

Spatial proximity amplifies valence in emotional memory and defensive approach-avoidance



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ARTICLE INFO

Article history:

Received 27 June 2014

Received in revised form

19 December 2014

Accepted 21 December 2014

Available online 23 December 2014

Keywords:

Peri-personal space

Startle

Skin conductance

Amygdala

Fear conditioning

Reward

ABSTRACT

In urban areas, people often have to stand or move in close proximity to others. The egocentric distance to stimuli is a powerful determinant of defensive behavior in animals. Yet, little is known about how spatial proximity to others alters defensive responses in humans. We hypothesized that the valence of social cues scales with egocentric distance, such that proximal social stimuli have more positive or negative valence than distal stimuli. This would predict enhanced defensive responses to proximal threat and reduced defensive responses to proximal reward. We tested this hypothesis across four experiments using 3-D virtual reality simulations. Results from Experiment 1 confirmed that proximal social stimuli facilitate defensive responses, as indexed by fear-potentiated startle, relative to distal stimuli. Experiment 2 revealed that interpersonal defensive boundaries flexibly increase with aversive learning. Experiment 3 examined whether spatial proximity enhances memory for aversive experiences. Fear memories for social threats encroaching on the body were more persistent than those acquired at greater interpersonal distances, as indexed by startle. Lastly, Experiment 4 examined how egocentric distance influenced startle responses to social threats during defensive approach and avoidance. Whereas fear-potentiated startle increased with proximity when participants actively avoided receiving shocks, startle decreased with proximity when participants tolerated shocks to receive monetary rewards, implicating opposing gradients of distance on threat versus reward. Thus, proximity in egocentric space amplifies the valence of social stimuli that, in turn, facilitates emotional memory and approach-avoidance responses. These findings have implications for understanding the consequences of increased urbanization on affective interpersonal behavior.

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1. Introduction

Humans are living in denser social environments than ever before (Dye, 2008). Urbanization has a multitude of beneficial effects on social organization and cultural identity, including wealth, global social status, artistic creativity, cultural artefacts, and access to critical resources, such as medical care and social support groups. At the same time, living in close quarters also increases the risk of interpersonal threats and social conflicts, suggesting that emotions are modulated by social proximity. Despite these important sociocultural implications of urbanization, surprisingly little laboratory research has been done on the role of egocentric distance on affective interpersonal behavior in humans.

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Personal space is a term that refers to interpersonal defensive boundaries around the body with the purpose of protecting oneself from harm (Horowitz et al., 1964). Approaching or infringing on an individual's personal space is associated with increased autonomic activity in humans and other species (McBride et al., 1963, 1965; Wilcox et al., 2006). Lesion studies indicate that the amygdala plays a critical role in establishing interpersonal defensive boundaries (Kennedy et al., 2009; Mason et al., 2006). However, it is not known how personal space violations interact with other amygdala-dependent learning processes in humans, such as fear conditioning.

A complementary literature on the evolution of defensive motivational systems also implicates an organization according to threat imminence. The spatial location of threats in egocentric space determines defensive repertoires in non-human animals. Proximal threats are more probable of inflicting harm than distal threats and thus induce more intense expression of defensive behavior (Blanchard and Blanchard, 1989). Threat imminence also

shifts neural signaling from cortical structures mediating precautionary behaviors to limbic and subcortical structures mediating post-encounter defensive responses and circa-strike “fight or flight” behaviors (Fanselow, 1994). Although there are fewer studies examining egocentric distance in defensive approach or reward contexts, the neural systems mediating defensive approach are also hypothesized to be organized according to distance (McNaughton and Corr, 2004), and proximal rewards tend to be valued more positively than distal rewards, as evidenced by spatial discounting in monkeys who prefer a smaller proximal reward to a larger distal reward (Kralik and Sampson, 2012; Stevens et al., 2005).

The hypothesis that egocentric distance may modulate defensive responses is also supported by studies suggesting differences in the neural representation of proximal and distal space (for reviews of neural representation of space, see Holmes and Spence, 2004; Previc, 1998). For instance, some patients with stroke have problems with perceiving and interacting with objects in near space but not far space (Halligan and Marshall, 1991), whereas others exhibit the opposite pattern (Brain, 1941). Neurophysiological studies in monkeys have also mapped the perception of graspable space, also termed ‘peripersonal space’, to the premotor cortex (Rizzolatti et al., 1996) and the posterior parietal cortex (Graziano et al., 2000). The neural representations of peripersonal space and defensive motor schemas overlap, as stimulation of ‘peripersonal space’-responsive areas in the premotor cortex evoke defensive responses such as moving the hand upwards and towards the midline of the body (Graziano and Cooke, 2006). Because of the tentative relationship between neural monitoring of peripersonal space and elicitation of bodily defense (Serino et al., 2009), we used a defensive reflex – the eye-blink startle response (Blumenthal et al., 2005) – as the outcome measure for the egocentric distance manipulation in three of the experiments described here. Startle is reliably modulated by valence such that responses increase with stimuli of negative valence and decrease with positive valence (Lang and Davis, 2006). Startle responses tend to habituate over time (Lang et al., 1990), but responses differentiate between negative and neutral stimuli even after repeated exposures to startle probes (Bradley et al., 1993). This makes startle a sensitive measure to study distance modulation of defensive responses. Indeed, painful stimulation to the hand while holding it near the face facilitates startle (Sambo et al., 2012; Sambo and Iannetti, 2013). Yet, it is not known whether startle in humans is influenced by spatial proximity to extra-personal affective stimuli.

