion

This study investigated potential gender differences in fear generalization, specifically investigating whether women exhibit enhanced fear generalization compared to men. Additionally, the research sought to uncover potential gender differences in related processes, including differential fear learning and the perceptual and memory representation of cues associated with threat or safety. Overall, this study found no robust evidence for gender differences in differential fear learning and perceptual fear generalization. However, the findings were mixed regarding gender differences in perception and recall memory accuracy.

Similar to Cooper et al. (2022a), we did not find gender differences in fear learning. Both genders successfully learned to associate cues to both threat and safety with strong statistical evidence for the absence of a gender effect in the speed at which differential learning occurred. Previous studies on gender differences in healthy volunteers either focused on contextual fear discrimination (Lonsdorf et al., 2015) or observed larger differential skin conductance responses (CS+ minus CS-) in men compared to women during cued fear conditioning (Milad et al., 2006). These previous findings suggest reduced differential learning in women compared to men. Various factors may contribute to divergent results between these previous studies and the present work, including differences in experimental paradigms, measurement techniques, considerations for the menstrual cycle, and distinctions between contraception use and free-cycling approaches. An essential distinction from these studies lies in the absence of hormone control in both the present study and Cooper et al. (2022a) 's research. Lonsdorf et al. (2015) reported that women using hormonal contraceptives exhibited impaired differential learning compared to both men and free-cycling women. Additionally, research suggested that elevated estradiol levels are associated with enhanced fear extinction, while lower levels are associated with extinction impairment. This phenomenon is supported by studies in both animals (Chang et al., 2009; Milad, Igoe, Lebron-Milad, & Novales, 2009) and humans (Graham & Milad, 2013; Milad et al., 2010; Zeidan et al., 2011). Notably, variations in women, contingent on the menstrual cycle or estrogen levels, have been explored in relation to gender differences in psychopathology (Cover, Maeng, Lebrón-Milad, & Milad, 2014).

Concerning gender differences in visual perception, the current literature offers mixed evidence where outcomes are contingent upon the specific perceptual task and stimulus dimension under examination (Abramov, Gordon, Feldman, & Chavarga, 2012; Shaqiri et al., 2018; Vanston & Strother, 2017). In the study by Shaqiri et al. (2018), employing a range of visual perceptual tasks, men demonstrated superior performance compared to women in tasks related to visual acuity, visual backward masking, motion direction detection, biological motion, and the Ponzo illusion. However, no gender differences were observed in tasks related to a contrast detection threshold, visual search, orientation discrimination, the Simon effect, and four other visual illusions (Shaqiri et al., 2018). In this study, we consistently measured real-time estimations of geometric size using a rating scale—a

methodology demonstrated in recent perceptual generalization research (Yu et al., 2023; Zaman et al., 2022, 2023) for effectively tracking the dynamic shifts in geometric perception during fear learning and generalization processes. Our findings revealed gender differences in both perceptual intercept and slope parameters through a statistical linear model, indicating a pattern where women exhibited greater perceptiveness than men. Yet, intriguingly, the computational non-linear model, which considers individual-level perceptual-physical mapping, revealed no differences in the perceptual slope parameter. This highlights the potential for biased interpretations of group differences in the current literature, where the common practice of averaging group-level responses may obscure the influence of individual variations (Estes, 1956; Estes & Maddox, 2005; see Supplementary Fig. 7 for individual perceptual patterns of the current study).

Regarding perceptual memory, our findings indicated that, relative to men, women exhibit a more precise memory of the safety cue, while displaying no notable difference in memory accuracy concerning the threat cue. Although we did not consistently observe more accurate memory in women compared to men across various conditions, this discovery raises questions about the generalizability of findings from animal studies indicating worse memory encoding and retrieval in women (Keiser et al., 2017; Lynch et al., 2013). Certainly, there are notable methodological differences between animal studies and our current human research that may temper the translational aspects. For instance, animal studies rely on contextual cues, with freezing behavior used to measure contextual memory precision indirectly. In contrast, our study employs perceptual cues, with the reproduction of these cues serving as a direct measure of perceptual memory. Yet, in the broader literature on gender differences in memory, it is established that men tend to outperform women in visual memory (De Frias, Nilsson, & Herlitz, 2006; Weiss, Kemmler, Deisenhammer, Fleischhacker, & Delazer, 2003), while the reverse is observed in auditory memory (Lewin, Wolgers, & Herlitz, 2001). It is noteworthy that these studies often utilize stimuli of higher complexity (e.g., human faces) compared to the simpler geometric sizes employed in our current study. Additionally, these studies were conducted in fear-free contexts, despite evidence suggesting that fear can modulate visual working memory (Curby, Smith, Moerel, & Dyson, 2019). Overall, there is a need for further systematic research to investigate comprehensively how women and men exhibit divergent patterns in perceptual memory encoding and retrieval within fear contexts, considering various modalities, stimulus dimensions, and memory tasks.

Finally, our investigation revealed the absence of gender differences in fear generalization, both with statistical and computational models. With the statistical model, evidence indicated no discernible gender differences in generalization patterns, aligning with the majority of recent findings (Tinoco-González et al., 2015; Torrents-Rodas et al., 2013; Xu et al., 2018) yet diverging from the findings reported by Cooper et al. (2022a). Notably, Cooper et al. (2022a) employed a 3-level categorical perceived risk scale to construct their generalization gradient, in contrast to our (and more commonly) use of the US expectancy scale ranging from 0 to 100. Moreover, their generalization test involved instrumental avoidance learning with a video game. These methodological differences may potentially modulate the results. To address potential concerns regarding differing trial numbers—given our larger trial count which might overshadow gender effect through more extinction—we conducted a reanalysis by restricting the dataset to include only the first 6 repetitions per TS (equating to the number of stimulus repetitions in Cooper et al., 2022a). However, this adjustment did not alter our original findings (see Supplementary Table 7). Moreover, in our attempt to replicate the findings of Xu et al. (2018), which reported slower extinction in women compared to men during the generalization stage, we specifically explored whether fear responses for the CS+ compared to the other stimuli evolved differently between genders throughout generalization trials. Our findings indicated no discernible effect (see Supplementary Table 8). On the computational front, the estimation of the generalization tendency parameter, crucial in the similarity generalization process (where mechanisms of learning and perception are considered), demonstrated no difference between women and men. Furthermore, there was no indication to suggest divergence in the probability of women and men being allocated to different latent groups of generalization patterns.

