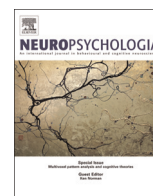




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Spatial proximity amplifies valence in emotional memory and defensive approach-avoidance



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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.

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

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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.

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