The present study bridges the social psychological literature on peri-personal space with the motivational literature on threat imminence by using immersive (3-D) virtual reality paradigms to manipulate the egocentric distance of conspecific threats in humans. Across four separate experiments, we wished to establish the valence gradient of conspecifics as a function of egocentric distance (Experiment 1), the learning-induced plasticity of

interpersonal defensive boundaries to conditioned threats (Experiment 2), the lasting effect of threat distance on the retention of fear memories (Experiment 3), and the influence of egocentric distance in establishing valence gradients across defensive approach and defensive avoidance contexts (Experiment 4). A design summary of the four experiments can be found in Table 1. Collectively, these studies can advance an understanding of how spatial proximity impacts interpersonal defensive behaviors in humans, alters long-term memory for threatening experiences, and magnifies the valence of rewards and punishments.

2. Methods

2.1. Participants

Twelve participants (Mean Age \pm SD = 22.3 \pm 6.3 years; 6 women) in Experiment 1, 21 participants (Mean Age \pm SD = 21.0 \pm 6.8 years; 11 women) in Experiment 2, 18 participants (Mean Age \pm SD = 20.3 \pm 3.7 years; 10 women) in Experiment 3 and 30 participants (Mean Age \pm SD = 25.1 \pm 8.4 years; 18 women) in Experiment 4 provided written informed consent in accordance with Duke University Medical Center Institutional Review Board guidelines. In Experiment 1, an additional 4 subjects participated, but no startle responses could be observed in these participants as evident from visual inspection of the EMG, and they were therefore excluded from the data analysis. In Experiment 3, 2 additional subjects participated, but no EMG was registered in these participants due to equipment failure. Data from these participants were excluded from analysis, leaving 12 participants (Mean Age \pm SD = 22.3 \pm 6.3 years; 6 women) in Experiment 1 and 18 participants (Mean Age \pm SD = 20.3 \pm 3.7 years; 10 women) in Experiment 3. In total, 81 subjects participated in the four experiments.

2.2. Fear-potentiated startle

The eye-blink startle response was recorded the same way in Experiments 1, 3 and 4. Electromyography (EMG) was continuously recorded from the right orbicularis oculi muscle at 1000 Hz using two cup electrodes filled with electrolyte gel. A ground electrode was attached to the left hand. Startle probes included a 100-dB 50-ms white-noise burst presented binaurally through headphones and jittered between 400 and 600 ms post-stimulus onset. Startle was quantified as the maximum EMG response 20–120 ms post-probe onset subtracted from the average EMG response during the immediate 500 ms preceding probe delivery. Responses were transformed to *T*-scores in Experiments 1, 3 and 4 (*T*-score = *z*-score \times 10 + 50) (Alvarez et al., 2007).

Table 1
Overview of experimental designs.

Experiment	Hypotheses	Experimental factors (levels)	Outcome measure
1	H1: Startle is facilitated at proximal distances.	Distance (0.6 m, 0.8 m, 1.2 m, and 2 m)	Startle
2	H1: Learned threat value increases interpersonal defensive boundaries. H2: Increased interpersonal defensive boundaries to learned threat generalize to new contexts.	Stimulus (CS+, CS-); context (conditioning, novel)	Interpersonal distance
3	H1: Fear memories formed at near interpersonal distance are resistant to extinction.	Distance (0.6 m, 3 m); stimulus (CS+, CS-); time (early, late)	Startle
4	H1: Proximity has opposing effects on defensive responses in defensive avoidance relative to defensive approach contexts.	Distance (0.6 m, 3 m); stimulus (defensive approach, defensive avoidance)	Startle

CS+, fear cue; CS-, control cue.

2.3. Distance measurement

In Experiment 2, the primary outcome measure was the distance (m) at which subjects would tolerate the virtual characters in egocentric space. Starting at a distance of 8 m, the character approached the subjects at a fixed velocity of 0.3 m/s. By pressing a response button, the participants could stop the approaching character at a distance where they would feel comfortable having a conversation with the character (see Section 2.6.2). We term this distance the “interpersonal defensive boundary”.

2.4. Skin conductance responses (SCRs)

In Experiment 2, SCR served as the autonomic measure of fear conditioning which allowed us to confirm that the CS acquired threat value prior to tests (see Section 2.6.2) of the interpersonal defensive boundaries (see Section 2.3). SCR served predominately as a manipulation check and was used in place of startle for convenience because it is less obtrusive and does not involve presentation of intense auditory startle probes. Skin conductance recording was controlled with the MP-150 BIOPAC system (BIOPAC Systems, Goleta, CA). Ag/AgCl SCR electrodes were placed on the palmar surface of the left hand. SCR analysis was carried out using AcqKnowledge software (BIOPAC Systems) using procedures previously described (Dunsmoor et al., 2009). Briefly, SCR was scored if the trough-to-peak response occurred 1–4 s following stimulus onset, lasted between 0.5 and 5.0 s, and was greater than 0.02 microSiemens. A trial that did not meet these criteria was scored as a zero.

2.5. Virtual reality contexts and stimuli

Two 3D environments that varied in color and texture were created in VirTools (Dassault Système, Paris, France). The virtual environments consisted of a floor, two walls, and a sky and were presented in a first-person perspective through 3-D goggles (eMagin Z800 3DVisor, Bellevue, Washington). In all Experiments (1–4), participants traveled through the virtual environments on a straight path at an average velocity of 0.3 m/s. Movement was paused during presentation of stimuli. Stimuli consisted of 4 different 3D characters that were imported into VirTools. All characters were 1.8 m tall in the virtual environment and exhibited neutral facial expressions. Characters were static during all presentations, except the two test phases in Experiment 2 during which they traveled toward the participant.

