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Examining Peripersonal Space: Representations Surrounding the Body and the Role of Threat

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M.A., Emory University, 2014
B.S., Furman University, 2012

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An abstract of
A dissertation submitted to the Faculty of the
James T. Laney School of Graduate Studies of Emory University
in partial fulfillment of the requirements for the degree of Doctor of Philosophy
in Psychology

2017

Abstract

Examining Peripersonal Space: Representations Surrounding the Body and the Role of Threat

By Samuel Bennett Hunley

Extensive work across numerous scientific fields provides strong evidence that human and non-human primates maintain a representation of the space and objects immediately surrounding the body, a region that is known as peripersonal space, which plays a critical role in coordinating both defensive and non-defensive perception-action processes. Despite diligent research, many open questions remain regarding the nature of peripersonal space, its function, and its relation to other representations of space and the body. In this regard, the current dissertation makes two primary contributions. First, it reviews emerging findings and highlights important open questions. Second, it presents findings from a novel auditory time-to-contact paradigm, used to examine peripersonal space in front of and behind the body. Across three experiments, participants estimated the arrival time of approaching sounds that were either threatening or nonthreatening in nature. Initial results suggested an effect of perceived loudness. When controlling for this effect, participants consistently underestimated the arrival time of stimuli approaching from the front as compared to those approaching for the rear across both threatening and nonthreatening contexts, and they underestimated more for threatening stimuli as compared to nonthreatening stimuli. These findings suggest larger peripersonal space representations in front of the body relative to the rear for both threatening and nonthreatening contexts as well as larger peripersonal space representations in response to threatening stimuli. We discuss these findings in relation to the non-defensive and defensive functions of peripersonal space representations.

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If I were to list every person who made a significant contribution to the completion of this project, this section would extend well beyond the length of the dissertation itself. In that regard, I will try to keep it brief.

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Table of Contents

List of Tables and Figures

Manuscript 1: A review of the peripersonal space literature: Emerging Findings and Unresolved Empirical Questions

Manuscript 2: Examining peripersonal space around the body using auditory looming stimuli

Manuscript 1

A Review of the Peripersonal Space Literature:

Emerging Findings and Unresolved Empirical Questions

Sam Hunley, M.A.

Emory University

Doctoral Dissertation

Abstract

Extensive work across numerous scientific fields provides strong evidence that humans and non-human primates maintain a representation of the space immediately surrounding the body, a region known as peripersonal space, that is differentiated from the space farther from the body, known as extrapersonal space. This distinction plays a critical role in coordinating both defensive and non-defensive perception-action processes relative to objects surrounding the body. Despite diverse and diligent research, many open questions remain regarding the nature of peripersonal space, its function, and its relation to other representations of space and the body. For example, are there separate systems for defensive and non-defensive behaviors? Is peripersonal space related to other constructs such as personal space or the body schema, and if so, how are these constructs related? Are there meaningful individual differences in how flexibly peripersonal space is represented? And how is peripersonal space represented around the body? In this review paper, we take up such questions and offer our suggestions for future research examining peripersonal space.

A Review of the Peripersonal Space Literature:

Emerging Findings and Unresolved Empirical Questions

Evidence from fields as varied as neuroscience, anthropology, zoology, and sociology indicate that human and non-human primates maintain a representation of the space immediately surrounding the body, a region known as peripersonal space, that is differentiated from the space farther from the body, known as extrapersonal space (e.g., Brain, 1941; Hall, 1968; Previc, 1998; Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981). This distinction plays a critical role in coordinating actions to objects surrounding the body for both defensive and non-defensive perception-action processes (e.g., Graziano & Cooke, 2006; Graziano & Gross, 1998). That is, successful coordinated action in relation to an object, whether it be a harmless coffee mug or an approaching angry lion, requires knowing that object's location relative to the body.

Despite decades of diligent research, many open questions remain regarding the nature of peripersonal space, its function, and its relation to other representations of space and the body. Such questions include: Are there separate systems for defensive and non-defensive behaviors? Is peripersonal space related to other constructs such as personal space or the body schema, and if so, how are these constructs related? Are there meaningful individual differences in how flexibly peripersonal space is represented? How is peripersonal space represented behind compared to in front of the body? In this review paper, we take up such questions and offer our suggestions for future research examining how humans think about, perceive, and act on the space immediately surrounding the body.

Two Functions of Peripersonal Space

Peripersonal space and its non-defensive function. In seminal work on peripersonal space, researchers examined spatial representations near the body of macaque monkeys for object-oriented, perception-action behaviors involving nonthreatening objects that did not require defensive action (Iriki, Tanaka, & Iwamura, 1996; Graziano & Gross, 1995; Rizzolatti, Matelli, & Pavesi, 1983; Rizzolatti et al., 1981). Multisensory neurons, sensitive to visual and tactile stimuli, were described in the monkey pariarcuate cortex that fired in response to objects placed at or near the skin and demonstrated maximal activation to objects placed a few centimeters above the skin. Furthermore, this mapping was anchored to particular body parts, such that specific groups of neurons fired for only objects near the hand, whereas others fired for only objects near the mouth (see Figure 1; Graziano, Hu, & Gross, 1997; Graziano, Yap, & Gross, 1994). Based on these findings, Graziano and Gross (1998) suggested that these neurons maintain a "body-part-centered" mapping of the space immediately surrounding the body, crucial for guiding effector-specific movement in relation to reachable objects.

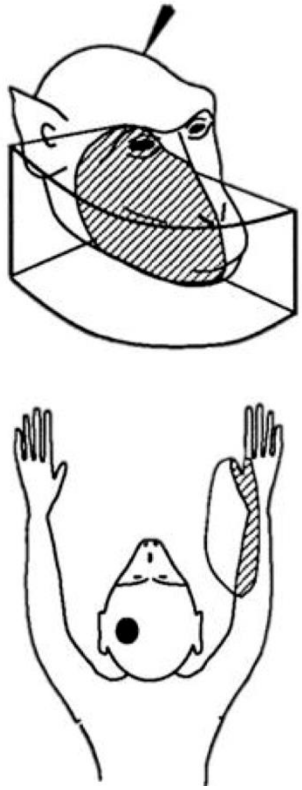

Figure 1. Receptive fields for bimodal visual-tactile neurons associated with the macaque face and hand, depicting the range for which these neurons activated. Black wedge and dot indicate the region from which the researchers conducted their recordings. Adapted from "Visuospatial Properties of Ventral Premotor Cortext" By M.S.A. Graziano, X.T. Hu, and C. G. Gross, 1997, *The Journal of Neurophysiology, 77,* p. 2274. Copyright 1997 by The American Physiological Society. Adapted with permission.

Behavioral studies of neurological patients, and studies utilizing fMRI and transcranial magnetic stimulation (TMS) with healthy participants provide strong evidence that humans also maintain populations of neurons, located within the intraparietal sulcus (IPS), supramarginal gyrus (SMG), and regions of the premotor cortex, that selectively represent the space near the body (Ackroyd et al., 2002; Berti & Frassinetti, 2000; Brozzoli, Gentile, Petkova, Ehrsson, 2011; Cowey, Small, & Ellis, 1994; Ferri et al. 2015; Serino, Canzoneri, & Avenanti, 2011). Moreover, much evidence suggests that human peripersonal space representations, like those of the macaque monkey, are multimodal in nature, responding to visual (e.g., Longo & Lourenco, 2006), visuo-tactile (e.g., Noel, Pfeiffer, Blanke, & Serino, 2015) and audio-tactile information (e.g., Canzoneri, Magosso, & Serino, 2012). And crucially, as in the monkey, these representations appear to be "body-part-centered," such that peripersonal space is at least partially defined by the location of the body, with bodily dimensions influencing the size of these representations. For example, it has been shown that individual differences in arm length predict differences in peripersonal space such that human participants with longer arms have correspondingly larger peripersonal spaces as measured by a line

Box 1. **Line Bisection as a Measure of Peripersonal Space.** The line bisection paradigm takes advantage of lateral attentional biases that differ as a function of distance from the body. Specifically, neurologically healthy participants are biased to bisect lines slightly to the left when those lines are presented in peripersonal space, a phenomenon known as pseudoneglect (Jewel & McCourt, 2000). Pseudoneglect is thought to be due to increased right parietal activation when objects are presented in peripersonal space, producing a left-oriented attentional bias (Longo, Trippier, Vagnoni, & Lourenco, 2015). Importantly, this bias shifts rightward as the line is presented at greater distances from the body (i.e., in extrapersonal space). Thus, the rate at which participants shift from left to right bias has been taken as a measure of the size of peripersonal space.

bisection paradigm (Longo & Lourenco, 2007; Lourenco, Longo, & Pathman, 2011; see Box 1 and Figure 2). Furthermore, there is evidence that peripersonal space representations associated with the arm are specifically affected by manipulations applied to the arm and not the torso, discussed further below (Lourenco & Longo, 2009).

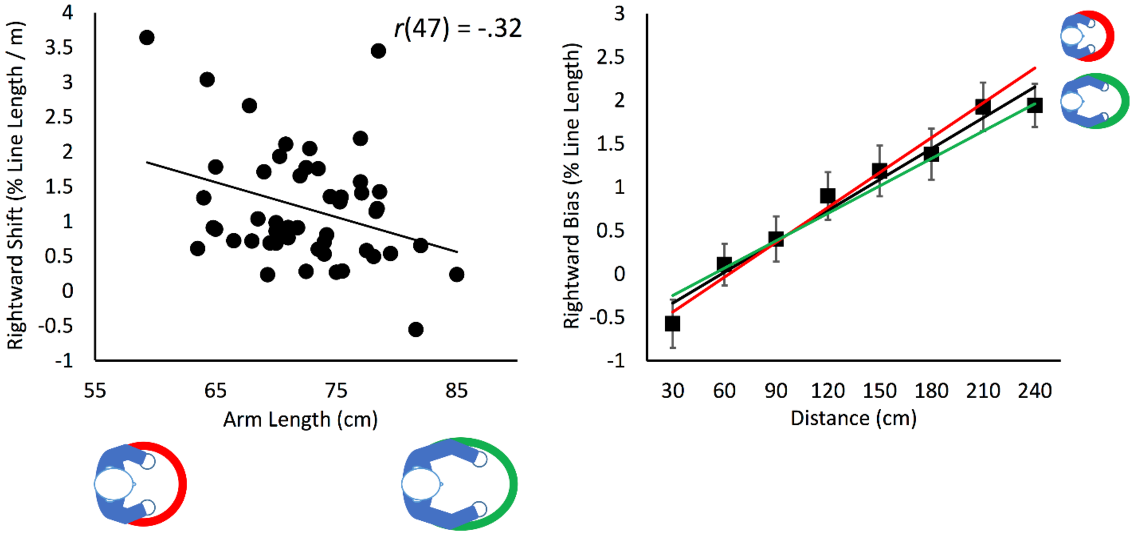

Figure 2. Both figures include data from the studies of Longo and Lourenco (2007) and Lourenco et al. (2011). Left figure: Scatterplot of the relation between arm length and the rate of participants' rightward shift on the line bisection task. Longer arms were associated with more gradual rightward shifts in bias, indicative of larger peripersonal spaces. Right figure: Participants' mean estimates (squares) of center at each distance (error bars 1 SEM). The black line is the mean slope across participants. The red line is the mean slope for participants with short arms (< 72.5 cm), and the green line is the mean slope for participants with long arms (≥ 72.5 cm). The difference between participants with shorter arms as compared to those with longer arms appears to be most apparent at the farthest distances from the line.

Evidence from both humans and monkeys also suggests that peripersonal space flexibly adapts to changing action capabilities. For example, research with paraplegic humans demonstrates that their representations of peripersonal space expand after simply seeing their paralyzed legs moved by another person (Scandola, Aglioti, Bonente, Avesani, & Moro, 2016). Moreover, hand tools that expand an animals' range of action have been shown to produce expansion of peripersonal space associated with the arm. After using a rake to complete a task, monkeys demonstrate expansion of peripersonal space (Iriki et al., 1996). Likewise, studies with humans demonstrate expansion following tool use by neurological patients (Ackroyd et al., 2002; Berti & Frassinetti, 2000) and healthy participants (Canzoneri, Marzolla, Amoresano, Verni, & Serino, 2013; Canzoneri, Ubaldi, Rastelli, Finisguerra, Bassolino, & Serino, 2013; Farnè, & Làdavas, 2000; Longo & Lourenco, 2006) using sticks, as well as by blind individuals when using a cane (Serino, Bassolino, Farnè, & Làdavas, 2007). The opposite effect has also been found in humans, such that impairing movement with arm weights (Lourenco & Longo, 2009) or barriers (Morgado, Gentaz, Guinet, Osiurak, & Palluel-Germain, 2013) produces contraction of peripersonal space. Taken together, these findings suggest representations of peripersonal space that flexibly adapt to changing physical capabilities. Of note, in the case of arm weights, this effect was restricted to peripersonal space associated with the arm in that weights worn on the back (in a backpack) did not result in detectable contraction of peripersonal space (Lourenco & Longo, 2009; mentioned above). In other words, manipulations applied to specific effectors (e.g., the arm) affected only representations associated with that specific effector, suggesting flexibility that may also be body-part-centered.

Peripersonal space and its defensive function. As described by Hediger (1955), perhaps the most important behavior of any animal is threat detection and avoidance. Though other behaviors, such as feeding and mating, can typically be safely delayed, defending against or fleeing from an active, physical threat cannot be postponed without deadly consequences (pg. 39). Hediger argued that a key goal in this endeavor is to keep potential threats at a safe distance by maintaining a “flight distance” or “flight zone” around the body that elicits fight-or-flight behaviors when crossed by a threatening object (e.g., a hungry predator, an aggressive conspecific). In his original account, Hediger reported that this distance appeared to be determined in part by an organism's body size (i.e., larger animals had larger flight zones) and defensive strategy (i.e., animals who relied on flight had larger flight zones), suggesting that animals' physical dimensions and capabilities play a role in defining the space close to the body – what we have referred to as peripersonal space.

More recently, Graziano and Cooke (2006) provided evidence that peripersonal space in primates was sensitive to defense-related information, describing a "margin of safety" represented in the primate brain. Graziano and colleagues have documented distinct startle responses in macaque monkeys for sudden air puffs presented near, but not far from, the face (Cooke & Graziano, 2003). Moreover, it was found that these startle responses were evoked when stimulating the ventral intraparietal area (VIP) and polyzensory zone (PZ), both of which are associated with the representation of peripersonal space in monkeys.

Behavioral work in humans dovetails with the findings from monkeys. More specifically, Sambo and Iannetti (2013) provided evidence for a "safety margin" in humans, like that described in monkeys, by taking advantage of a human defensive reflex known as the hand blink reflex (HBR) (see also, Bufacchi, Liang, Griffin, & Iannetti, 2016; Sambo, Foster, Williams, & Iannetti, 2012; Sambo, Liang, Cruccu, & Iannetti, 2012). In the HBR, humans produce defensive eye-blinks when the hand is stimulated, but this effect, as measured by muscular response using electromyography (EMG), is strongest when the hand is in proximity to the face and weaker when farther away from the face. Similarly, De Paepe and colleagues (2017) described hand-centered representations of peripersonal space related to pain detection that were “spatially locked” to the stimulated hand. Taken together, these findings suggest peripersonal space representations as related to defense of the body that may be body-part-centered.