Gender differences are well-documented in several anxiety-related clinical disorders (Bekker & Van Mens-Verhulst, 2007), many of which have increasingly been linked to fear generalization behavior (Dymond et al., 2015; Fraunfelter et al., 2022). Our findings, which showed an absence of gender differences in fear generalization, suggested that fear generalization may not be the primary modulator of the well-established gender differences observed in anxiety-related disorders. Yet, further research is needed to confirm this conclusion. Despite the methodological considerations mentioned earlier, another plausible explanation for our findings could be the lack of significant gender differences in trait anxiety within our sample (Supplementary Note 5). Extensive prior research has consistently indicated that women tend to report higher levels of trait anxiety compared to men (Costa, Terracciano, & McCrae, 2001; Egloff & Schmukle, 2004), and this discrepancy often corresponds with more pronounced fear generalization (Sep et al., 2019). Hence, the absence of a discernible gender gap in trait anxiety within our study might account for the lack of observable distinctions in fear generalization between genders. Moreover, the precise causal relationship between fear generalization and anxiety-related disorders remains uncertain. It is unclear whether fear generalization precedes the onset of anxiety disorders or if existing anxiety disorders amplify fear generalization tendencies. Consequently, there is a need to explore whether gender works differently on fear generalization and its associated mechanisms within clinical populations.

5. Limitations

In the computational model, building on prior research (Yu et al., 2023), the Overgeneralizers group is defined as individuals who retain at least 70% of learning to all stimuli encountered in the environment. However, this cutoff point has not been tested for clinical relevance. Future studies could design experiments to establish the selective influence of the generalization rate parameter on clinical samples and determine a clinically relevant cutoff point for individuals who exhibit extreme generalization tendencies.

Additionally, the current research falls short of conducting a holistic examination of the distinctions between biological sex and psychological gender. The latter, recognized as a multifaceted psychological construct (Hyde, Bigler, Joel, Tate, & Van Anders, 2019), is limited by our approach of only allowing participants to self-report a binary categorical gender. Although this aligns with recent research investigating gender differences in human fear generalization (Cooper et al., 2022a; Xu et al., 2018), it remains intriguing to explore whether specific psychological elements, transcending traditional binary distinctions, could contribute to systematic changes in fear generalization behavior or its underlying mechanisms. In the current study, all participants identified with the gender corresponding to their biological sex. However, we did not control for sex-oriented factors that could potentially influence hormones, such as estrogen levels and the use of contraceptives. This aspect warrants attention in future research, especially considering past studies indicating the impact of these hormonal factors on fear learning (Lonsdorf et al., 2015; Milad et al., 2006). By not measuring hormone levels or documenting menstrual cycle phases, we may have overlooked crucial variables that could affect our observations. Future research should incorporate hormonal assessments and consider menstrual cycle phases to provide a more comprehensive understanding of gender differences in fear conditioning.

Furthermore, the conclusions drawn regarding gender differences in perception and perceptual memory are exclusively based on visual stimuli. This approach, however, overlooks research suggesting varied

sensory encoding and retrieval abilities between genders across different sensory modalities (Abramov et al., 2012; Shaqiri et al., 2018; Vanston & Strother, 2017). Additionally, fear responses in this study are confined to the behavioral US expectancy measure, despite studies revealing inconsistent results in fear learning when employing psychological, physiological, and neurological measures (LeDoux & Brown, 2017; LeDoux & Pine, 2016; Lipp & Purkis, 2005; Rossi & Berglund, 2011). To derive a more comprehensive understanding of gender differences in fear generalization, future research should incorporate multiple response channels to measure fear responses.

6. Conclusions

In this work, we concurrently assessed fear learning and generalization behavior, perception, and perceptual memory within a classical conditioning experiment. Employing both statistical and computational modeling approaches, our findings revealed an absence of evidence supporting distinct patterns of fear learning and generalization behaviors between genders. Additionally, we found no compelling evidence for differences in how individuals perceive and remember visual features of stimuli during the fear learning and generalization phases. This work, consistent with recent research trends (Tinoco-González et al., 2015; Torrents-Rodas et al., 2013; Xu et al., 2018), challenges hypotheses derived from animal studies regarding gender differences in fear generalization behavior and questions assumptions about women having worse memory accuracy as the underlying cause of such differences (Keiser et al., 2017; Lynch et al., 2013). However, a more systematic investigation with a consistent methodology to measure fear responses and the underlying processes is necessary for a clearer understanding of how biological sex, psychological gender, and their interaction influence generalization behavior. Until then, it is premature to rely on animal studies or limited human evidence to determine whether gender can effectively guide tailored treatments for clinical symptoms related to fear generalization.

CRediT authorship contribution statement

Kenny Yu: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Tom Beckers:** Writing – review & editing, Conceptualization. **Francis Tuerlinckx:** Writing – review & editing, Supervision, Methodology. **Wolf Vanpaemel:** Writing – review & editing, Supervision, Methodology. **Jonas Zaman:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

I have shared the link to both data and codes in the cover letter and also in the manuscript.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.brat.2024.104640.

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