2.6. Procedure

2.6.1. Experiment 1: Proximity modulates magnitude of defensive responses

Participants were instructed that they would see two different virtual characters that appear at different distances. The two 3D characters were presented at a distance of 0.6 m, 0.8 m, 1.2 m, or 2.0 m from the position of the participant in the virtual environment. These distances were chosen based on prior literature to span the defensive interpersonal boundary (Kennedy et al., 2009; Little, 1965). The characters appeared for 1 s, during which time forward navigation down the alleyway was paused. Each character was presented 4 times at each of the four distances, resulting in a total of 32 presentations. The inter-trial interval (ITI) between stimulus presentations was 5 ± 1 s. A startle probe was delivered between 400 and 600 ms following stimulus onset for each presentation. Before the experiment started, 9 startle probes were presented alone to allow startle responses to habituate. Startle responses were transformed to *t*-values and averaged for each distance before data was entered in a repeated-measures ANOVA

with Distance as within-group factor. Startle responses were of similar magnitude to the two virtual characters ($P > 0.60$), so the data were collapsed over the characters.

2.6.2. Experiment 2: Acquired fears increase interpersonal defensive boundaries

Following a short habituation phase in which two virtual characters were presented four times without reinforcement (data not analyzed), fear conditioning proceeded with presentations of one of the characters (CS+) co-terminating with a brief electric stimulation to the wrist (US) on 50% of the trials in a pseudorandom order. Partial reinforcement slows extinction rate (partial reinforcement extinction effect) (LaBar et al., 1998; Phelps et al., 2004), which was desirable to maintain the acquired threat value of the CS+ across the two test phases following acquisition. US duration was 6 ms, and US intensity was calibrated to each participant's tolerance prior to the start of the experiment using an ascending staircase procedure so that the shocks were subjectively rated as annoying but not painful (Dunsmoor et al., 2009). Another virtual character was never paired with shock and served as the control stimulus (CS−). The character serving as CS+ and CS− was counterbalanced across participants. Participants viewed 12 presentations of each CS-type presented in a pseudo-randomized order so that no more than two presentations of any CS-type would follow in a row, in order to avoid mood induction effects. Each CS was presented for 6 s followed by an ITI of 10 ± 2 s. Mean SCR to the CS+ compared to the CS− served as the primary index of fear conditioning.

Two test phases of interpersonal defensive boundaries to the CS+ and the CS− followed the fear conditioning phase. These two test phases differed as to whether CSs were presented in the original fear conditioning context or a novel context. We tested whether the difference in interpersonal defensive boundaries between CSs was greater in the conditioning context than the novel context, consistent with personal space being context dependent (Little, 1965), or whether the CS+ related increased interpersonal defensive boundaries was similar across contexts, consistent with findings on fear generalization across contexts (Bouton et al., 2006). The two contexts were both alleyways, but differed with respect to the texture and color of the ground, walls and sky (see Fig. 3 for example contexts). Presentation order of contexts was counterbalanced across subjects. Participants were detached from the shock electrodes before the test of defensive distance started.

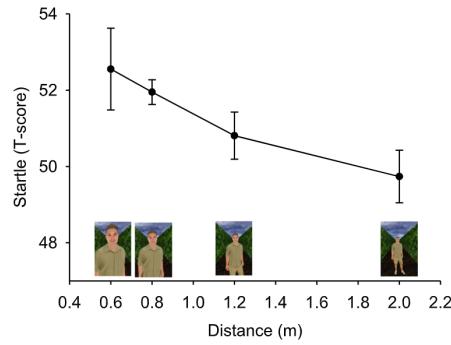


Fig. 1. Startle response to virtual characters appearing at varying egocentric distances in Experiment 1. The startle response increased with smaller defensive distance in the 3D virtual reality environment.

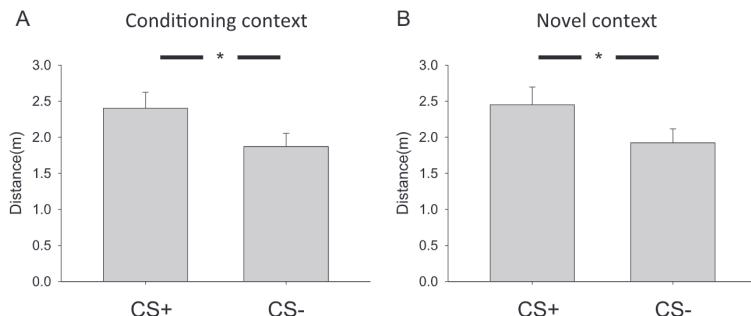


Fig. 2. Defensive distance following fear conditioning in Experiment 2. (A) Interpersonal defensive boundaries were greater to the fear cue (CS+) than the control cue (CS-) when tested in the virtual fear conditioning context. (B) Interpersonal defensive boundaries were also greater to the fear cue relative to the control cue in a novel virtual context. * $p < 0.05$.

They were told that they would see the two characters (CS+, CS-) moving towards them and were asked to stop the characters at a distance they would feel comfortable at having a conversation with the character by pressing a mouse button. The character approached the subjects at fixed rate (0.3 m/s) starting at a distance of 8 m. The primary outcome measure in the test phases was the distance (m) at which participants stopped the encroaching virtual character, which we termed the "interpersonal defensive boundary" (see Section 2.3).