As described in the case of non-defensive behaviors, individual differences in arm length have been shown to relate to the size of peripersonal space (Longo & Lourenco, 2007; Lourenco et al., 2011). There is also evidence that individual differences in trait anxiety or fear may be similarly related to peripersonal space. For instance, higher trait claustrophobic fear has been associated with larger peripersonal spaces, as measured by a line bisection task (Hunley, Marker, & Lourenco, 2017; Lourenco et al., 2011; see Box 1). Similarly, individual differences in anxiety have been shown to predict the size of peripersonal space as measured by an HBR-based task, such that greater anxiety predicts larger peripersonal spaces (Sambo & Iannetti, 2013). Sambo and Iannetti (2013), however, failed to find a correlation between peripersonal space and claustrophobic fear, which they suggested might reflect task-specific differences in the studies. Whereas Lourenco and colleagues (2011) used a line bisection task to capture peripersonal space representations, which Sambo and Iannetti (2013) proposed primed non-defensive responses, Sambo and Iannetti (2013) used a HBR-based task, which may have primed defensive responses. Accordingly, specific fears and general anxiety may have different relations to peripersonal space representations depending on the corresponding function relevant to the task. Another possibility is that the relation between peripersonal space and anxiety depends on which body-part is utilized in the task. For instance, the line bisection task seems to specifically measure peripersonal space as related to the arm (Lourenco & Longo, 2009), whereas the HBR task may measure peripersonal space specifically associated with the face (e.g., Sambo et al., 2012). Given the accumulating evidence for body-centered representations, it would follow that peripersonal space associated with the arms, which may be more sensitive to restricted movement, could be more strongly associated with claustrophobic fear, whereas peripersonal space associated with the face, a particularly sensitive somatosensory region, could be specifically associated with a general tendency towards anxiety. Taken together, the extant data are consistent with peripersonal space representations that are at least partially defined by individual differences in sensitivity to threatening contexts (i.e., trait anxiety, trait fear). However, future research is necessary to determine why the reported relations appear to be task specific.

Like peripersonal space for non-defensive behaviors, there is evidence that peripersonal space representations are flexible in defensive contexts, reacting to contextual factors. For instance, Vagnoni and colleagues (2012) reported that, in a visual looming task, participants judged threatening stimuli (i.e., snakes, spiders) as arriving sooner than nonthreatening stimuli (i.e., rabbits, butterflies). These findings have since been extended to infants, where infants displayed earlier defensive blinks to looming threatening snakes and spiders as compared to nonthreatening rabbits and butterflies (Ayzenberg, Longo, & Lourenco, 2015). One interpretation is that this effect could result from participants experiencing larger representations of peripersonal space in the presence of threatening animals as compared to nonthreatening animals, leading them to judge the former as making contact with themselves sooner. This interpretation is bolstered by findings indicating that participants demonstrate larger peripersonal space representations, as measured by audio-tactile (Taffou & Viaud-Delmon, 2014) and visuotactile (de Haan, Smith, Stigchel, & Dijkerman, 2016) interaction tasks, in response to approaching threatening stimuli (e.g., angry dog growls, images of spiders) than to nonthreatening stimuli (e.g., sheep bleats, images of butterflies). In all of these studies, greater trait fear of the target was associated with greater expansion of peripersonal space representations. In addition to responding flexibly to threats near the body, other research suggests that peripersonal space representations flexibly incorporate tool use related information, even in defensive contexts. Rossetti and colleagues (2015) reported that humans showed earlier autonomic fear responses to an approaching dangerous stimulus (i.e., a needle) after using a tool that extended their reach. These findings suggest that peripersonal space representations as related to defense of the body respond not only to threat-related information but also to the changing motor capabilities of the body.

One or two systems of peripersonal space? Though peripersonal space would seem to incorporate both defensive and non-defensive functions, it remains an open question whether these behaviors are supported by *one* or *two* separate systems. One possibility is that there is a single, unified system for representing peripersonal space that enables both defensive and non-defensive behaviors. After all, both types of behaviors require coordinating perception-action processes in relation to objects (e.g., coffee mugs, angry lions, other people) surrounding the body, and as such, it might make most sense for such behaviors to recruit resources from one system that handles the demands presented by these contexts. A single system could allow for an efficient representation of space, reducing the cognitive and neural resources to map the area around the body. Such an interpretation is supported by evidence from monkeys, suggesting that defensive and non-defensive behaviors recruit common neural networks (Cooke & Graziano, 2003;

Rizzolatti et al., 1981). Furthermore, there are common psychological effects reported for peripersonal space representations across defensive and non-defensive contexts. Specifically, such representations seem to flexibly respond to contextual changes to action capabilities (i.e., tool use) under both threatening (Rossetti et al. 2015) and nonthreatening (e.g., Ackroyd et al., 2002; Longo & Lourenco, 2006) conditions, providing support for the view that defensive and non-defensive functions rely on a single system of peripersonal space representation.

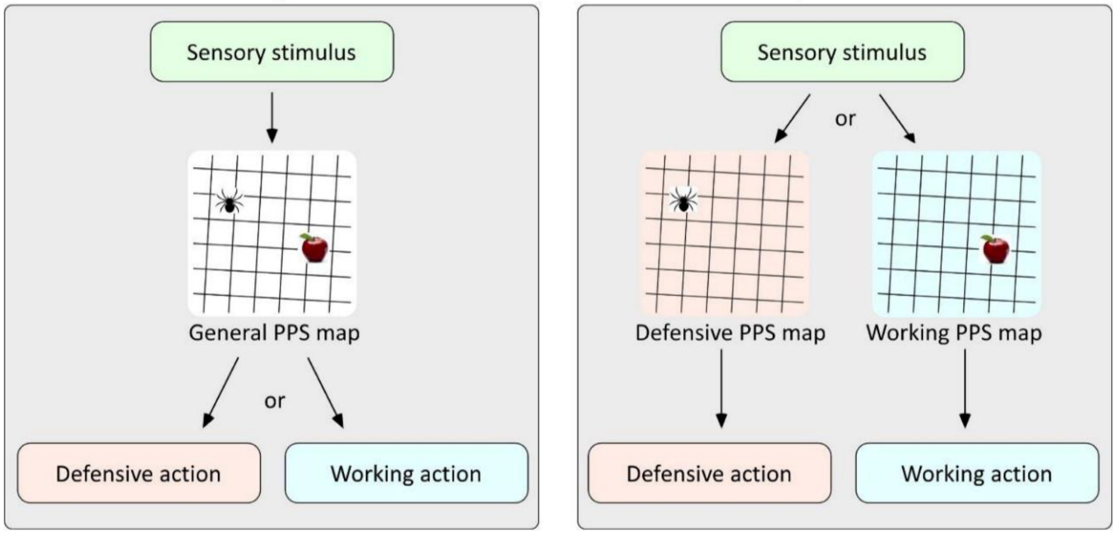

Figure 3. Graphic depicting the two peripersonal space systems discussed by de Vignemont & Iannetti (2015). One possibility is that there is a single system (left) representing both threatening (e.g., a spider) and nonthreatening objects (e.g., an apple), which helps to organize both defensive and “working” non-defensive behaviors. The other possibility (right) is that there are separate “maps” for each set of behaviors. Adapted from “How Many Peripersonal Spaces?” By F. de Vignemont and G.D. Iannetti, 2015, *Neuropsychologia, 70*, p. 328. Copyright 2014 by Elsevier Ltd. Adapted with permission.

Another possibility, as suggested by de Vignemont and Iannetti (2015), is that peripersonal space is represented by two distinct systems, one of which is specialized for the “goal-directed” non-defensive behaviors and the other of which is specialized for “protective actions” (see Figure 3). In support of this position, the authors point to evidence that non-defensive behaviors are organized quite distinctly from defensive behaviors. For instance, non-defensive behaviors are largely organized *toward* a target object that is the intended recipient of an action, whereas defensive actions are geared *away from* a target, such as ducking out of the way of a projectile or avoiding obstacles (Bracha, 2004; Dosey & Meisels, 1969; Graziano & Cooke, 2006). These behaviors might necessitate different levels of motor precision. For instance, grasping an object with the hand requires slower, precise motor guidance, whereas protective actions may require rapid, less fine-grained, responses to keep a threat away from the body. These differences also extend to the sensory features of peripersonal space where non-defensive behaviors may necessitate fine-grained sensory feedback. By contrast, defensive behaviors would operate perfectly well with less fine-grained depictions of space (e.g., Liang, Mouraux, & Iannetti, 2013). Rather, defensive behaviors necessitate more rapid sensory feedback, relative to non-defensive behaviors, given the more immediate consequences for survival.

As it stands, no study (to our knowledge) has directly pitted the two accounts against one another. Additionally, we would suggest a third possibility that should be tested in future research. In this third model, peripersonal space is represented by a single system with defensive and non-defensive “modes” that allow the system to accommodate to these distinct demands across contexts. The advantage of a single system with access to defensive and non-defensive modes is that it would allow for an efficient representation of space, as provided by a single mapping, while still allowing the flexibility to adapt to the requirements of specific contexts, as provided by the two system account.

Dissociating between these accounts. One way to begin disentangling these accounts would be to examine whether separate tasks, one priming the non-defensive function of peripersonal space and the other priming the defensive function, are affected in the same way by manipulations known to affect peripersonal space. For example, Sambo and Iannetti (2013) argue that HBR-based tasks prime the defensive function whereas line bisection task primes the non-defensive function. Thus, if non-defensive and defensive behaviors rely on a single representational system that behaves the same under all conditions, then performance on these tasks should be affected by manipulations in similar ways. For instance, threat-related stimuli (e.g., angry dog barks) should produce expansion on both tasks (Taffou & Viaud-Delmon, 2015). Likewise, motor-related manipulations, such as having participants wear arm weights (Loureno & Longo, 2009), should produce contraction on both the line bisection task as well as the HBR task. If non-defensive and defensive behaviors rely on distinct, dissociable systems, then performance on these tasks should not be affected in the same way by these manipulations. Threat-related information should produce expansion on only the HBR task, and the motor restriction caused by arm weights should produce compression on only the line bisection task. In fact, motor restriction should produce *expansion* of peripersonal space on a defense-related task given that motor restriction would make it more difficult to respond to threats. This latter possibility is supported by Vagnoni and colleagues (2017) who reported greater underestimation for looming objects when participants' movements were restricted by a chin rest, possibly indicating an expanded peripersonal space as related to defense of the body. This expansion, rather than contraction as one would expect under non-defensive circumstances (Lourenco & Longo, 2009), is consistent with both the two system account, with dissociable systems of peripersonal space for defensive and non-defensive behaviors, as well as a hybrid model where motor restriction could result in expansion when the defensive mode is primed. As such, a necessary task for future research is to determine means of distinguishing between these accounts.

One way to do so would be to apply conflicting defense- (e.g., threatening sound that causes expansion) and non-defense-related (e.g., arm weights that cause contraction) manipulations. If peripersonal space representations are subsumed by the hybrid system detailed above, then competing defensive and non-defensive information should disrupt performance on tasks examining peripersonal space, regardless of which specific function (i.e., defensive, non-defensive) was activated. However, if peripersonal representations are subsumed by two systems, then task performance should be affected only by the manipulation relevant to the function activated by the task at hand. Thus, by implementing such approaches, researchers will be in position to shed light on the cognitive and neural underpinnings of peripersonal space representations, providing important insight into how such representations guide and coordinate behavior under differing circumstances.

Distinguishing Peripersonal Space from Other Constructs

Peripersonal vs. personal space. Drawing from Hediger's (1955) concept of the flight zone, it was hypothesized that humans maintain a representation of the space immediately surrounding the body that defines a comfortable distance between one's self and other people. Early research found evidence for such a representation, demonstrating that participants maintained a consistent boundary between themselves and social partners, referred to as their preferred interpersonal distance (Sommer, 1959), which was greater than the space they maintained in relation to objects (Horowitz, Duff, & Stratton, 1964). Research demonstrates that humans produce reliable preferences for interpersonal distances (Hayduk 1983; Holt et al., 2014; but see Hayduk, 1985) and that incursions of these distances into personal space produce feelings of discomfort and anxiety (Hayduck, 1981).

Given that personal space involves managing interpersonal distances between both familiar friends (i.e., nonthreatening persons) and unfamiliar strangers (i.e., potential threats), and that peripersonal space representations play a role in guiding perception-action behaviors towards innocuous (e.g., Graziano & Gross, 1998) and potentially harmful objects (e.g., de Vignemont & Iannetti, 2015), it would seem plausible that the two constructs should be related. Indeed, parallels between performance on tasks measuring peripersonal and personal space suggest that the underlying representations rely on shared or causally related mechanisms. For instance, higher trait anxiety and fear have been associated with both larger peripersonal spaces (Lourenco et al., 2011; Sambo & Iannetti, 2013) and larger personal space preferences (Bogovic, Mihanovic, Jokic-Begic, & Svagelj, 2013; Dosey & Meisels, 1969). Moreover, evidence from fMRI with humans suggests that intrusions into personal space caused by social looming stimuli (i.e., faces) activates brain regions (Holt et al., 2014) that are similarly implicated in the representation of peripersonal space (e.g., di Pellegrino & Làdavas, 2015).

To this end, Iachini and colleagues (2014) specifically investigated whether and how the two constructs are related. In this study, participants completed two versions of a stop-approach task where they interacted with virtual avatars, consisting of three different “actors” (i.e., person, anthropomorphic robot, and cylinder) in a virtual reality (VR) environment. In one condition, participants completed a standard stop-approach task, examining personal space, which required indicating the distance they first became uncomfortable with the avatar. In another condition meant to measure peripersonal space representations, participants indicated at which distance they could physically reach the avatar with their hand. Both tasks involved a passive condition, in which participants waited while the avatar walked towards them, and an active condition, in which participants walked to the avatar. The researchers hypothesized that the relation between personal and peripersonal space representations would be most readily apparent when participants had to plan and enact motor actions relative to a social target, perhaps priming the motor guidance function of peripersonal space. In line with their predictions, the researchers reported that, in the passive condition, participants' performance differed on the comfort distance and reachability tasks, whereas performance did not differ in the active condition. Specifically, in the passive condition, participants reported that they could reach the avatars at a significantly further distance than their preferred comfort distance to the avatars. However, in the active condition, participants' estimates of reachability did not differ from their preferred comfort distance. This pattern of results has since been replicated in VR and real environments as well as on a paper-and-pencil task where participants estimated their comfortable distance and their range of reach (Iachini, Coello, Frassinetti, Senese, Galante, & Rugiero, 2016). In all cases, the authors argue that their results suggest peripersonal and personal space representations may rely on shared or causally related mechanisms.

In another study, Quesque and colleagues (2016) found that tool use, which produces expansion of peripersonal space (e.g. Ackroyd et al., 2000; Canzoneri, Ubaldi, et al., 2013; Longo & Lourenco, 2006; Rossetti et al., 2015), also results in expanded personal space in relation to a virtual human-like walker, created by a projected point-light display. More specifically, participants reported larger preferred interpersonal distances between themselves and the virtual walker when it crossed in front of them after having used a tool to complete a task, providing additional support for the claim that peripersonal and personal space rely on shared or causally related mechanisms.

Yet other research examining the effect of tool use suggests a dissociation between peripersonal and personal space. For example, Patané and colleagues (2016) found that, though tool use produced expansion of peripersonal space as measured by a reachability task, it had no effect on a task measuring participants' preferred comfort distance to a social partner. In more recent work, Patané and colleagues (2017) examined the effect of social tool use in which a participant completed a cooperative tool use task with a confederate. In this case, the results were consistent with a dissociation between peripersonal and personal space. Participants reported an increased range of reachability following cooperative tool use, again suggesting expansion of peripersonal space representations, but smaller preferred comfort distances between themselves and the confederate (the same as from the tool use task), suggesting *contraction* of personal space. Thus, whereas Quesque and colleagues report expansion of personal space after non-social tool use, here the authors argue that social tool use produced the opposite effect, providing evidence for a dissociation between the two constructs. Thus, it remains an open question whether peripersonal and personal space involve shared or causally related systems, meaning that there is more work to be done.

Considerations for future research. One potential reason for the discrepant findings regarding the connection between peripersonal and personal space could be the influence of context-specific considerations in managing interpersonal interactions. When determining one’s “comfortable” distance between the body and a social partner, it is not simply a matter of determining the proper distance to maintain physical comfort and safety for the self. Instead, one must manage the social expectations of others and calculate their level of comfort as well. These calculations may differ substantially depending on one’s relationship with his or her social partner(s), as well as the context in which they are interacting. One’s comfortable distance is likely to vary when interacting with an unfamiliar grocery store employee as compared to a long-term romantic partner, and interactions between both individuals are likely to vary by context. For instance, listening to positively-valenced music has been shown to decrease participants’ preferred interpersonal distances to a stranger (Tajadura-Jiménez, Pantelidou, Rebacz, Västfjäll, & Tsakiris, 2011), suggesting that external cues that affect a person’s mood can influence preferred interpersonal distances. In this vein, the contraction of personal space after tool use reported by Patané and colleagues (2017) could be due to the social nature of the researcher’s task and not the tool use itself. That is, participants may have felt more comfortable with the confederate after the tool use task, resulting in contraction of their preferred interpersonal distances.

An intriguing possibility is that, if personal space is highly affected by social and contextual variables, then the strength of the relation between personal and peripersonal space representations may be moderated by individual differences in sensitivity to these variables. For instance, persons with high levels of psychopathic traits, who are less empathic (Ali, Amorim, & Chamorro-Premuzic, 2009), might be less sensitive to social cues associated with managing interpersonal distances and, as such, might demonstrate a stronger relation between their representations of personal and peripersonal spaces. In fact, psychopathic traits have already been associated with distinct patterns of response on an interpersonal distance task, such that individuals high in Coldheartedness as measured by the Psychopathic Personality Inventory (PPI; Lilienfeld, Widows, & Staff, 2005) preferred smaller interpersonal distances (Vieira & Marsh, 2013). The same may be true for individuals diagnosed with Autism Spectrum Disorder (ASD), which is characterized by dramatic social deficits (American Psychiatric Association, 2013). An important avenue for future research will be to determine whether traits associated with psychopathy or disorders such as ASD moderate the relation between peripersonal and personal spaces.

Conclusions. Given that managing peripersonal space requires planning and enacting actions in relation to objects surrounding the body (i.e., other people) as well as tracking and responding to the potential threats posed by these objects, both required in managing personal space, it would be reasonable to expect a deep connection between the two constructs—either through shared or causally related mechanisms. Indeed, initial research suggests that this may be the case, at least under active conditions when participants are required to plan and/or enact motor actions relative to another person (Iachini et al., 2014; Iachini et al., 2016) or when using a tool relative to a looming point-light display of a person (Quesque et al., 2016). However, discrepant findings exist in the literature, with some researchers reporting that tool use has either no effect on personal space (Patané et al., 2016) or the opposite effect, causing contraction of personal space instead of expansion as is the case with peripersonal space (Patané et al., 2017). One potential reason for these discrepant findings could be the influence of context-specific considerations associated with managing personal space. As such, future research may benefit from including populations who are less sensitive to these factors, such as individuals with high levels of psychopathy or individuals diagnosed with ASD. Such work could lead to a clearer understanding of the relation between peripersonal and personal space representations.

Peripersonal space and body representations. When coordinating perception-action processes, the brain not only needs a representation of the objects surrounding the body but also a representation of the body's location in space. This statement is true both in relation to non-defensive (e.g., checking a watch on the wrist) and defensive (e.g., swatting a spider on the hand) actions. In this regard, scientists have long theorized the presence of an "organized model" of the body, referred to as the body schema, which is used for controlling action and posture as well as locating stimuli on the body (Head & Holmes, 1911, p. 189; Martel, Cardinali, Roy, & Farné, 2016; Medina & Coslett, 2010). This representation, which remains largely unconscious, is thought to be distinct from the body image, which refers to conscious conceptual (e.g., body ownership), linguistic (e.g., "fat", "skinny"), and visuospatial descriptions of body parts (e.g., "My hand is connected to my forearm.") and their location (e.g., "I am holding my hand above my head.") (Coslett, Saffran, Schwoebel, 2002; Gallagher, 2005; Schilder, 1935; Schwoebel & Coslett, 2005; Sirigu et al., 1991).

Given that peripersonal space is at least partly defined by the body's physical dimensions (e.g., arm length; Longo & Lourenco, 2007; Lourenco et al., 2011) and location in space relative to other objects (Graziano & Gross, 1998; Rizzolatti, et al., 1981), a reasonable hypothesis, as some researchers have suggested, is that peripersonal space and the body schema may actually be reflections of the same or causally related underlying systems (Cardinali, Brozzoli, & Farné, 2009). That is, peripersonal space and body schema could be two names for the same representational system, or at least, the two systems may be causally related such that changes to one affect the other. Per this view, the expansion of peripersonal space caused by tool use (e.g. Ackroyd et al., 2000; Canzoneri, Ubaldi, et al., 2013; Longo & Lourenco, 2006; Rossetti et al., 2015) may be a reflection of the tool being incorporated into the body schema, which itself causes the remapping of space (Maravita & Iriki, 2004). As evidence for this position, active tool use has been shown to affect the body schema, impacting free-hand reaching kinematics, with participants adjusting the velocity of their reach as if they perceived their forearm as longer (Cardinali, Frassinetti, Brozzoli, Urquizar, Roy, & Farné, 2009). When directly tested, participants view their forearms as longer and skinnier after using a tool to complete a task, suggesting that the tool was incorporated into their body schema (Cardinali, Frassinetti, et al., 2009; Canzoneri, Marzolla, et al., 2013). Furthermore, the use of prosthetic limbs by amputees has been shown to produce changes to the body schema (Mayer, Kudar, Bretz, & Tihanyi, 2008) as well as peripersonal space (Canzoneri, Ubaldi, et al., 2013). Such findings imply that these constructs could be the result of the same or causally related systems.

However, another possibility is that peripersonal space and the body schema both are derived from somatosensory mappings of the body’s location in space but are ultimately separate systems that are not causally related. In this view, findings using the cross-modal congruency task suggest a dissociation between peripersonal space and the body schema. This task relies on the cross-modal congruency effect, a facilitating effect where a visual stimulus appearing near the hand produces a speeded response to tactile stimuli presented to the same hand (Spence, Pavani, & Driver, 1998, 2004; Spence, Pavini, Maravita, & Holmes, 2004). Researchers have found the cross-modal congruency effect in relation to the end of a tool after that tool has been used to complete a task, suggesting expansion of peripersonal space (Maravita, Spence, & Driver, 2003). However, if peripersonal space and the body schema relied on a single or causally related system, then one would expect that peripersonal space would expand to include the length of the tool. That is, because tool use results in a continuous extension of the body schema (Canzoneri, Ubaldi et al., 2013; Cardinali, Frassinetti, et al., 2009), one would anticipate that peripersonal space would also incorporate the tool in a continuous manner. However, Holmes and colleagues (2007) found that this expansion included only the tip of the tool that had been actively used, not the middle section of the tool. These findings have been replicated in behavioral (Holmes, Sanabria, Calvert, & Spence, 2007) and fMRI (Holmes, Spence, Hansen, Mackay, & Calvert, 2008) paradigms, and extended to show that peripersonal space will expand to include the middle sections of a tool but only when that section had a functional feature used to complete the task (Park, Strom, & Reed, 2013; but see, Bonifazi, Farné, Rinaldesi, & Làdavas, 2007). Thus, rather than a continuous expansion as one would expect if peripersonal space and body schema were products of the same or causally related underlying systems, these results suggest that peripersonal space “projects” in a discontinuous manner to functionally relevant parts of the tool (Holmes, 2012). As such, peripersonal space and the body schema may reflect dissociable systems.

Conclusions. Because peripersonal space is at least in part defined by the location (e.g., Graziano & Gross, 1998) and capabilities of the body (e.g., Longo & Lourenco, 2007), researchers initially proposed that it may be tightly related to the body schema, the cognitive and neural representation of the body (Cardinali, Brozoli, et al., 2009; Maravita & Iriki, 2004). However, evidence regarding the relation between the two constructs is currently mixed. Although early research suggested a connection between the two constructs in that tool use causes expansion both of peripersonal space (e.g., Ackroyd et al., 2002; Longo & Lourenco, 2006) as well as the body schema (Canzoneri, Ubaldi et al., 2013; Cardinali et al., 2009), evidence from the cross modal congruency task (Holmes, Calvert, et al., 2007; Holmes, Sanabria, et al., 2007) and an fMRI study (Holmes et al., 2008) suggests that the two representations may be dissociable to some degree. Specifically, tools appear to produce continuous expansion of the body schema but discontinuous expansion of peripersonal space. Additional research is necessary to understand if and under what circumstances these constructions dissociate. By better understanding how the two constructs interact, researchers can produce a clearer picture of the cognitive and neural underpinnings of both peripersonal space and the body schema.

Open Questions in Peripersonal Space Research

Individual differences in the flexibility of peripersonal space. As discussed above, peripersonal space appears to respond flexibly to contextual information, both in regard to motor-related changes (e.g., tool use and arm weights; Ackroyd et al., 2002; Lourenco & Longo, 2009) and threat-related information (e.g., angry dog barks, approaching spiders; de Haan et al., 2016; Taffou & Viaud-Delmon, 2014). However, an open question is whether there are meaningful individual differences in this flexibility. For instance, given that individuals high in trait fears and anxiety (e.g., claustrophobic fear, general trait anxiety) (Lourenco et al., 2011; Sambo & Iannetti, 2013) have larger, distorted peripersonal spaces, a possibility is that these individuals are also hampered by limited flexibility (i.e., expansion, contraction) in their peripersonal space representations. In addition, a growing body of research suggests that high trait anxiety is associated with deficits in attentional flexibility (Derryberry & Reed, 2002; Eysenck, Derakshan, Santos, & Calvo, 2007; Pacheco-Unguetti, Acosta, Callejas, & Lupiáñez, 2010) and disruptions in neural activation in fronto-parietal networks associated with attention (Bishop, 2009; Sylvester et al., 2012) as well as peripersonal space (Brozzoli et al., 2011; Serino et al., 2011). These individual differences in attentional flexibility could be associated with individual differences in the flexibility of peripersonal space as well.

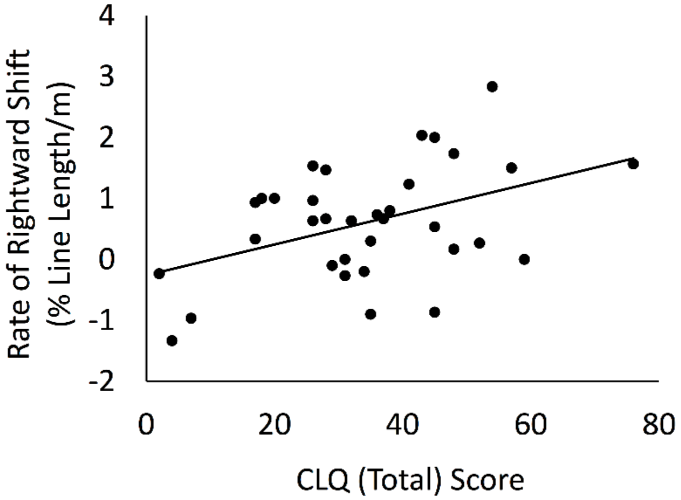

Figure 4. Scatterplot of the relation between trait claustrophobic fear, as measured by the Claustrophobia Questionnaire (CLQ), and rate of rightward shift of participants estimates on the line bisection task from Hunley et al. (2017). More rapid rightward shifts are indicative of smaller peripersonal space representations. When using a stick to bisect the line, greater claustrophobic fear was associated with smaller peripersonal space representations, suggesting decreased flexibility (i.e., decreased expansion) of peripersonal space in individuals high in claustrophobic fear.

Along these lines, research from our lab suggests that trait fear, specifically trait claustrophobic fear, is associated with individual differences in the flexibility of peripersonal space as measured by a line bisection task (Hunley et al., 2017). Previous work has shown that participants demonstrate expansion of peripersonal space when using a stick to bisect lines compared to when using a laser pointer (Longo & Lourenco, 2006). However, Hunley and colleagues (2017) found that higher trait claustrophobic fear was associated with less expansion when using the stick to bisect lines (see Figure 4). In other words, participants high in claustrophobic fear demonstrated less flexibility in the size of their peripersonal space representations, providing initial evidence for individual differences in the flexibility of peripersonal space representations.

Given these findings, an open question is whether other cognitive (e.g., trait anxiety; Sambo & Iannetti, 2013) and physical (e.g., arm length; Longo & Lourenco, 2007) factors that have been associated with the size of peripersonal space also play a role in defining the flexibility of these representations. As previously mentioned, trait anxiety is associated with decreased attentional flexibility (e.g., Derryberry & Reed, 2002; Eysenck et al., 2007; Pacheco-Unguetti et al., 2010), which may also relate to decreased flexibility of peripersonal space. Likewise, in the case of arm length, because individuals with longer arms can act on a broader range of space, an intriguing possibility is that they may also have more flexible representations of space. However, such links could depend on which function of peripersonal space is primed (i.e., non-defensive, defensive) (Sambo & Iannetti, 2013), as well as which body-part is utilized in the task (i.e., arms, trunk). For instance, peripersonal space representations may be more flexible under non-defensive circumstances when simply coordinating actions towards objects and less flexible under defensive circumstances when maintaining a safe distance to a threat. Likewise, the representation of the arm, which is frequently used to complete actions, may be more flexible than that for the trunk, which is rarely used to complete actions. Future studies will be crucial for testing the extent to which such individual differences play a role in determining the flexibility of peripersonal space.

How is peripersonal space represented around the body? In most studies of peripersonal space, one major limitation is that researchers examine only the space in front of the body. However, humans exist and act in a 3D world and must – and often do – interact with objects at all positions around the body. We sit in chairs simply by using the feel of the chair against our legs or the knowledge that the chair is behind us, and we can reach behind us to grab objects as small as a set of keys on a countertop without turning to visually locate the keys. We also routinely navigate space while accommodating objects both in front of (e.g., pushing a strollers) as well as behind the body (e.g., pulling wheeled luggage). Such actions require a representation of where these objects are in space relative to the body in order to act. Likewise, threats are not limited to approaching from the front of the body. As such, to defend against incoming attackers, humans must maintain vigilance at all points around the body and be able to organize defensive behaviors in relation to threats from different directions. In this vein, researchers have demonstrated that peripersonal space representations extend around the body (Van der Stoep, Nijboer, Van der Stigchel, & Spence, 2015), both in monkeys (Graziano, Reiss, & Gross, 1999) as well as humans, including both neurological patients (Farnè & Làdavas, 2002) and healthy participants (Kitagawa, Zampini, & Spence, 2005).