2.6.3. Experiment 3: Spatial proximity delays extinction of fear potentiated startle

The experiment was separated into three phases: fear conditioning, extinction, and 24-h delayed re-extinction. Participants

were told prior to the experiment that they would be walking down a long alleyway and would encounter four different individuals along the way; two of which were dangerous, and would sometimes deliver a brief shock, whereas the other two were safe and would never deliver a shock. However, they were not told which characters were dangerous and which were safe. The same calibration procedure was used as in Experiment 2 to determine the intensity of the electric stimulation that served as US (see Section 2.6.2). The characters appeared for 1 s, during which time forward navigation down the alleyway was paused. A short habituation phase involving two presentations of each character occurred prior to conditioning. Prior to conditioning, 9 startle probes were presented to habituate baseline startle responses (data not analyzed).

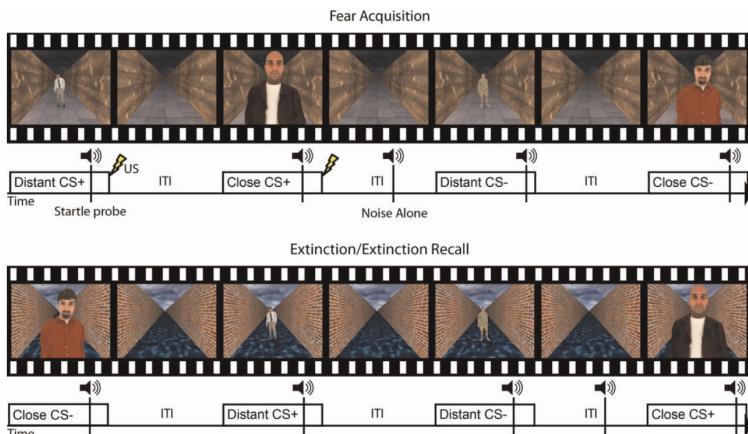


Fig. 3. Fear conditioning design in Experiment 3. Four 3-D virtual characters, appearing either at a proximal interpersonal distance that invades personal space or farther away, served as conditioned stimuli (CS). One character from each distance (CS+) was paired with an electrical shock unconditioned stimulus during acquisition training, whereas one character from each distance was unreinforced (CS-) throughout the experiment. Acquisition and extinction occurred in separate virtual contexts. Twenty-four hours later, re-extinction was tested in the extinction context. Fear-potentiated startle responses served as the dependent measure of fear conditioning. ITI = inter-trial interval.

Each phase included 40 trials: 10 proximal CS+s, 10 distal CS+s, 10 proximal CS-s, and 10 distal CS-s. During fear conditioning, 60% of the CS+ stimuli co-terminated with shock (partial reinforcement schedule). Partial reinforcement of the CS+ was used to delay rapid extinction that normally occurs in human participants following 100% CS+ reinforcement (LaBar et al., 1998; Phelps et al., 2004). This procedure decreases the likelihood of floor effects that would preclude observing the effect of the distance manipulation during extinction testing. The ITI was 12 ± 2 s, during which time participants were passively guided down the alleyway on a fixed rate and forward path with a velocity of 0.3 m/s, with no CSs present. Extinction followed conditioning and included the same 40 trials but with no US. Contingency awareness was assessed at the end of the Day 1, and all subjects demonstrated knowledge of which characters had (and had not) been paired with shock. Subjects returned 24 h later for a test of re-extinction and were reconnected to the shock electrodes; however, no shocks were delivered on Day 2. In all phases, stimulus order was pseudorandomized such that characters did not appear more than twice in a row. Four counterbalanced stimulus order presentations were used, and the assignment of contexts to training phases was also counterbalanced across subjects.

During each phase, startle probes were delivered on 6 of 10 trials for each of the four stimulus conditions. Six noise-alone startle probes were delivered during the ITIs of each phase to

make probe delivery uncorrelated to CS presentations. ITI startle data were not analyzed, as the CS- itself provides a matched control condition. Normalized average response to each stimulus (proximal and distal CSs) was categorized as early (startle probes 1, 2, and 3) and late (startle probes 4, 5, and 6) for each training phase. Repeated-measures ANOVA was used in the statistical analyses of data, with distance, CS-type, and time (early, late) as within-subject factors. Proximal and distal CS+ trials were then subtracted from their respective distance-matched CS- to create conditioning scores that were used in data graphs (Fig. 4) to depict CSxdistance interactions. We predicted greater startle responses to the CS+ than the CS- during the late part of the acquisition phase, consistent with conditioning. We also predicted greater difference between CS+ and CS- in the proximal relative to the distal location during the late part of extinction and re-extinction, consistent with the hypothesis that proximal location delays extinction.

At the end of the experiment on Day 1, participants rated the valence (range: 1–9, 5 being neutral) and arousal (range: 1–9, 5 being neutral) of each character. Ratings were performed on a computer where all characters were displayed in 2D at the same distance (0.6 m). Due to software malfunction, arousal and valence ratings for two participants were not registered. These participants were excluded from the statistical analysis of rating data leaving 16 participants.

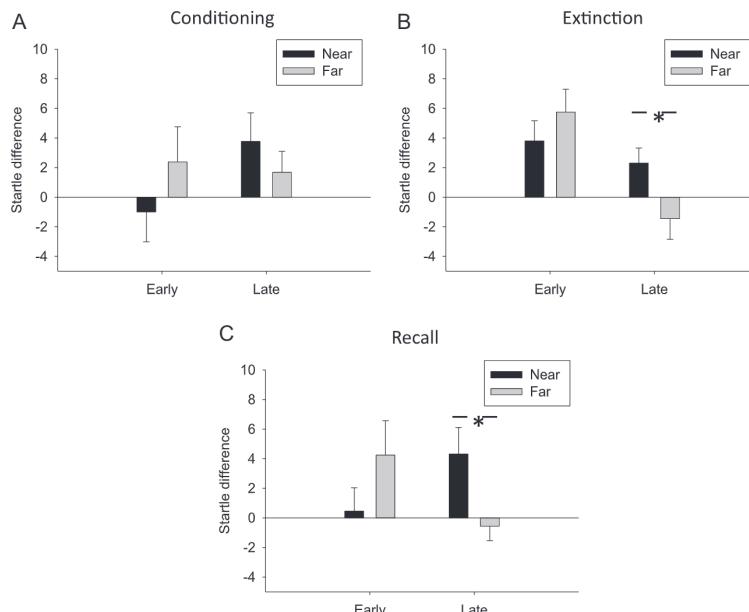


Fig. 4. Fear-potentiated startle during conditioning and extinction in Experiment 3. Bars show mean startle difference (\pm SEM) between the proximal (near) CS+ and CS-, as well as between the distal (far) CS+ and CS-. Left panels show early responses (average of responses 1–3) and right panels show late responses (average of responses 4–6). (A) Similar startle magnitudes were observed to the CS+ and CS- during the early stage of fear conditioning. Conditioned responses were observed to both the near and far CS+ relative the distance-matched CS- during late acquisition. (B) During initial extinction, greater responses to both the near and far CS+ relative the CS- were observed. During late trials, however, differential responding was only observed to the near CS+, suggesting resistance to extinction of proximal fear memories. (C) No difference in startle magnitude between near and far CSs was observed during early trials when re-extinction was tested 24 h later. However, differential responding to the near CS+ again persisted in the late stage of testing, whereas the far CS+ was re-extinguished. * $p < 0.05$.

2.6.4. Experiment 4: Opposing valence gradients across defensive approach and avoidance

Experiments 1–3 investigated threat modulation of defensive behavior. In Experiment 4, we examine the influence of spatial proximity on both threats and rewards in avoidance and approach contexts. In contrast to threats, the presence of rewards weakens defensive responses, and we thus expected attenuated startle responses to proximal relative to distal rewards during approach. To test this hypothesis, participants encountered characters that signaled shock or monetary reward together with shock, at proximal or distal locations. Characters that signaled a combination of threat and reward were used instead of characters that signaled only reward, as this type of incentive conflict has been theorized to be sensitive to distance manipulations (McNaughton and Corr, 2004). We term this motivational condition Defensive Approach, in line with previous literature (McNaughton and Corr, 2004, 2014).

The experiment was separated into two runs to allow participants a brief pause (~1 min) between runs to reduce fatigue. Four characters were displayed for 2 s each with a variable inter-trial interval with an average of 10 s (range: 8–12 s). Each character was displayed 25 times in pseudo-random order so a character would not be shown twice in a row. Every character presentation ended with an electric shock unless a button was pressed in which case no shock was delivered. Participants were informed that they always could avoid the shock by pressing the button. Four characters were displayed during the experiment. Two of the characters, one proximal (0.6 m) and one distal (3 m), were displayed concurrently with an icon on the left side of the screen signaling how much money would be rewarded if the shock was not avoided (defensive approach condition). The two other characters, also one proximal (0.6 m) and one distal (3 m), were displayed without the money icon signaling that no reward would be given if the shock was not avoided (defensive avoidance condition). Thus, no incentive was given for not avoiding the shock during defensive avoidance. During the Defensive Approach condition, the reward amounts were 1¢, 5¢, 50¢, \$1, or \$3, and each reward amount was displayed on 5 of the 25 presentations for the proximal and distal character. Startle probes were delivered on 4 out of 5 (80%) of these presentations, adding up to 20 startle probes per character. Startle probes were jittered between 400 and 600 ms following stimulus onset, as in Experiments 1 and 3. Before each run, 8 startle probes were presented without any of the characters on the screen to allow for the startle response to habituate before the experiment began. Startle responses were transformed to t-scores and averaged for the proximal and distal defensive avoidance and defensive approach conditions. At the end of the experiment, participants rated the valence (range: 1–9) and arousal (range: 1–9) of each character. Ratings were performed on a computer where the characters were displayed in 2D at the same distance, as in Experiment 3.

2.7. Statistical analysis

Repeated measures analysis of variance (ANOVA) was performed in SPSS 18 (IBM Corporation, New York, USA) to evaluate the main effect of distance (0.6 m, 0.8 m, 1.2 m, and 2.0 m) on startle in Experiment 1, the effect of CS-type (CS+, CS−) on defensive distance in Experiment 2, the CS-type \times distance interaction in Experiment 3 and the Condition (Defensive Approach, Defensive Avoidance) \times distance interaction in Experiment 4. Post-hoc two-sample t-tests were used to compare differential startle responses in Experiment 3 (CS+ versus CS−). Statistical significance was set to $\alpha=0.05$.

3. Results

3.1. Experiment 1: Proximity modulates magnitude of defensive responses

We found that startle was enhanced with decreasing distance ($F_{3,36}=3.18$, $P=0.03$; Fig. 1), indicating that proximity of conspecifics in egocentric space increases the vigor of defensive reflexes in a graded fashion.

3.2. Experiment 2: Acquired fears increase interpersonal defensive boundaries

Participants exhibited greater SCR to the CS+ than the CS− ($F_{1,20}=13.50$, $P=0.002$; Fig. S1), indicating successful discriminatory fear learning. Following fear learning, we tested how close subjects would tolerate each virtual character in egocentric space. Defensive interpersonal boundaries were enhanced to the fear cue relative to the control cue across the conditioning context and the novel context ($F_{1,20}=8.70$, $P=0.008$; Fig. 2). Defensive boundaries were similar across contexts ($F_{1,20}=0.68$, $P=0.42$) and no interaction between context and CS-type was noted ($F_{1,20}=0.15$, $P=0.71$). Accordingly, differences in defensive boundaries between the fear cue and control cue were found both when participants were tested within the fear conditioning environment (mean difference: 0.53 m, $t_{20}=3.09$, $P=0.006$; Fig. 2) and the novel virtual environment (mean difference: 0.56 m, $t_{20}=2.76$, $P=0.01$; Fig. 2), suggesting that fear memory modulation of defensive interpersonal boundaries generalizes across contexts. This set of results shows that learned threat value changes the preferred distance to a stimulus and suggests that amygdala-dependent fear learning shapes defensive distance monitoring.