An open question, then, is how peripersonal space representations differ around the body. One possibility is that peripersonal space representations are equally as large in the rear as compared to the front, such that space is represented equally at all points around the body (i.e., symmetrically) (see Figure 5). Representing space in such a fashion may be an efficient and straightforward use of cognitive and neural resources. Another possibility is peripersonal space representations are larger in front of the body as compared to the rear. Most human perception-action capabilities are oriented towards the frontal plane, meaning that it may be advantageous to have a greater amount of attentional resources allocated in this direction to coordinate complex actions, producing a larger peripersonal space in front of the body as compared to behind it. Finally, a third possibility is that how peripersonal space is represented around the body varies by context. For instance, as argued above, given that most human perception-action capabilities are frontward-oriented, it could be that a larger frontward representation of peripersonal space would be advantageous under non-defensive conditions when simply guiding perception-action behaviors in relation to objects. Defensive conditions may require a redistribution of

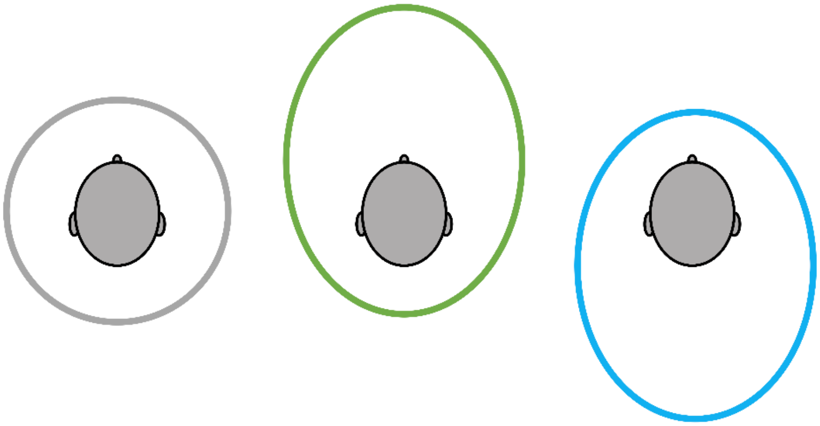

Figure 5. Graphic depicting possible “shapes” of peripersonal space around the body. One possibility is that space is represented symmetrically (gray). However, given the orientation of human perception-action capabilities, a larger frontal representation is possible as well (green). Finally, it is possible that the shape of peripersonal space representations vary by defensive context. In this case, a larger frontal representation may be beneficial under non-defensive contexts, whereas a larger rear representation (blue) may be beneficial under defensive contexts.

attentional resources, though. Again, because human perception-action capabilities are frontward-oriented, any response to a threat approaching from the rear would necessarily take more time, potentially making that threat more dangerous than if it had approached from the front. As such, a larger representation behind the body could be adaptive in preparing for oncoming threats.

As it stands, evidence suggests that peripersonal space is represented asymmetrically, with a larger representation of space in front of the body, both under non-defensive and defensive contexts. For instance, research examining the processing of multisensory information, particularly audio-tactile stimuli, has found differences in how such information is integrated in front of as compared to behind the body under non-defensive circumstances (Gillmeister & Forster, 2012; Kóbor, Füredi, Kovács, Spence, & Vidnyánszky, 2006; Occelli, Spence, & Zampini, 2011). Specifically, this research has shown that, though interfering information (e.g., crossing the arms) affects the processing of multisensory stimulation both in front of and behind the body, this effect may be weaker behind the body (Kóbor et al., 2006). In addition, attentional effects on performance seem strongest behind the body when the hands are held close to the body, whereas they are strongest in front of the body when the hands are held farther away (Gillmeister & Forster, 2012). Given that peripersonal space representations are multisensory in nature (Graziano & Gross, 1995), these differences in processing of multisensory information for the front as compared to the rear are suggestive of differences in peripersonal space as well, suggesting that a greater amount of attentional resources may be directed towards the front of the body, such that interfering attentional information has a stronger effect at least in a non-defensive context.

In addition to this work examining multisensory integration under non-defensive contexts, Bufacchi and colleagues (2016) examined peripersonal space representations behind the body as compared to that in front under defensive circumstances. Peripersonal space representations were assessed using a HBR-based task where participants were asked to place their hand at various locations relative to the face, including placing the hand behind the head. Participants demonstrated larger peripersonal space representations in front of the body as compared to the rear, consistent with an asymmetric representation of peripersonal space. However, this conclusion could be specific to facially-centered representations, which may be inherently frontward oriented given the location of the face. Additional work is necessary to examine whether asymmetries exist for representations centered on other body parts (e.g., arm, trunk), which more readily interact with front and back.

Another limitation is that the researchers examined peripersonal space representations only in relation to defensive behaviors and not non-defensive behaviors. By including threat-level as a factor, future studies examining peripersonal space representations around the body will be able to shed light on whether, and how, these representations shift to accommodate the different contextual demands these situations produce. Finally, the researchers did not take into account individual differences. As previously mentioned, individual differences in body dimensions (i.e., arm length; Longo & Lourenco, 2007), trait fears (Lourenco et al., 2011), and anxiety (Sambo & Iannetti, 2013) are associated with distinct differences in peripersonal space representations in front of the body. But it is an open question whether such differences exist behind the body as well. Work from Noel and colleagues (2015) demonstrating that expansion of peripersonal space representations in front of the body is associated with contraction behind the body suggests that these representations may rely on common resources. As such, these individual differences may exist behind the body as well. However, work examining individual differences in peripersonal space representations is only just emerging and more research is needed with different paradigms to better understand these relations. By examining individual differences in how peripersonal space is represented around the body, researchers can better understand the role they play in determining the nature of such representations.

Conclusions

In summary, research has long documented neural and cognitive evidence of representations of the space immediately surrounding the body, known as peripersonal space. Such representations have been shown to be multimodal in nature (e.g., Canzoneri et al., 2012; Graziano & Gross, 1995) and to provide a “body-part-centered” mapping of space that is anchored to individual body parts (e.g., the face, arms) (Graziano & Gross, 1998; Lourenco & Longo, 2009; Sambo et al., 2012). Furthermore, representations of peripersonal space are sensitive to both the actions available to an organism (e.g., Iriki et al., 1996; Longo & Lourenco, 2006; Morgado et al., 2013) as well as threat-related information (e.g., angry dog sounds) present in the environment (de Haan et al., 2016; Taffou & Viaud-Delmon, 2014). However, it remains to be seen whether these functions rely on the same or separate representational systems (de Vignemont & Iannetti, 2015). In this vein, evidence is mixed regarding whether the constructs of peripersonal and personal space rely on the same or causally related systems (e.g., Iachini et al., 2014; Quesque et al., 2016) or whether the systems are dissociable to some degree (e.g., Patané et al., 2017; Patané et al., 2016). Likewise, though peripersonal space is in part defined by body dimensions (Longo & Lourenco, 2007) and its location in space (Graziano & Gross, 1998), evidence suggests that peripersonal space may be distinct from body representations such as the body schema (e.g., Holmes, 2012).

The current literature also leaves open important questions regarding the nature of peripersonal space, which should shape the agenda for future research in this area. Though Hunley and colleagues (2017) documented individual differences in the flexibility of peripersonal space representations in relation to claustrophobic fear, it remains unclear whether such differences occur in relation to other cognitive (e.g., trait anxiety) and physical (e.g., arm length) factors that define peripersonal space. In addition, an emerging area of study is how peripersonal space is represented around the body and whether these representations vary under non-defensive versus defensive contexts. Investigating these issues promises to shed light on the cognitive and neural systems undergirding peripersonal space as well as how such systems play a role in determining behavior.

The Current Dissertation

The current dissertation seeks to extend peripersonal space literature by specifically investigating representations of peripersonal space surrounding the body in defensive and non-defensive contexts. To this end, we developed a novel paradigm, utilizing auditory looming stimuli (i.e., sounds specifying an object on a collision course with the body) to quantify the size of peripersonal space both in front of and behind the body, with both threatening and nonthreatening stimuli. In addition, individual differences in the flexibility of peripersonal space in relation to both trait anxiety as well as arm length are examined.

Experiment 1 first establishes an auditory time-to-contact (TTC) paradigm, where participants estimated the arrival time of threatening sounds (i.e., a car on a collision course) both from the front and rear. After establishing that participants were able to consistently complete the task, Experiments 2 and 3 were conducted to examine performance in relation to both a nonthreatening control sound (Experiment 2) as well as threatening and nonthreatening animal sounds (i.e., a bee buzzing, an owl call) (Experiment 3). When stimuli were controlled for perceived loudness, we found that participants consistently underestimated the arrival time of stimuli approaching from the front as compared to those approaching for the rear across both threatening and nonthreatening contexts, suggestive of larger peripersonal space representations in front of the body relative to the rear. In addition, participants consistently underestimated for the threatening car sound as compared to the nonthreatening, low-pass filtered control sound, suggestive of a larger peripersonal space representation in response to a threatening stimulus. We discuss these findings in relation to the defensive and non-defensive functions of peripersonal space representations and how these functions are manifested neurally and cognitively.

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Manuscript 2

Examining Peripersonal Space around the Body using Auditory Looming Stimuli

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Doctoral Dissertation

Abstract

Researchers from disciplines as varied as neurology, neuroscience, anthropology, and psychology have long documented neural and cognitive representations of space immediately surrounding and within actionable range of the body, known as peripersonal space, that are differentiated from representations for the space outside this range, known as extrapersonal space. The current studies investigated how peripersonal space is represented around the body, particularly in regard to threatening and nonthreatening stimuli, using a novel auditory time-to-contact paradigm. Across three experiments, participants estimated the arrival time of approaching sounds that were either threatening or nonthreatening in nature. Initial results suggested an effect of perceived loudness. When controlling for this effect, participants consistently underestimated the arrival time of stimuli approaching from the front as compared to those approaching for the rear across both threatening and nonthreatening contexts, and they underestimated more for threatening stimuli as compared to nonthreatening stimuli. These findings suggest larger peripersonal space representations in front of the body relative to the rear for both threatening and nonthreatening contexts, suggesting that the defensive and non-defensive functions of peripersonal space may rely on a single representational system. In addition, our findings suggest larger peripersonal space representations in response to threatening stimuli, replicating previous findings. We discuss these findings in relation to the defensive and non-defensive functions of peripersonal space representations.

Examining Peripersonal Space around the Body using Auditory Looming Stimuli

Over the past century, researchers across multiple disciplines have differentiated the space immediately surrounding and within actionable range of the body, known as peripersonal space (Brain, 1941; Hall, 1968; Graziano & Cooke, 2006; Previc, 1998; Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981) from the space outside this range, known as extrapersonal space. Growing evidence suggests that this distinction plays a crucial role in coordinating actions in relation to objects surrounding the body, both for everyday, innocuous behaviors, as well as those needed for defense of the body (de Vignemont & Iannetti, 2015). Despite decades of attention, a number of important questions remain regarding the nature of peripersonal space. The current paper seeks to address three of these questions: How is peripersonal space represented around the body? Do representations of peripersonal space vary in accordance with the threateningness of a given scenario? And finally, are there individual differences in how peripersonal space is represented and how flexibly it shifts across contexts?

The Role of Peripersonal Space in Non-Defensive Behaviors

The initial work examining peripersonal space described its function primarily in reference to non-defensive, perception-action processes. For instance, single-unit recording studies with monkeys documented neurons in the pariarcuate cortex that responded only when objects were near the monkey’s body or, in other words, within its reach (Iriki, Tanaka, & Iwamura, 1996; Rizzolatti, Matelli, & Pavesi, 1983; Rizzolatti et al., 1981). Likewise, in humans, through behavioral studies of neurological patients and studies utilizing fMRI and transcranial magnetic stimulation (TMS) with healthy participants, researchers identified brain regions implicated in representing objects immediately surrounding the body (Berti & Frassinetti, 2000; Brozzoli, Gentile, Petkova, Ehrsson, 2011; Cowey, Small, & Ellis, 1994; Ferri, et al., 2015; Serino, Canzoneri, & Avenanti, 2011), including the intraparietal sulcus (IPS), supramarginal gyrus (SMG), and regions of the premotor cortex. This work has been extended to show that, in humans, the size of peripersonal space, what is considered near the body, is partly defined by a person's actionable range. Specifically, longer arms are associated with larger peripersonal space representations (e.g., Longo & Lourenco, 2007; Lourenco et al., 2011).

The Role of Peripersonal Space in Defensive Behaviors

Another basis for the distinction between the space immediately surrounding the body from that farther away can be derived from the defensive function of spatial representations. Hediger (1955) was the first to propose such a function, arguing for a "flight distance" or "flight zone" among nonhuman animals that elicited fight-or-flight behaviors when crossed by a threatening object (e.g., a hungry lion). More recent work has provided evidence for a "margin of safety" in macaque monkeys (Cooke & Graziano, 2003; Graziano & Cooke, 2006). For example, Cooke and Graziano (2003) reported that sudden air puffs presented within peripersonal space (i.e., close to the body) produced highly stereotyped startle responses.

A number of studies have indicated that peripersonal space representations in humans are indeed sensitive to threat, as well as individual differences in anxiety or fear. For instance, Sambo and Iannetti (2013) provided evidence for a "safety margin" in humans, similar to that described in monkeys, by taking advantage of a human defensive reflex known as the hand blink reflex (HBR) (Bufacchi, Liang, Griffin, & Iannetti, 2016;

Sambo, Foster, Williams, & Iannetti, 2012; Sambo, Liang, Cruccu, & Iannetti, 2012). In the HBR, humans produce defensive eye-blinks when the hand is stimulated, but this effect is strongest when the hand is near the face and weaker when farther away from the face. In this vein, they reported individual differences in peripersonal space as measured by the HBR that scaled with trait anxiety (Sambo & Iannetti, 2013). Specifically, greater trait anxiety was associated with larger peripersonal spaces. A similar relation was reported by Lourenco and colleagues (2011) who found that higher trait claustrophobic fear was associated with larger peripersonal spaces in a line bisection task. Together, these studies suggest an association between trait levels of anxiety or fear and the size of one's peripersonal space.

Flexibility of Peripersonal Space

The size of peripersonal space adapts flexibly to a given context, regardless of whether relevant to defensive or non-defensive behaviors. For example, Iriki and colleagues (1996) found that neurons in macaque monkeys that formerly fired only for objects placed near the hand subsequently fired to the tip of a tool after that tool had been used to complete a task, suggesting expansion of peripersonal space after tool use. Similar findings have been reported in humans, using the line bisection task, where researchers have demonstrated expansion of peripersonal space in humans after tool use (Ackroyd et al., 2002; Berti & Frassinetti, 2000; Longo & Lourenco, 2006) as well as contraction of peripersonal space when reach was impeded with arm weights (Lourenco & Longo, 2009). Such flexibility in non-defensive contexts has since been documented using a number of methodologies, including audio-tactile interaction tasks (e.g., Canzoneri, Ubaldi, Rastelli, Finisguerra, Bassolino, & Serino, 2013; Noel, Pfeiffer, Blanke, & Serino, 2015), estimates of reachability (e.g., Morgado, Gentaz, Guinet, Osiurak, 2013) and fMRI-based measures (e.g., Serino, Canzoneri, Marzolla, di Pellegrino, & Magosso, 2015). In addition, initial evidence suggests that peripersonal space flexibly incorporates information regarding threat, expanding in relation to both auditory (Taffou & Viaud-Delmon, 2014) and visual (de Haan, Smith, Stigchel, & Dijkerman, 2016) threatening stimuli. Taken together, these findings indicate that peripersonal space adapts flexibly to changing motor capabilities (Maravita & Iriki, 2004) as well as to defense-related information.

Individual differences in the flexibility of peripersonal space. An open question in this literature is whether there are individual differences in the flexibility of peripersonal space. That is, do individuals vary in the degree to which they are able to flexibly represent the space surrounding the body? Given that individuals high in trait fears and anxiety (e.g., claustrophobic fear, general trait anxiety) (Lourenco, Longo, & Pathman, 2011; Sambo & Iannetti, 2013) have larger, distorted peripersonal space representations, they might also suffer in their ability to flexibly represent space. Initial research from our lab suggests that this assumption holds in relation to claustrophobic fear. Hunley and colleagues (2017) found that individuals high in trait claustrophobic fear demonstrated less expansion when using a tool to complete a line bisection task than individuals low in trait claustrophobic fear. This finding suggests that individuals high in trait claustrophobic fear possess less flexible representations of peripersonal space.