3.3. Experiment 3: Spatial proximity delays extinction of fear potentiated startle

Experiment 3 investigated the effect of spatial proximity on the persistence of fear memories. Results from late Acquisition revealed significantly greater startle to the CS+ versus the CS− ($F_{1,17}=4.43$, $P=0.05$; Fig. 4). There was no difference in the mean level of conditioning (CS+ versus CS−) during late Acquisition across distances ($p>0.35$), indicating an equivalent level of learning regardless of personal distance of the CS+. We also replicated the finding from Experiment 1 of a main effect of distance on startle, such that startle to proximal CSs were greater overall than to distal CSs ($F_{1,17}=9.89$, $P=0.006$).

During extinction and re-extinction, we observed an interaction among CS-type, distance and time ($F_{1,17}=7.79$, $P=0.01$; Fig. 4) due to differential startle remaining elevated to proximal stimuli during the later stage of each phase (extinction: $t_{17}=2.16$, $P=0.04$, re-extinction: $t_{17}=2.42$, $P=0.03$; Fig. 4). Differential startle to the distal stimuli on the other hand, was non-significant during the later stage of each phase indicating full extinction ($P<0.21$). When CS+ responses were analyzed separately, we found robust differences in the startle response to the near and distant CS+ during late extinction ($t_{17}=3.71$, $P=0.002$) and re-extinction ($t_{17}=4.90$, $P<0.001$). This pattern suggests that the CS-type \times Distance interaction during the second half of each phase was driven by differences in startle between the close and distant CS+ rather than distance-related differences in response to the CS−. In contrast to the facilitation of startle to the near CS+ during the later stage of Extinction and Re-extinction, the difference in startle between the CS+ and CS− during the early stages of Extinction and Re-extinction was similar across proximal and distal distances ($P>0.17$). The finding of an increased differentiation between the

proximal fear cue and the distance-matched control cue during the later stages of Extinction and Re-extinction shows that conditioned fear associations acquired at a near personal distance were harder to extinguish (and re-extinguish) than those at a farther distance, despite equivalent levels of initial learning. Importantly, these results cannot be attributed to a general facilitating effect of proximal distance on startle responses, as the CS⁻ was distance-matched to the CS⁺.

To assess whether participants experienced the fear cues differently from the control cues, evaluative ratings for each CS were retrospectively collected after extinction training on Day 1 (Fig. S2). The characters serving as the CS⁺ stimuli were rated as more negative (Close: $t_{12}=9.48$, $P<0.001$; Distant: $t_{12}=7.28$, $P<0.001$) and arousing (Close: $t_{12}=8.33$, $P<0.001$; Distant: $t_{12}=7.32$, $P<0.001$) than characters serving as the CS⁻. Egocentric distance did not affect these retrospective subjective ratings of valence or arousal (P s > 0.70).

3.4. Experiment 4: Opposing valence gradients across defensive approach and avoidance

As a behavioral check of the motivational manipulation, we compared the proportion of trials that were successfully avoided by the participants across the defensive approach and defensive avoidance conditions. As expected, shocks were avoided to a larger degree during defensive avoidance (90% of trials) than during defensive approach (35% of trials) ($F_{1,29}=97.27$, $P<0.001$). We observed an interaction between motivation condition (defensive approach, defensive avoidance) and egocentric distance (proximal, distal) on startle responses ($F_{1,17}=7.58$, $P=0.01$; Fig. 5). The interaction was driven by an increase in startle to the proximal relative to the distal character during Defensive Avoidance, and a decrease in startle to the proximal relative to the distal character during defensive approach. The average startle response to the proximal and distant character during defensive avoidance was greater than that during defensive approach ($F_{1,29}=5.83$, $P=0.02$), suggesting that cues predicting reward inhibit startle relative to unrewarded cues, as could be expected if startle tracks valence. The observation that close proximity facilitated startle during defensive avoidance and inhibited startle during Defensive Approach suggests that spatial proximity amplifies the valence of stimuli.

Retrospective ratings of valence and arousal for each character, taken at the end of the experiment (Fig. S3), showed that stimuli

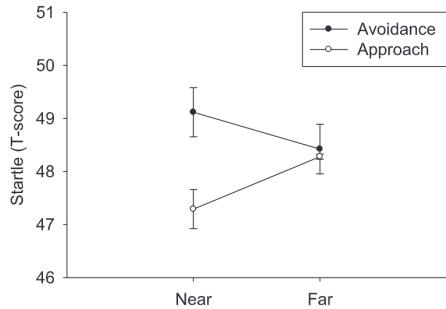


Fig. 5. Distance modulation of defensive responses during defensive avoidance and approach in Experiment 4. Startle increased when participants were exposed to proximal relative to distal threats during defensive avoidance trials. In contrast, startle decreased with spatial proximity when participants were exposed to reward during defensive approach.