A growing literature suggests that high trait anxiety is associated with decreased attentional flexibility (Derryberry & Reed, 2002; Eysenck, Derakshan, Santos, & Calvo, 2007; Pacheco-Unguetti, Acosta, Callejas, & Lupiáñez, 2010) and disrupted activation in fronto-parietal networks associated with attention (e.g., Bishop, 2009; Sylvester et al., 2012). Importantly, regions that fall within these networks have also been associated with peripersonal space in studies utilizing fMRI (Brozzoli et al., 2011) and transcranial magnetic stimulation (TMS) (Serino et al., 2011). Consequently, the decreased flexibility in peripersonal space reported by Hunley and colleagues (2017) may be rooted in the decreased attentional flexibility seen in individuals high in trait anxiety.

Spatial Representations around the Body

Despite the progress made in understanding peripersonal space, it remains an open question how peripersonal space is represented *around* the body, particularly behind compared to in front of the body. Given that humans and other organisms exist in three-dimensional space, it is important to generalize beyond the frontal plane in order to fully understand the role of peripersonal space in guiding behavior. Though evidence demonstrates that peripersonal space representations exist for the rear as well as the front (Farnè & Làdavas, 2002; Graziano, Reiss, & Gross, 1999, Kitagawa, Zampini, & Spence, 2005; Van der Stoep, Nijboer, Van der Stigchel, & Spence, 2015), it is unclear whether these representations differ in character for the front and rear, specifically in regard to their size. Such differences could indicate differences in how attention is allocated around the body.

In this vein, there is reason to believe that representations of peripersonal space may differ in size around the body. For instance, research examining the processing of multisensory information around the body has found differences in how audiotactile information is integrated in front compared to behind the body (Gillmeister & Forster, 2012; Kóbor, Füredi, Kovács, Spence, & Vidnyánszky, 2006; Occelli, Spence, &

Zampini, 2011; Zampini, Torresan, Spence, & Murray, 2007). Specifically, Kóbor and colleagues (2016) reported that interfering information (e.g., crossing the arms) had a stronger effect in front of the body as compared to the rear. In a similar vein, Gillmeister and Forster (2012) found that attentional effects on performance in the rear are strongest when the hands are held close to the body, whereas they are strongest in front when the hands are held farther away from the body. Given that peripersonal space involves the integration of multisensory stimuli (Graziano & Gross, 1995), these differences in processing of multisensory information for the front as compared to the rear may suggest differences in peripersonal space as well.

However, only two studies (to our knowledge) have specifically examined characteristics of peripersonal space representations in front of the body as compared to behind. In the first, Noel and colleagues (2015) examined changes in peripersonal space behind the body after they induced expansion in the front of the body (Noel et al., 2015). In this paradigm, participants were tasked with responding as quickly as possible to a vibro-tactile stimulus applied to the trunk, either the chest for frontward trials or the mid-back for rear trials. Meanwhile, task-irrelevant sounds were presented on a number of speakers. These sounds moved from speaker to speaker towards the participant producing an effect of looming (i.e., the sounds appeared to be moving towards participants). Previous work with this paradigm found that sounds close to the body produced speeded responses to the vibro-tactile stimulus, whereas sounds far from the body did not (e.g., Canzoneri et al., 2012). Studies had utilized this paradigm in the past to examine space in front of the body, but Noel and colleagues (2015) built upon these designs such that sounds and vibro-tactile stimuli could be presented behind the body. These researchers reported that peripersonal space expansion in the frontal plane was accompanied by simultaneous contraction behind the body, suggesting that the representations for the front and rear rely on common resources. However, they did not directly compare the size of peripersonal space in front of the body relative to that in the rear. Another study reported larger peripersonal spaces in front of the body compared to the rear, but this study used HBR for the face (Bufacchi et al., 2016), which might be inherently biased towards a larger frontal representation. It is unclear whether peripersonal space, when assessed more generally, would show a similar bias.

Individual differences in peripersonal space representations around the body. Crucially, neither Noel and colleagues (2015) nor Bufacchi and colleagues (2016) examined individual differences in peripersonal space, particularly how differing levels of anxiety might affect peripersonal space representations. This omission is important because previous work suggests that differences in body morphology (Longo & Lourenco, 2007) as well as trait fear and anxiety (Lourenco et al., 2011; Sambo & Iannetti, 2013) are associated with differences in representations in front of the body. Yet, it remains unknown whether such differences exist in the rear plane as well. Given evidence from Noel and colleagues (2015) suggesting that peripersonal space in the front and rear of the body share cognitive resources, a possibility that would follow is that these individual differences in body morphology and anxiety would predict differences in peripersonal space representations behind the body as well.

How do spatial representations surrounding the body vary under threatening and nonthreatening contexts? Given the role that peripersonal space plays both in guiding defensive and non-defensive behaviors, it is crucial for researchers to establish how space is represented around the body under both contexts. As previously mentioned, peripersonal space in the frontal plane shows greater expansion for threatening compared to nonthreatening objects, and, importantly, the degree of expansion has been shown to be positively correlated with the fear of the target object (de Haan et al., 2016; Taffou & Viaud-Delmon, 2014). However, the difference between threatening and nonthreatening contexts may extend beyond simple expansion in the frontal plane.

One possibility is that that the overall shape of peripersonal space surrounding the body differs under threatening and nonthreatening contexts. For instance, under nonthreatening contexts, a larger frontal representation, as compared to the rear, might be adaptive, given that the majority of human perception-action capabilities are frontward-oriented. Specifically, precise behaviors oriented towards innocuous, safe objects may necessitate greater attentional resources oriented towards the front of the body in order to enable precise movements (e.g., grasping the small handle of a coffee mug). By contrast, circumstances in which there is a direct threat may require a redistribution of attentional resources. Though threats can approach from all directions, a threat approaching from behind the body is potentially *more* threatening because, due to the orientation of most human perception-action capabilities, such objects require a greater time to identify, are more difficult to track, and take greater time to properly react to. Thus, a larger representation behind the body would be adaptive when remaining vigilant for approaching threats, allowing for enough time to prepare a defensive response (i.e., fight, flight). Yet another possibility is that both threatening and nonthreatening contexts require similarly sized representations of space in front of the body as compared to the rear. Thus, given these possibilities, it is crucial for researchers to establish how space is represented around the body under both contexts.

The Current Paper

The current paper sought to extend the extant literature by establishing a novel paradigm for examining peripersonal space both in front of and behind the body, under threatening and nonthreatening conditions. By examining performance under varying degrees of threat, we were able to test whether and how peripersonal space representations differed under these different contexts. Furthermore, as part of this extension, we examined the role of individual differences in predicting peripersonal space around the body.

Experiment 1

Though a number of studies have examined peripersonal space in front of and behind the body (Farnè & Làdavas, 2002; Graziano et al., 1999, Kitagawa, et al., 2005; Van der Stoep et al., 2015) and others have examined multisensory interactions in front of and behind the body (Gillmeister & Forster, 2012; Kóbor et al., 2006; Zampini, Torresan, Spence, & Murray, 2007; Occelli et al., 2011), comparatively few have directly compared peripersonal space representations across both regions of space (Bufacchi et al., 2016; Noel et al., 2015), and these studies are not without limitations. Bufacchi and colleagues (2016) report a larger representation in front of the body as compared to the rear; however, this finding could be limited to the region surrounding the face, which may be biased to produce a larger frontal representation due to the location of the face. In another study, Noel and colleagues (2015) required that participants stand between two, closely placed “walls” of speakers, which may be problematic because barriers to movement have been shown to affect peripersonal space (Morgado et al., 2013) and may not generalize to non-restrictive conditions. Thus, the goal of Experiment 1 was to develop a task that allowed for unambiguous comparisons between front and rear representations of peripersonal space.

In developing a new task, looming stimuli (Gibson, 1957, 1958, 1979), visual or auditory stimuli that specify objects on a direct collision course with the body, offer particular promise for investigating peripersonal space as related to defense of the body. Indeed, a large variety of species and populations have been shown to produce defensive responses (e.g., blinking, swatting, ducking) to visual looming stimuli, including macaque monkeys (Ghazanfar & Maier, 2009; Schiff et al., 1962), human infants (Ball & Tronick, 1971), adult humans (Regan & Beverly, 1978), amphibians such as frogs, and even invertebrates such as fiddler crabs (Schiff, 1965). Given this sensitivity, researchers have used such stimuli to probe at what distance an organism considers an object to be “close to” the body or, in other words, within peripersonal space (e.g., Canzoneri et al., 2012; de Haan et al., 2016; Noel et al., 2014; Rossetti, Romano, Bolognini, & Maravita, 2015).

In humans, one such means for examining participants’ reactions to looming objects is within the context of a time-to-contact (TTC) task. In a visual TTC task, participants are presented with objects that appear briefly before disappearing. These stimuli specify objects approaching the participant from different distances and at varying speeds, producing different TTCs. After the object disappears, participants are asked to estimate the arrival time of the object, given a stable trajectory. A common pattern is for participants to underestimate the TTC of approaching visual stimuli, especially when the stimulus takes longer to arrive (Vagnoni, Lourenco, & Longo, 2012). Whether visual or auditory, both types of looming stimuli prime defensive behaviors and serve as salient warning cues in humans and other species (Bach, Neuhoff, Perrig, & Seifritz, 2009; Gibson, 1979; Schiff & Oldak, 1990). Furthermore, participants' performance on TTC tasks varies as a function of the level of threat specified by a looming object, with participants consistently underestimating the arrival time of approaching threatening objects (e.g., snakes, spiders) relative to less threatening objects (e.g., butterflies, rabbits) (Vagnoni et al., 2012). This finding highlights that, though looming stimuli are inherently threatening, context modulates participants' responses, producing differential performance across stimuli that involve threatening or nonthreatening content. Importantly, these findings mirror the results of studies in the peripersonal space literature that demonstrate an increased size of peripersonal space for threatening stimuli (de Haan et al., 2016; Taffou & Viaud-Delmon, 2014). Taken together, this evidence suggests that the underestimation seen in TTC studies for threatening stimuli reflects expanded peripersonal space representations.

Though visual looming stimuli are inherently restricted to the front of the body in humans, auditory looming stimuli, which humans can perceive from any direction, can be used to examine space behind the body as well. Crucially, humans are capable of using auditory information to identify an object's distance from the body (Moore & King, 1999), allowing us to examine what participants consider "near" the body – or within peripersonal space. Thus, auditory looming stimuli provide a crucial methodological strategy by which to examine space behind the body as effectively as in front of the body. Furthermore, given that previous work has demonstrated differential responses to threatening versus nonthreatening looming stimuli (Vagnoni et al., 2012), such a task could be used to examine differences in peripersonal space representations across both contexts.

For the current study, an auditory TTC task was developed, similar to that used by Neuhoff and colleagues (e.g., Neuhoff, 2001; Neuhoff et al., 2009), using threatening sounds (i.e., car horns) to examine space in front compared to behind the body. Participants sat between two speakers, one in front of the body and one behind the body. Stimuli were designed to signal an approaching car at varying speeds. Participants were tasked with pressing a response key right before the car would make contact with the body. In addition, given the evidence that peripersonal space is sensitive to trait anxiety (Sambo & Iannetti, 2013) and body morphology (Longo & Lourenco, 2007), measures of trait anxiety and measurements of height and arm length were collected.

Methods

Participants

Forty-six undergraduate students (39 female) between 18 and 26 years of age participated for research credit or payment ($15). All participants had normal or corrected-to-normal vision, and all reported having normal hearing. This sample size was determined *a priori* using G*Power statistical software (Faul, Erdfelder, Lang, & Buchner, 2007). Given the exploratory nature of this project, a medium effect size ($\eta^2 \approx .15$) was assumed.

Apparatus and Stimuli

Auditory TTC task. Each participant sat between two Yamaha HS5 Studio speakers placed exactly 1 m in front of and behind him or her. A decibel meter

(RadioShack) was used to confirm that all sounds were produced at the same intensities from both speakers. Participants responded to sounds using a keyboard placed atop a small, mobile desk.

Stimuli for this experiment were created using the recording of a car horn (a 1996 Chevy Blazer; downloaded from soundsnap.com). To produce the effect of looming, the intensity of this single sound clip was increased logarithmically from 0 dB to 65 dB, a manipulation that has proven effective in simulating movement towards the listener (Bach et al., 2009; Bach et al., 2008). The rate at which sounds increased in intensity was varied to create five different stimulus “arrival times” or TTCs (i.e., 3000 – 7000 ms, 1000 ms increments). These specific speeds were chosen to enable analyses across a variety of TTCs as has been done in previous studies (e.g., Vagnoni et al., 2011). Sound clips lasted the same amount of time as their designated TTC. Consequently, the “arrival” of stimuli occurred when the sound ceased. Sounds could approach from one of two possible directions, front or back, such that there were 10 different stimuli. Participants completed two blocks of 50 trials, for a total of 100 trials, with front and back trials presented in a randomized order.

Participants were given feedback on each trial throughout the task. Specifically, they were told “too late” if they responded after the sound had ceased and “too early” if they responded more than 500 ms before the TTC for a given sound. If they responded within the 500 ms window, no feedback was given. Feedback was included in this first experiment to ensure that participants understood and completed the task reliably. Having found that participants had little difficulty with the task (see results below), we conducted the subsequent experiments without this feedback (see Experiments 2 and 3).

Psychological measure of trait anxiety. To examine trait anxiety, the State-Trait Anxiety Inventory Trait subscale was utilized (STAI-T; Speilberger, Gorsuch, Lushene, Vagg, & Jacobs, 1983), which has been previously shown to correlate with the size of peripersonal space (Sambo & Iannetti, 2013). The STAI-T is a 20-item scale in which participants are asked to indicate how they “generally” feel by rating their agreement to a number of statements. These items describe both positive (e.g., “I feel pleasant”) and negative (e.g., “I feel inadequate”) feelings regarding the presence or absence of anxiety. Participants ranked their experience of items using a scale ranging from 1 (“Almost Never”) to 4 (“Almost Always”). The STAI-T has been shown to have a high internal reliability with a Cronbach’s Alpha of .92 (Ramanaiah, Franzen, & Schill, 1983).

Physical measures. To account for individual differences in body morphology, each participant’s arm length (from the right acromion to tip of right middle finger) and height (without shoes) were measured. Previously, arm length was found to predict the size of one’s peripersonal space, with longer arms predicting larger peripersonal spaces (Longo & Lourenco, 2007). It has been argued that this relation exists because arm length effectively predicts an individual’s ability to act on the space around the body. However, one difficulty is properly accounting for body proportions. For instance, it is entirely possible that a tall person and a short person could have the same arm length, one that is proportionally short for the tall person but proportionally long for the shorter person. Consequently, the taller person may have a perceived range of action that is comparatively small, whereas the shorter person’s perceived range of action may be comparatively large – despite having the same arm length. To address this, arm length was calculated as a proportion of height in the current work.