presented in the context of defensive approach were rated as more positive than stimuli presented in the context of defensive avoidance ($F_{1,29}=12.23$, $P=0.002$). We also observed a tendency for a Distance by Stimulus interaction ($F_{1,29}=2.80$, $P=0.10$) in the same direction as our startle findings, with greater differences in valence as a function of motivational context to characters presented in near-body space. When conditions were ranked according to mean valence ratings and mean startle responses, the correlation between valence and startle was significant (Spearman's $\rho=-1.0$; $P<0.01$). No main effect of Distance was observed ($F_{1,29}=0.18$, $P=0.67$). Arousal ratings were greater to reward-related stimuli ($F_{1,29}=21.42$, $P<0.001$) as well as to near stimuli ($F_{1,29}=7.33$, $P=0.01$). We also observed a Distance by Stimulus interaction ($F_{1,29}=4.18$, $P=0.05$). The interaction effect was driven by a larger difference in arousal ratings between stimuli at the far location than at the near location. As such, they were in the opposite direction of the startle data. Accordingly, when conditions were ranked according to mean arousal ratings and mean startle responses, the correlation between arousal and startle was non-significant (Spearman's $\rho=-0.8$; $P>0.20$). Thus, the pattern of startle reflex modulation is more similar to subjective valence modulation across conditions than subjective arousal.

4. Discussion

Results from four experiments demonstrate that the near-body localization of potentially threatening cues in egocentric space increases startle responses, defensive boundaries, fear memory persistence, and hedonic state during approach and avoidance of an aversive stimulus. Experiment 1 showed that startle responses were potentiated as virtual characters encroached upon the personal space of the research participant, even without a threat being present. Experiment 2 further showed that interpersonal defensive boundaries are flexibly allocated according to the potential threat value of an encroaching conspecific, even when the threat is encountered in a novel environment. Experiment 3 revealed that conditioned threats invading personal space are more resistant to extinction and re-extinction processes relative to distal threats, despite equivalent arousal levels at the time of learning. Experiment 4 extended these findings to the domain of defensive approach and avoidance, with opposing egocentric gradients of hedonic value being established across these motivational contexts. Overall, our findings suggest that egocentric distance establishes an important behavioral value gradient that influences fear learning and approach-avoidance behavior.

4.1. Defensive responses scale with spatial proximity

Prior studies using live actors found that proximity to the actor enhanced autonomic activity (McBride et al., 1965). These effects of invasion of personal space on autonomic activity were recently replicated using VR applications (Wilcox et al., 2006). From these previous investigations of autonomic activity and spatial proximity, we predicted facilitation of defensive startle reflexes to social stimuli at close range. Our findings indicate a progressive increase in startle with proximity to characters that were presented at distances between 2 and 0.6 m. This indicates that the vigor of defensive responses is enhanced with spatial proximity, in line with animal research on threat imminence (Blanchard and Blanchard, 1989; Fanselow et al., 1994). Interestingly, this effect is graded in the range chosen, which spans from distances where most individuals are comfortable speaking with strangers to those that clearly invade personal space. Thus defensive boundaries appear to be coded in a continuous rather than a discrete fashion along a gradient of egocentric distance.

4.2. Adaptation of interpersonal defensive boundaries to acquired fear

In Experiment 2, a previously neutral stimulus acquired a negative valence following fear conditioning. We found that the character that served as the fear cue was tolerated at 0.5 m further distance than the safe character. This shows that defensive space is adaptive and can change with the valence of stimuli. This finding also helps in interpreting the findings from Experiment 1, and suggests the facilitation of startle with proximity was due to change in valence of the proximal stimuli.

We further assessed the influence of context on interpersonal defensive boundaries. Prior studies on personal space have found that the setting in which a person is being approached modulates inter-personal boundaries. For example, inter-personal boundaries are greater in a setting where you experience the scrutiny of others than in a private setting (Little, 1965). From this line of research, it could be expected that the inter-personal boundaries would differ between a dangerous context in which one has experienced aversive shocks and a novel context. On the other hand cued fear generalizes to new contexts (Bouton et al., 2006), and it is therefore possible that cued fear is context-independent resulting in enlarged inter-personal boundaries to fear cues across contexts. In our experiment, the distance at which the threatening character was tolerated did not change between the conditioning context and a novel context. This generalized pattern suggests that the information determining the plasticity of the interpersonal defensive boundaries was signaled by the fear cue rather than the conditioning context. This is in line with studies on fear generalization showing that fear memories extend across different contexts (Bouton et al., 2006).

4.3. Spatial proximity increases the persistence of fear memory

In Experiment 3, we found that egocentric distance is a mediating factor for the selective retention of acquired fears. This finding is in line with a large body of fear conditioning literature in humans showing that certain classes of stimuli are more resistant to extinction than other stimuli (preparedness theory) (Ohman and Mineka, 2001; Seligman, 1971). Such stimuli include fearful animals like snakes or spiders (Ohman et al., 1976), and faces belonging to an ethnic out-group (Olsson et al., 2005). Here, we show that a contextual factor, egocentric distance, can also determine the persistence of a fear memory. This finding is important as it may inform an understanding of inter- or intra-subject differences in the persistence of real-world fear memories, as these events are typically encoded from an egocentric perspective embedded in a spatial context. For instance, the effect of egocentric distance appeared at tests of extinction and re-extinction, whereas acquisition was not affected by distance. This finding is in keeping with human conditioning research showing that fear-relevance of a CS appears to play a larger role during stages of learning that are more ambiguous than acquisition (Bouton et al., 2006), such as extinction learning (Olsson et al., 2005). Future studies could determine whether distance affects inhibitory processes at work during extinction or consolidation processes or both.

These results could aid in uncovering potential mechanisms involved in experience-induced anxiety conditions such as post-traumatic stress disorder (PTSD). Slowed extinction of de novo fears is a hallmark of PTSD (Milad et al., 2009), and a prospective study reported that impaired extinction may be a predisposing risk factor rather than a consequence of PTSD upon exposure to trauma (Guthrie and Bryant, 2006). As a factor modulating extinction, egocentric distance could be an environmental parameter influencing PTSD development at the time of trauma by engaging a neural circuitry that form extinction-resistant memory traces.