Procedure

Prior to beginning the study, the experimenter took arm and height measures of each participant. Next, participants were seated in between the two speakers for the auditory TTC task. Participants were told that their task was to imagine themselves as pedestrians in traffic and that they would hear cars on a direct collision course with their body, blaring their horns as they approached. This backstory was used to ensure that participants experienced the looming stimuli as threatening. They were instructed that the only way to stop the car from hitting them was to wait until the very last second to hit the response key (i.e., to let the car get as close to their body as possible before responding). Participants heard sounds approach from both the front and rear. Previous evidence suggests that humans sometimes confuse front and rear presented auditory stimuli under minimal conditions (Brungart, Durlach, & Rabinowitz, 1999; Middlebrooks & Green, 1991). As such, the experimenter specified the direction of approach on each trial. After completing the auditory looming task, participants were given the STAI-T questionnaire.

Results

Out of all trials, < 1% were removed due to participant error (e.g., forgetting to respond). Of the remaining trials, 1.8% were identified as outliers (> 2.5 standard deviations from individual means) and subsequently removed. One participant was removed from the analyses for producing responses > 2.5 standard deviations from the sample mean for both front and rear trials.

Performance on the TTC Task

As a preliminary analysis, we examined whether participants' TTC estimates scaled according to the actual TTCs, as would be expected if they performed the task according to the instructions. Participants' estimates of TTC were regressed on the actual TTC to compute the slope of the best-fitting line. One-sample *t*-tests revealed that the slope of participants responses differed significantly from zero for both directions (Front: *M* = .78, *SD* = .09, *t*[44] = 58.39, *p* < .001, *d* = 8.70; Rear: *M* = .78, *SD* = .09, *t*[44] = 60.88, *p* < .001, *d* = 9.08), indicating that participants appropriately scaled their estimates of TTC in accordance with the actual TTC. Further analyses demonstrate that participants' performance had a high internal consistency (Cronbach's Alpha = .94), providing additional evidence that participants were able to reliably complete this task.

Front versus rear performance. We then compared participants' performance for front and rear trials to test for differences across the two conditions. Given that we did not have an *a priori* reason to expect participants' responses to vary by TTC across front and rear trials, participants' mean response times were collapsed across TTC. A paired samples t-test revealed no difference in participants' estimates for front (*M* = -567.18 ms, *SD* = 174.05) and rear (*M* = -600.91 ms, *SD* = 195.68) trials, *t*(44) = 1.56, *p* = .13, *d* = .23, with significant underestimation in both cases as revealed by one sample *t*-tests (all *t*'s > 20.6; all *p*'s < .001). However, given that feedback was provided on every trial, one potential concern is that practice could have masked the effect of direction. To account for this possibility, we also compared participants' responses in just the first block, at which point they had received less feedback on their performance. Again, though, there was similarly no difference between front (*M* = -670.58 ms, *SD* = 193.34) and rear (*M* = -700.37 ms, *SD* = 214.43) trials, *t*(44) = 1.26, *p* = .21, *d* = .19, suggesting that the lack of a direction effect was likely not due to participants receiving feedback across trials.

Trait Anxiety

The relation between trait anxiety and performance on the auditory TTC task was examined in correlation analyses. Given that, on average, participants did not differ in their performance for front and rear, we first examined the relation between anxiety and participants' average estimates, collapsed across front and rear trials. However, our analyses revealed no relation between trait anxiety and participants' estimates when collapsed across front and rear trials, $r(43) = .08$, $p = .61$. Next, we examined whether anxiety was associated with a bias to underestimate more for one direction over the other. To examine this possibility, difference scores (rear estimate – front estimate) were calculated to capture the relative bias across planes. Positive scores indicate greater underestimation on front trials relative to rear trials, and negative scores indicate a greater underestimation on rear trials relative to front trials. This analysis revealed a significant

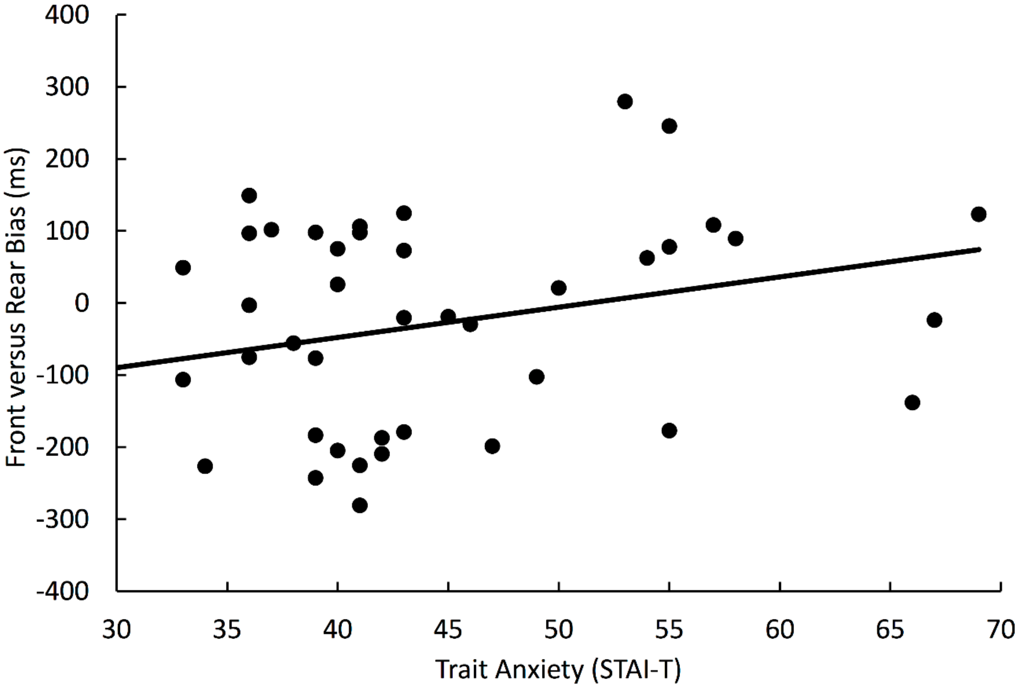


Figure 1. Scatterplot relating participants' trait anxiety scores to their performance on the auditory TTC task. Higher trait anxiety scores were associated with higher front versus rear difference scores, indicating greater front bias. No bivariate outliers were present in this analysis.

correlation between differences scores and trait anxiety, *r*(43) = .30, *p* = .05 (see Figure 1). That is, higher anxiety was associated with greater front than rear underestimation, providing preliminary support for a larger peripersonal space representation in front of the body as compared to the rear under threatening circumstances for individuals high in anxiety.

Arm Length

The relation between arm length as a proportion of height and performance on the auditory TTC task was examined in correlation analyses. Again, given that, on average, participants did not differ in their performance for front and rear, we first examined the relation between arm length and participants' average estimates collapsed across front and rear trials. Correlational analyses revealed a marginally significant negative relation between arm length and participants' estimates when collapsing across front and rear trials, *r*(43) = -.28, *p* = .06. In other words, there was a trend for longer arms to be associated with greater underestimation, or larger peripersonal space representations, in both directions. Next, arm length was examined in relation to difference scores of participants' performance on front versus rear trials. Correlation analyses revealed a significant relation between these two variables, *r*(43) = -.48, *p* = .001 (see Figure 2). Participants with proportionally longer arms had a tendency to underestimate more for behind the body than the front, suggesting that individuals with longer arms may have larger peripersonal space representations behind the body under threatening circumstances.

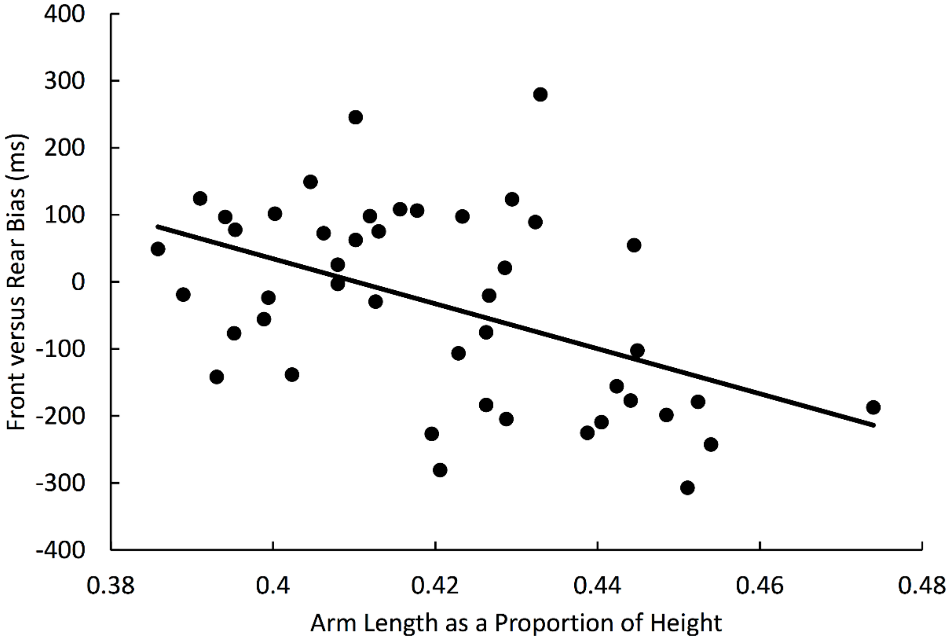


Figure 2. Scatterplot relating participants' arm length to their performance on the auditory TTC task. Longer arms were associated with lower front versus rear difference scores, indicating greater rear bias. No bivariate outliers were present in this analysis.

Discussion

In summary, participants significantly underestimated the TTC of approaching car sounds from both the front and the rear, and this underestimation did not differ between front and rear trials. These findings could be taken as evidence for symmetrical representations of peripersonal space, with equally sized representations of front and rear space. However, open questions remain regarding whether these findings are limited to threatening contexts or whether they are the result of the feedback participants received on each trial. As such, further testing is needed.

In regard to individual differences, there was a marginally significant relation between arm length and general underestimation (collapsed across front and rear), such that longer arms were associated with greater underestimation for both directions. These findings suggest that longer arms were associated with larger peripersonal space representations, replicating previous findings (Longo & Lourenco, 2007). Furthermore, analyses of individual differences in trait anxiety and arm length revealed associations between these variables and different patterns of performance. Specifically, higher trait anxiety was associated with a greater tendency to underestimate the arrival time of sounds approaching from the front relative to the rear, and longer arms in proportion to one's height was associated with a greater tendency to underestimate the arrival time of sounds approaching from the rear relative to the front.

Given that these results were not predicted, we can only speculate regarding their potential implications, and they will need to be investigated further. One possible explanation is that these findings could be indicative of differences in peripersonal space flexibility. For instance, high trait anxiety is associated with decreased attentional flexibility (e.g., Bishop, 2009; Derryberry & Reed, 2002; Eysenck et al., 2007), and decreased flexibility in tasks measuring peripersonal space (Hunley et al., 2016). Thus, a potential explanation for our finding is that participants high in trait anxiety have difficulty allocating attentional resources across contexts, leaving them "stuck" representing space in such a way that would be adaptive under non-defensive conditions (i.e., a larger front representation) rather than switching to representing space in such a way that would be adaptive for defensive conditions (i.e., a larger rear representation). A similar explanation could hold for the relation between arm length and peripersonal space. Longer arms relative to one's height also means that a given individual is capable of acting on more space relative to their height. Routinely acting on a larger region of space may lead to increased flexibility of spatial representations. Consequently, it is possible that these individuals are more capable of switching between peripersonal spaces intended for non-defensive and defensive behaviors, leading longer arms to be associated with greater underestimation behind the body on a threatening looming task.

Notably, however, these correlations have not been reported in previous studies, and in the case of anxiety, the relation appears to be weak. As such, additional research is necessary to ensure that they replicate (Open Science Collaboration, 2015). In addition, one difficulty in interpreting these findings is that the effects were observed under only threatening conditions caused by an approaching car sound, whereas the proposed explanations assume shifting representations between threatening and nonthreatening circumstances. For the proposed explanations to hold, trait anxiety and arm length will need to account for differences between threatening and nonthreatening conditions. Thus, the goal of Experiment 2 was to replicate the findings of Experiment 1 while examining performance under nonthreatening conditions as well.

Experiment 2

Experiment 2 sought to replicate the findings of Experiment 1 and extend the auditory TTC paradigm from our first experiment by including nonthreatening stimuli in the task. This study utilized a within-subjects design to capture individual differences in performance with threatening and nonthreatening stimuli while accounting for trait anxiety and body morphology. This experiment had two primary goals: 1) to investigate how representations of peripersonal space differ in response to threatening and nonthreatening stimuli, and 2) to provide a strong test of the hypothesis that trait anxiety and arm length are associated with differences in the flexibility of peripersonal space.

Specifically, if higher trait anxiety predicts decreased peripersonal space flexibility, then high anxiety participants should demonstrate difficulty switching between representations useful for non-defensive behaviors (i.e., a larger frontal representation as compared to the rear) to those useful for defensive behaviors (i.e., a larger rear representation as compared to the front). Along similar lines, longer arms should predict greater flexibility in switching between representations for non-defensive and defensive contexts. In addition, Experiment 2 removed feedback from trials to reduce potential practice effects.

Methods

Participants

Fifty-two undergraduate students (35 female) between the 18 and 42 years of age participated for course credit. All participants had normal or corrected to normal vision, and all reported having normal hearing. This sample size was determined with G*Power statistical software (Faul et al., 2007), assuming effect sizes similar to those found in Experiment 1.

Apparatus and Stimuli

Auditory TTC task. As in Experiment 1, each participant sat between two Yamaha HS5 Studio speakers placed exactly 1 m in front of and behind him or her. Readings from a decibel meter (RadioShack) confirmed that all sounds were produced at the same intensities from both speakers. Participants again responded to sounds using a keyboard placed atop a small mobile desk.

In addition to the threatening car stimuli used in Experiment 1, this experiment included a matched set of nonthreatening, control stimuli. These stimuli were created by applying a low-pass filter to the car horn sound file, which preserved frequencies from

200 to 400 Hz with a smoothing factor of one (Praat; Boersma, 2002). Consequently, we were able to preserve some of the low-level properties of the original file while also masking the identity of the original sound source. To confirm that listeners could not recognize the control sound and that this sound was perceived as less threatening, 10 volunteer raters were recruited to evaluate the car and control sounds. None of the volunteers were able to correctly identify the control sound file as a car horn, and all participants rated the car horn as more threatening than the control sound, $t(9) = 6.50$, $p < .001$, $d = 2.11$. As with the threatening stimuli from Experiment 1, these sounds were modified such that they increased logarithmically from 0 to 65 dB to produce the effect of looming towards participants with five possible TTCs (i.e., 3000 - 7000 ms, 1000 ms increments).

Sounds were presented in two blocks of 50 trials each. Trials were blocked by threat-level (threatening, nonthreatening) and the order of presentation was counterbalanced across participants. Front and rear trials were presented in a randomized order throughout. In addition, participants did not receive feedback on their performance to prevent significant practice effects. Instead, participants were presented with example sounds (one from each direction) prior to each block. Participants simply listened to these examples without responding and were told that, during the task, they were to respond to the sound at the very last moment.

Psychological measure of trait anxiety. The STAI-T (Speilberger et al., 1983) was again used to measure trait anxiety. The STAI-T was presented prior to or after the TTC task (order counterbalanced across participants).

Physical measures. Measurements of participants arm length and height were collected to calculate arm length as a proportion of height as in Experiment 1. These measurements were always taken immediately prior to the completion of the STAI-T.

Procedure

In the threatening condition, the procedure followed that described in Experiment 1. In the nonthreatening condition, participants were asked to imagine that a small, light-weight object was approaching them on a direct collision course (from the front or rear) and informed that this object posed no threat of bodily harm. Again, participants were tasked with using the response key to “stop” the object right before it made contact with their body (i.e., to let the object get as close to their body as possible before responding). Participants were informed that the objects could approach from either the front or rear and that they would be told the direction of approach prior to each trial. In both conditions, participants were presented with two example sounds, one from each direction, to listen to without responding. They were also reminded to respond right before the sound “made contact,” represented by the sound’s cessation.

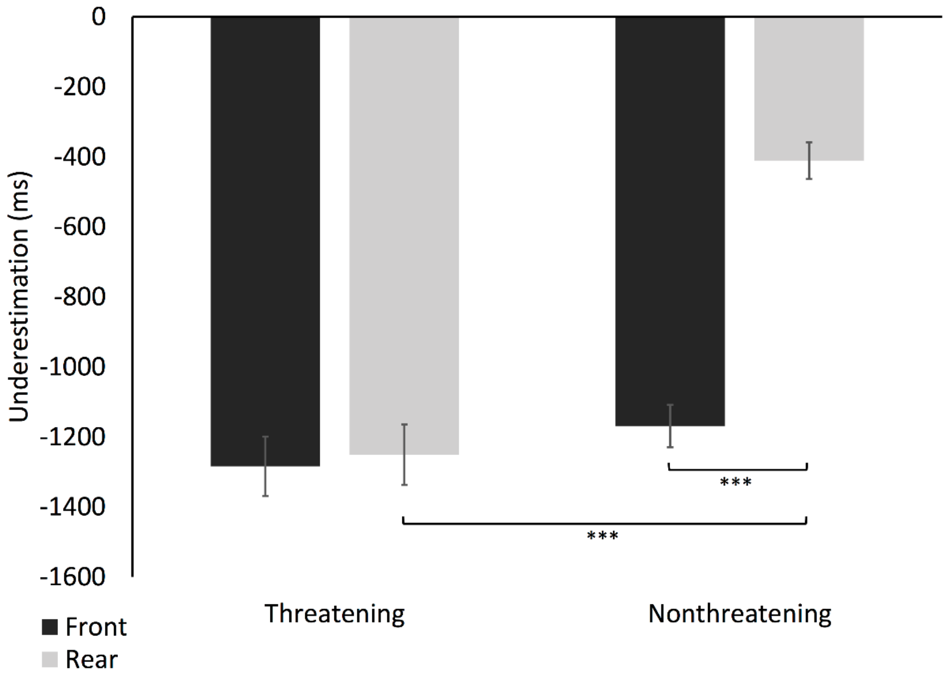
Results

Two participants were removed for failing to follow directions (i.e., responding immediately after sound presentation). Of the remaining 50 participants, < 1% of trials were removed due to participant error (e.g., forgetting to respond). Of the remaining trials, < 1% were identified as outliers (> 2.5 standard deviations from individual means) and subsequently removed.

Performance on TTC Task

As a preliminary analysis, we examined whether participants' TTC estimates scaled according to the actual TTCs, as would be expected if they performed the task according to the instructions. Participants' estimates of TTC were regressed on the actual TTC to compute the slope of the best-fitting line. One-sample *t*-tests revealed that the slope of participants responses differed significantly from zero for both directions for both the threatening (Front: $M = .65$, $SD = .14$, $t[49] = 34.01$, $p < .001$, $d = 4.81$; Rear: $M = .67$, $SD = .15$, $t[49] = 32.54$, $p < .001$, $d = 4.60$) and nonthreatening trials (Front: $M = .69$, $SD = .12$, $t[49] = 42.67$, $p < .001$, $d = 5.89$; Rear: $M = .77$, $SD = .13$, $t[49] = 43.23$, $p < .001$, $d = 6.12$), indicating that participants appropriately scaled their estimates of TTC in accordance with the actual TTC. Further analyses demonstrate that participants' performance had a high internal consistency (Cronbach's Alpha = .87). Thus, participants' TTC estimates scaled in accordance with veridical TTCs and their performance was reliable across trials.

Front versus rear performance. We then conducted a 2 × 2 repeated measures ANOVA, with direction (front, rear) and threat level (threatening, nonthreatening) as independent variables, and participants' mean responses (calculated as the mean difference between participants estimates of TTC and the actual TTC) as the dependent variable. As in the previous experiment, we collapsed across TTC in this analysis, given that there was no *a priori* reason to expect a difference as a function of TTC. This analysis yielded significant main effects of direction, $F(1, 49) = 318.24$, $p < .001$, $\eta_p^2 = .87$, and threat level, $F(1, 49) = 36.67$, $p < .001$, $\eta_p^2 = .43$, as well as a significant interaction, $F(1, 49) = 426.44$, $p < .001$, $\eta_p^2 = .90$. To shed light on this interaction, we conducted *post hoc* comparisons (Bonferonni corrected). These analyses revealed that, in the nonthreatening condition, participants underestimated more for sounds coming from the front (M = -1251.49 ms, SD = 609.76) than the rear (M = -409.73 ms, SD = 370.77): M_{diff} = 759.31 ms, SE_{diff} = 32.63, 95% CI (-824.88, -693.75), $t(49) = 23.27$, $p < .001$, d = 1.14 (see Figure 3). By contrast, in the threatening condition, there was no such difference between performance for sounds coming from the front (M = -1284.20 ms, SD = 598.94) as compared to the rear (M = -1169.04 ms, SD = 426.69): M_{diff} = 32.71 ms, SE_{diff} = 23.23, 95% CI (-79.40, 13.99), $t(49) = 1.41$, $p = .663$, $d = .05$. Furthermore, participants underestimated significantly more for rear trials in the threatening condition as compared to rear trials in the nonthreatening condition: M_{diff} = 841.76 ms, SE_{diff} = 82.90, 95% CI (-1008.35, -675.18), $t(49) = 10.15$, $p < .001$, $d = 1.76$. Whereas no such difference existed for front trials: M_{diff} = 115.16 ms, SE_{diff} = 78.94, 95% CI (-273.79, 43), $t(49) = 1.46$, $p = .604$, $d = .16$. Overall, participants demonstrated significant underestimation for both stimulus types from both directions as revealed by one-sample *t*-tests, (all *t*'s > 7.81; all *p*'s < .001). Thus, participants demonstrated symmetrical underestimation for front and rear trials in the threatening condition, whereas they exhibited asymmetrical underestimation in the nonthreatening condition, underestimating more for front trials relative to rear trials, suggesting a larger representation of peripersonal space in front of the body as compared to the rear at least when the stimuli were nonthreatening in nature.



***$p < .001$

Figure 3. Participants' mean underestimation for each condition from the front and rear. Error bars are ± SEM.

Trait Anxiety

The relation between trait anxiety and performance on the auditory TTC task was examined in correlation analyses. Following Experiment 1, we first examined the relation between anxiety and participants average estimates, collapsed across front and rear trials. However, correlation analyses again revealed no significant relation between trait anxiety and participants' estimates collapsed across front and rear trials for either the threatening condition, $r(48) = .03$, $p = .824$, or the nonthreatening condition, $r(48) = .10$, $p = .495$. Following the findings of Experiment 1, we calculated difference scores (mean rear estimate - mean front estimate) for participants' performance for both the threatening and the nonthreatening conditions. For the threatening condition, correlation analyses revealed that difference scores and trait anxiety were not significantly related, *r*(48) = .01, *p* = .947, failing to replicate the findings of Experiment 1, which found a significant positive relation. Likewise, in the nonthreatening condition, we found that there was no relation between participants' difference scores and trait anxiety, *r*(48) = -.04, *p* = .774.

Arm Length

The relation between arm length as a proportion of height and performance on the auditory TTC task was examined in correlation analyses. Given the marginal relation found in Experiment 1, we first examined the relation between arm length and participants average estimates collapsed across front and rear trials. However, correlation analyses revealed no significant relations between arm length and participants' estimates for either the threatening, *r*(48) = -.22, *p* = .131, or the nonthreatening, *r*(48) = .06, *p* = .662, condition. We also examined the relation between arm length and participants difference scores in both conditions. In the threatening condition, correlation analyses revealed no significant relation between arm length and participants' differences scores, *r*(48) = .073, *p* = 613, failing to replicate the findings of Experiment 1, which found a significant negative relation between the variables. Likewise, in the nonthreatening condition, arm length and participants' difference scores were again not significantly related, *r*(48) = .10, *p* = .492.

Discussion

Our results revealed that participants' performance on our TTC task depended on the threat level of the stimuli (approaching car or nonthreatening control sound) and the direction of approach (front versus back). Specifically, participants underestimated the

TTC equally for front and rear car sounds on a collision course with the body, whereas they exhibited greater underestimation in the frontal plane compared to the rear when stimuli posed no harm to the body. However, unlike Experiment 1, we found no relation between individual differences in trait anxiety or arm length and participants' TTC performance. Moreover, examining the distributional properties of the measures used in both experiments suggests that the different findings could not be attributed to such factors, suggesting perhaps that these relations are not robust and may not reflect genuine effects.

On the surface, participants' patterns of underestimation in the current experiment fit what one might expect for representations of peripersonal space under varying levels of threat. When under no threat of physical harm, participants seemed to maintain a larger frontal representation, which would be adaptive given that the majority of human perception-action capabilities are frontward-oriented, necessitating greater attentional resources in this direction. However, when under threat of bodily harm by an approaching car, having a symmetrical representation of space, such that attention is distributed equally around the body, would allow participants to maintain vigilance around the body, possibly enabling more rapid responses to threats approaching from any direction. Thus, participants' pattern of responses may reflect context-dependent changes to peripersonal space representations. Notably, this finding differs from Bufacchi and colleagues (2016), who reported a larger frontal representations of peripersonal space when examining defensive behaviors.

However, another possibility, and concern, is that this result reflects low-level sound properties that are unrelated to threat or peripersonal space. For instance, although all of the sounds were matched for absolute loudness using a sound meter, it is possible that the sounds differed in *perceived* loudness (Plack & Carlyon, 1995; Siegel & Stefanucci, 2011). A number of participants spontaneously reported that the car horn sound appeared louder than the low-pass filtered car horn (control sound), and a few individuals specifically remarked that this effect appeared stronger in the rear. If true, then the findings in the current study could reflect differences in judgement based on perceived loudness rather than differences in peripersonal space as related to threat. In other words, given that sound intensity is the primary means by which humans make TTC judgements for auditory stimuli (Bach et al., 2009; Bach et al., 2008), the decreased underestimation in the rear for the control sound might not be due to its nonthreatening nature but because participants perceived the sound as quieter and, consequently, perceived the object as farther away. A follow-up study in which ratings of perceived loudness were collected confirmed these anecdotal accounts (see Supplemental Materials), with participants perceiving the control sound as significantly quieter behind the body as compared to the front. In light of the differences in perceived loudness, we conducted a third experiment, replicating the methods of Experiment 2, in which we took into account both perceived loudness and threat ratings. By taking both variables into account, we could precisely determine the differences between participants' estimates of TTC for multiple sounds approaching from the front or rear.

Experiment 3

Experiment 3 used the same TTC paradigm as Experiments 1 and 2, but it included stimuli that were matched for perceived loudness, across both direction (i.e., front, rear) and stimulus categories (i.e., threatening, nonthreatening). In addition, we sought to examine whether our effects generalized across different types of threatening and nonthreatening stimuli. Experiment 2 included a single threatening stimulus produced by an artifact (i.e., a car) with little evolutionary relevance. Previous work examining the effect of threat on estimates of visual TTC utilized images of evolutionarily threatening animals (i.e., snakes, spiders), perhaps making them more perceptually salient (Vagnoni et al., 2012). Experiment 3 included sounds produced by both a threatening animal (i.e., a bee buzzing) and a nonthreatening animal (i.e., an owl call) as well to ensure generalizability of our findings across stimulus types.

Methods

Participants

Fifty-one undergraduate students (40 female) between 18 and 21 years of age participated for research credit. All participants had normal or corrected to normal vision, and all reported having normal hearing. This sample size was determined with G*Power statistical software (Faul et al., 2007), anticipating effect sizes similar to those found in Experiment 1.

Apparatus and Stimuli

Auditory TTC task. As in Experiments 1 and 2, each participant sat between two Yamaha HS5 Studio Speakers placed exactly 1 m in front of and behind him or her. Participants again responded to sounds using a keyboard placed atop a small mobile desk.

The current experiment utilized a new set of threatening and nonthreatening sounds that included sounds produced both by a human-made artifact (i.e., a car) and biological sources (i.e., animals). Specifically, the threatening sounds included a car horn (used in Experiments 1 & 2) and a bee buzzing, and the nonthreatening sounds included a new low-pass filtered version of the car horn (control sound) and an eastern screech owl (*Megascops asio*) call. A separate group of 22 participants (see Supplemental Materials) verified that the threatening sounds (i.e., car horn, bee buzzing) were indeed perceived as significantly more threatening than the nonthreatening sounds (i.e., control sound, eastern screech owl) and that they were matched for perceived loudness in front and rear presentations (see Supplemental materials). Though these new sounds were balanced for front and rear loudness perception, they were not matched for perceived loudness across categories. An additional 30 participants were recruited to select versions of the sounds that were matched for perceived loudness across categories. We created multiple versions of each sound ranging in intensity (-2 dB to +2 dB relative to the original 60 dB sound file), and participants rated each sound on its perceived loudness. We then selected the sounds from each stimulus category that were rated as equally loud to be used in the experiment. A Bayesian repeated measures ANOVA analyzing participants' ratings of perceived loudness for each sound found strong evidence for the null hypothesis, indicating that the sounds we selected did not differ in their perceived loudness, BF_{01} = 15.78. Given that the sounds were matched for perceived loudness, they now differed in their maximum absolute loudness. As such, when creating the looming sound clips, the sounds now increased logarithmically from 0 dB to 58 dB for the car horn, 0 dB to 57 dB for the bee buzzing, 0 dB to 57 dB for the control sound, and 0 dB to 63 dB for the eastern screech owl.

Sounds were presented in four blocks of 50 trials each. Trials were blocked by sound, with order of presentation alternating between threatening and nonthreatening trials. Prior to beginning the task, participants were presented with example sounds (one from each direction) and reminded that the sounds’ cessation represented the point at which it made contact with the body. However, as in Experiment 2, participants received no feedback on their performance during test trials.

Psychological measure of trait anxiety. The STAI-T (Speilberger et al., 1983) was again used to measure trait anxiety. Following the procedure of Experiment 2, participants were randomly assigned to either complete the auditory TTC task or STAI-T first.

Physical measures. Measurements of participants arm length and height were collected to calculate arm length as a proportion. These measurements were again taken immediately prior to the completion of the STAI-T.

Procedure

The instructions for the car horn and the control sound were identical to those used in Experiment 2. For the bee buzzing sound, participants were asked to imagine that a bee was flying directly towards them on a direct collision course (from the front or rear) and informed that it would sting them if it made contact. For the eastern screech owl call, participants were asked to imagine that a tiny owl was flying directly towards them on a direct collision course (from the front or rear). They were assured that the owl posed no threat of bodily harm. For all sound types, participants were again tasked with using the response key to “stop” the object right before it made contact with their body (i.e., to let the object get as close to their body as possible before responding). Participants were informed that the objects could approach from both the rear and the front and that they would be told which the direction the object would come from.