Supporting this hypothesis, the three types of traumas associated with most risk for developing PTSD are kidnapping, rape, and domestic violence, whereas other traumas, such as natural disasters or automobile accidents, are less likely (Darves-Bornoz et al., 2008). All of the former traumas involve another individual using force within the near-body space of the victim. The present results thus provide a possible explanation for the increased risk of developing PTSD following close assault in that fear associations formed in near space are harder to extinguish over time.

4.4. Opposing egocentric gradients of hedonic value across approach and avoidance

In Experiment 4, spatial proximity attenuated startle during defensive approach, and facilitated startle during avoidance. This finding suggests that spatial proximity amplifies valence. Supporting this interpretation, we observed a tendency for retrospective valence ratings to decrease with proximity for avoidance stimuli and increase with proximity for defensive approach stimuli, yielding maximal differences across conditions in near-body space. The startle findings clearly did not track retrospective arousal ratings, as these showed an increase to both avoidance and defensive approach stimuli in near-body space, yielding maximal differences across conditions in far-body space. Results from the ratings tests should be interpreted with caution, however, as they were obtained retrospectively, whereas the startle responses were obtained on-line. Moreover, the valence rating interaction term was only significant at a trend-level.

The increased startle response with proximity during avoidance of shock could be interpreted as increased intensity in escape responses when threat is near (Blanchard and Blanchard, 1989; Fanselow, 1994; Mobbs et al., 2007). The decrease in startle to approaching rewards, on the other hand, could be related to spatial discounting (Kralik and Sampson, 2012; Stevens et al., 2005), meaning that near rewards have greater motivational value than far rewards. A recent study in rats has shown that striatal dopamine may signal the increased motivational value of proximity to reward, as dopamine concentration increases with spatial proximity to reward (Howe et al., 2013). Our finding of a decrease in startle responses to the proximal character during defensive approach might therefore be due to increased mesolimbic activity signaling proximity to reward and concurrently inhibiting the startle response, as has been observed in rodents (Munro and Kokkinidis, 1997).

4.5. Limitations

One limitation of the present experimental design was the use of slightly different conditioning parameters across Experiments 2 and 3. These experiments differed with respect to the distance at which characters were presented during fear conditioning (2 m versus 0.6 and 3 m), and fear conditioning indices (SCR versus startle). Although we do not make direct comparisons between experiments here, future studies could integrate these designs to study how persistence of fear memory (Experiment 3) relates to interpersonal defensive boundaries (Experiment 2).

4.6. Synthesis

Previous theories explaining how proximal threat enhances defensive responses have focused on threat imminence (Fanselow, 1994; Mobbs et al., 2007). These theories could explain the findings of facilitation of startle to proximal characters in Experiment 1 and the increase in interpersonal defensive boundary to the threatening character in Experiment 2. The findings from Experiment 3 would also adhere to threat imminence theory, in that fear acquired at close range should be more extinction-resistant.

However, the threat imminence theory cannot explain why defensive responses would decrease with proximity to a cue signaling reward during an approach-avoidance task. Bringing together theories on threat imminence with theories on behavioral inhibition during defensive approach (McNaughton and Corr, 2004), we have therefore proposed the more general idea that proximity amplifies the valence of stimuli signaling either reward or threat. The neural systems responsible for this change in valence level with proximity are not fully understood, but it seems reasonable to suppose that fear and reward circuits together with cortical areas monitoring peri-personal space are involved.

Given that the amygdala is central to fear conditioning (LaBar et al., 1998), the sense of personal space (Kennedy et al., 2009), and proximity to threatening spiders (Mobbs et al., 2010; Nili et al., 2010), this region is likely involved in mediating the increased fear memory persistence to proximal threats shown here, along with related brainstem nuclei implicated in a circa-strike mode of defensive responding (Fanselow, 1994). The amygdala also plays a central role in reward behavior (Schultz, 1998), and amygdala-brainstem circuits are thought to contribute to defensive approach behaviors in near space (McNaughton and Corr, 2004). In addition, parietal lesions can give rise to attentional deficits restricted to near space (Halligan and Marshall, 1991), and stimulation of prefrontal motor areas evoke defensive blocking behaviors characteristic for protection from close threat (Cooke and Graziano, 2004). A parieto-frontal network therefore is involved in guiding visuomotor operations in near-body space (Graziano and Cooke, 2006; Holt et al., 2014). We speculate that many of the behavioral effects observed across our experiments depend on interactions between this fronto-parietal circuit monitoring the interpersonal defensive boundaries around the body (Graziano and Cooke, 2006) and an amygdala-brainstem circuit for defensive approach-avoidance behaviors and fear learning (Fanselow, 1994; McNaughton and Corr, 2004).

4.7. Conclusion

Urban environments increase the proximity of conspecifics, which, as shown here, magnify interpersonal defensive behaviors. At smaller social scales, our findings have relevance for establishing appropriate dyadic distances to optimize interpersonal affective interactions. Given that defensive buffer zones are sensitive to the threat value of conspecifics, efforts to enhance positive interactions among individuals working or living in close range should promote more healthy social environments.

Acknowledgments

We thank Michal Farruggia and Tori Polo for help with data collection. This study was funded by NSF grant 0745919 and NIH grants R01 DA027802 and F31 MH090682. FA received grants from the Swedish Research Council and the Sweden-America Foundation.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.neuropsychologia.2014.12.018>.

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