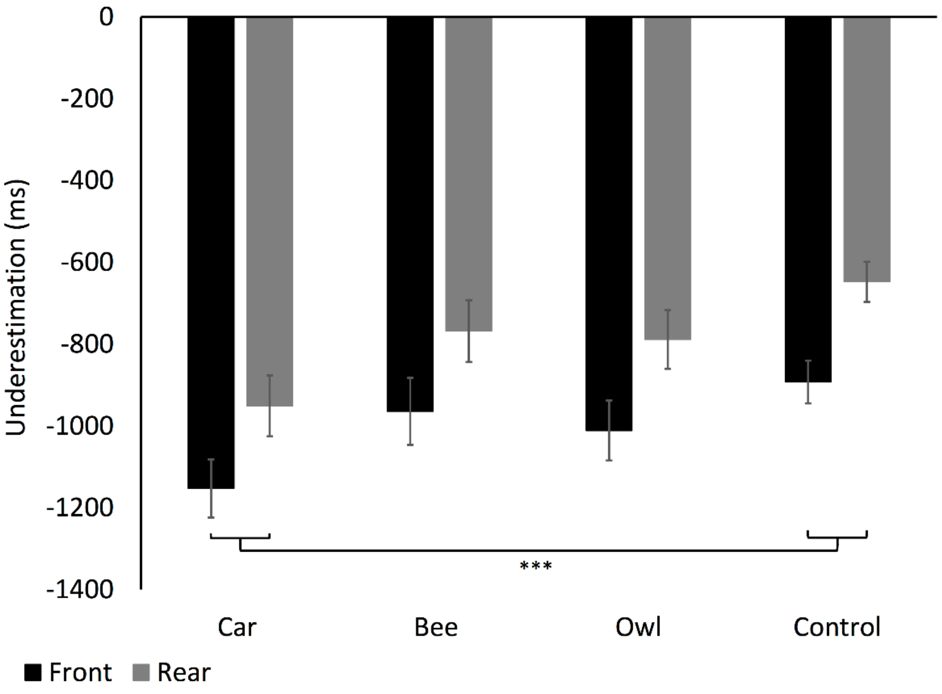
Results

Out of all trials, < 1% of trials were removed due to participant error (e.g., forgetting to respond). Of the remaining trials, 2% were identified as outliers (> 2.5 standard deviations from individual means) and subsequently removed.

Performance on TTC Task

As a preliminary analysis, we examined whether participants' TTC estimates scaled according to the actual TTCs, as would be expected if they performed the task according to the instructions. Participants' estimates of TTC were regressed on the actual TTC to compute the slope of the best-fitting line. One-sample *t*-tests revealed that the slope of participants responses differed significantly from zero for all sounds in both directions: car horn (Front: *M* = .68, *SD* = .13, *t*[50] = 38.06, *p* < .001, *d* = 5.33; Rear: *M* = .70, *SD* = .13, *t*[50] = 38.52, *p* < .001, *d* = 5.40), bee buzzing (Front: *M* = .73, *SD* = .19, *t*[50] = 27.96, *p* < .001, *d* = 3.92; Rear: *M* = .78, *SD* = .19, *t*[50] = 30.21, *p* < .001, *d* = 4.23), eastern screech owl (Front: *M* = .66, *SD* = .13, *t*[50] = 37.28, *p* < .001, *d* = 5.22; Rear: *M* = .72, *SD* = .14, *t*[50] = 36.98, *p* < .001, *d* = 5.18), and control sound (Front: *M* = .65, *SD* = .12, *t*[50] = 37.30, *p* < .001, *d* = 5.22; Rear: *M* = .71, *SD* = .14, *t*[50] = 36.93, *p* < .001, *d* = 5.17). These results indicate that participants appropriately scaled their estimates of TTC in accordance with the actual TTC of the stimuli across all categories. Further analyses demonstrate that participants' performance had high internal consistency (Cronbach's Alpha = .88), again demonstrating that participants were able to reliably complete this task even without explicit feedback.

Front versus rear performance. We then conducted a 2 × 4 repeated measures ANOVA, with direction (front, rear) and sound type (car horn, bee buzzing, eastern screech owl, control sound) as independent variables and participants' mean responses (calculated as the mean difference between participants estimates of TTC and the actual TTC) as the dependent variable. This analysis yielded a significant main effect of direction, $F(1, 50) = 287.72$, $p < .001$, $\eta_p^2 = .85$, such that participants showed significantly greater underestimation for sounds that approached from the front ($M = -1005.40$ ms, $SD = 362.20$) compared to the rear ($M = -788.94$ ms, $SD = 346.19$): $M_{diff} = 216.43$ ms, $SE_{diff} = 12.76$, 95% CI (-242.05, -190.80). There was also a significant main effect of sound type, $F(3, 150) = 4.51$, $p = .005$, $\eta_p^2 = .08$, with pairwise comparisons (Bonferonni corrected) revealing significantly greater underestimation for the car horn ($M = -1051.93$ ms, $SD = 514.91$) as compared to the control sound ($M = -770.33$ ms, $SD = 346.38$): $M_{diff} = 281.60$ ms, $SE_{diff} = 58.97$, 95% CI (-443.60, -119.61), $t(50) = 4.78$, $p = .001$, $d = .64$ (see Figure 4), but no other significant effects (all p's > .35). There was no



***$p = .001$

Figure 4. Participants' mean underestimation for each condition from the front and rear. Error bars are ± SEM.

significant interaction between these factors, $F(3, 150) = .87$, $p = .457$, $\eta_p^2 = .02$. Overall, participants consistently underestimated the TTC for all stimulus types for both directions (all *t*'s > 10.16, all *p*'s < .001).

Trait Anxiety

Following Experiments 1 and 2, we conducted correlation analyses to test for a relation between trait anxiety and participants' estimates of TTC on the auditory TTC task. These analyses revealed no significant relation between anxiety and performance whether examining performance when collapsing across direction (car horn: *r*[49] = .11, *p* = .464; bee buzzing: *r*[49] = -.24, *p* = .090; control sound: *r*[49] = -.05, *p* = .710; eastern screech owl: *r*[49] = -.19, *p* = .187) or examining difference scores (mean rear estimate – mean front estimate) (car horn: *r*[49] = .06, *p* = .700; bee buzzing: *r*[49] = .13, *p* = .366; control sound: *r*[49] = -.12, *p* = .410; eastern screech owl: *r*[49] = .23, *p* = .108). These latter results again fail to replicate the findings of Experiment 1, which utilized only the car horn, and indicates that such relations do not generalize to other sounds.

Arm Length

Again, following Experiments 1 and 2, we conducted correlation analyses to test for a relation between arm length as a proportion of height and participants' estimates of TTC on the auditory TTC task. These analyses revealed no significant relation between arm length and performance when examining performance when collapsing across direction (car horn: *r*[49] = .05, *p* = .721; bee buzzing: *r*[49] = .15, *p* = .407; control sound: *r*[49] = .08, *p* = .575; eastern screech owl: *r*[49] = -.04, *p* = .809). Likewise, correlation analyses revealed no significant relation when examining difference scores (mean rear estimate – mean front estimate) (car horn: *r*[49] = -.18, *p* = .218; control sound: *r*[49] = .15, *p* = .294; eastern screech owl: *r*[49] = -.06, *p* = .671), again failing to replicate the findings from Experiment 1 in relation to the car horn. However, here there was a significant relation in the case of the bee buzzing condition (*r*[49] = -.347, *p* = .012), such that participants with longer arms were more likely to underestimate more behind the body as compared to participants with shorter arms.

Discussion

In summary, participants consistently underestimated sounds approaching from the front compared to sounds approaching from the rear for both threatening and nonthreatening approaching objects. Moreover, we found evidence that threat produced an expansion of peripersonal space, with participants significantly underestimating for the threatening car horn relative to the nonthreatening control sound, which, crucially, were matched for perceived loudness such that this finding cannot be explained simply by differences in low-level properties. When examining across stimulus categories and direction (front vs. back), we found consistent underestimation for the front as compared to the rear for *all* stimulus types. These findings suggest that peripersonal space representations are larger in front compared to rear across both threatening and nonthreatening stimuli.

Though there was a significant effect for threat when comparing the threatening car horn to the nonthreatening, low-pass filtered car horn (control sound), which possessed similar low-level properties, there were no other significant differences for the other sounds. Likewise, we again failed to find a significant relation between either anxiety or arm length and performance in any condition, except for a significant negative relation between arm length and performance in the bee buzzing condition. This finding mirrors that of Experiment 1, which reported a similar relation for performance relative to an approaching car sound. Though interesting and perhaps suggestive of a relation between arm length and performance on this task, we note that this correlation was not predicted to occur for only the bee buzzing stimulus. Furthermore, we did not correct for multiple comparisons. As such, it requires replication.

Consistent Underestimation for Front Compared to Rear Trials

These findings indicate that participants consistently underestimated for approaching sounds in the front of the body as compared to those coming from the rear. And crucially, this difference cannot be explained by differences in perceived loudness, as stimuli were judged as equally loud in front of and behind the body (see Supplemental Materials). One interpretation of these findings is that they reflect an asymmetry in peripersonal space representations such that there is a larger default representation of space in front of the body as compared to the rear of the body. This asymmetry could be a result of the fact that the majority of human perception-action capabilities are frontward-oriented. As such, greater attentional resources are allocated to the front of the body as compared to the rear of the body, leading participants to underestimate for the front relative to the rear across both threatening and nonthreatening contexts. This interpretation is bolstered by work examining the processing of multisensory stimuli under non-defensive contexts, which, as discussed above, reports differences in how this information is integrated in front of the body as compared to the rear (e.g., Gillmeister & Forster, 2012; Kóbor et al., 2006; Zampini et al., 2007; Occelli et al., 2011). Likewise, it is supported by the work of Bufacchi and colleagues (2016) who report larger frontal peripersonal space representations relative to the rear under a defensive context.

Is it possible, however, that participants' estimates in these experiments reflect a behavioral strategy completed unrelated to peripersonal space? For instance, prior research has shown that humans are capable of estimating the arrival time of looming auditory stimuli based on intensity alone (Bach et al., 2009; Bach et al., 2008), such that participants could simply respond to stimuli once they achieve a certain intensity. Such a strategy cannot account for the results in the current experiment given that sounds were matched for perceived loudness both in front of and behind the body. In other words, on such a strategy participants would have perceived the intensity as increasing at equal rates for both directions, resulting in symmetrical underestimation. Instead, we found asymmetrical performance, suggesting that these results are due to differing underlying spatial representations for the front as compared to the rear of the body.

Above, it was suggested that threatening contexts may result in a redistribution of attentional resources, such that peripersonal space is represented differently around the body under threatening and nonthreatening contexts. Indeed, Experiment 2 found evidence for this possibility, demonstrating symmetrical underestimation under threatening conditions, suggesting that attention may be allocated equally at all points around the body in this context. However, here we show that, in response to both threatening (i.e., car horn, bee buzzing) and nonthreatening (i.e., control sound, eastern screech owl) sounds, there was consistent underestimation in the front relative to the back, suggesting a larger frontal representation of space relative to the rear. What might account for the difference in performance for the car sound from Experiment 2 relative to

Experiment 3? One possibility is that the car horn used in Experiment 3 reached a lower maximum loudness in Experiment 3 (58 dB) than in Experiment 2 (65 dB). As such, the car in Experiment 2 would appear to approach closer to the body, perhaps making it difficult to discern differences in peripersonal space for the front as compared to the rear. Future studies should investigate this possibility through including sounds with different maximum loudness ratings.

An Effect of Threat?

The fact that participants consistently underestimated the threatening car horn as compared to the nonthreatening, low-pass filtered version of the horn (control sound) suggests that they were sensitive to the threat value of the car stimulus. In other words, they underestimated for the more threatening stimulus. However, though participants displayed similar patterns of performance (i.e., greater underestimation for the front as compared to the rear) for all stimulus types, we found no difference between the threatening bee buzzing sound and the nonthreatening eastern screech owl call. This finding is perhaps surprising given that the bee buzzing was rated as significantly more threatening than all other stimuli (see Supplemental Materials). As such, one might have expected greatest underestimation for this sound. However, whereas the control sound maintained many of the low-level properties of the car horn, the bee buzzing sound and eastern screech owl call were not. Thus, these differences could have masked the effect of threat. Furthermore, another possibility is that, though rated as less threatening, a quickly approaching car may represent a less avoidable threat than a quickly approaching bee. That is, one may more easily escape from or swat away a threatening bee than a threatening car. Future studies will need to take these possibilities into account when choosing and designing auditory stimuli for looming tasks.

General Discussion

The current paper sheds light on the nature of peripersonal space representations surrounding the body as related to threatening and nonthreatening contexts. We find that, when sounds were matched for perceived loudness, participants consistently underestimated the TTC of approaching stimuli from the front as compared to the rear and that participants underestimated more for threatening sounds as compared to nonthreatening sounds. We argue that these findings are reflective of larger peripersonal space representations in front of the body and larger peripersonal space representations in response to threatening stimuli. These findings are consistent with previous work which reports asymmetries in peripersonal space representations (Bufacchi et al., 2016) as well as larger peripersonal space representations in response to threats (de Haan et al., 2016; Taffou & Viaud-Delmon, 2014). Furthermore, we suggest that the current findings dovetail with work examining the integration of multisensory stimuli, which reports asymmetries in how such stimuli are processed in the front and rear (Gillmeister & Forster, 2012; Kóbor et al., 2006; Zampini, Torresan, Spence, & Murray, 2007; Occelli et al., 2011).

Peripersonal Space around the Body

Why might peripersonal space be represented as larger in front of the body as compared to the rear? One possibility is that given that the majority of human perception-action capabilities are frontward-oriented. It is adaptive to allocate a greater amount of attentional resources in this direction. Representing space in such a way could be adaptive under both threatening and nonthreatening circumstances in that doing so would allow for more precise control of motor behaviors in relation to targets.

Recently, de Vignemont and Iannetti (2015) proposed that the non-defensive and defensive functions of peripersonal space are subsumed by two separate representational systems. Specifically, they argue that non-defensive behaviors are largely organized *toward* a target object that is the intended recipient of an action, whereas defensive actions are geared *away from* a target, such as ducking out of the way of a projectile or avoiding obstacles (Bracha, 2004; Dosey & Meisels, 1969; Graziano & Cooke, 2006). These behaviors might necessitate different levels of motor and sensory precision. For instance, grasping an object with the hand requires slower, precise sensorimotor guidance, whereas protective actions may require rapid, less fine-grained, responses to keep a threat away from the body (Liang, Mouraux, & Iannetti, 2013). Such distinctions could result in differences in how attention is allocated around the body under different defensive contexts, producing differently shaped representations of peripersonal space and necessitating separate representational systems. However, the current study suggests that the defensive and non-defensive functions of peripersonal space rely on similarly shaped representations of space, with both contexts producing a larger frontal representation of space as compared to the rear, an effect clearly observed when controlling for perceived loudness (Experiment 3). Our findings suggest that, under both threatening and nonthreatening circumstances, humans maintain larger peripersonal space representations in the front, which would allow for precise control of perception-action capabilities. This finding suggests that such motor precision may be adaptive under both circumstances. An alternative possibility, though, is that because we utilized looming stimuli, which may be inherently threatening, we only examined the defensive function of peripersonal space. As such, our results with even nonthreatening stimuli may not reflect the non-defensive function of peripersonal space. However, we have some evidence that performance on our task was modulated by the threat value of the stimuli (i.e., car vs. control), as was the case in previous experiments using visual looming stimuli, where participants underestimated more for threatening stimuli relative to nonthreatening stimuli (e.g., snakes vs. rabbits, Vagnoni et al., 2012). Thus, these findings suggest that the defensive and non-defensive functions of peripersonal space were likely differentially primed.

Given that sighted humans primarily rely on visual input, an additional concern is that an auditory task might not be an ecologically valid test of human spatial perception. As such, a visual task may be more appropriate. Because visual information is restricted to the front of the body, though, an exclusively visual task would make it impossible to examine space behind the body. In addition, there is a large body of evidence suggesting that humans and non-human primates are sensitive to the location of complex sounds presented behind the body under both defensive (e.g., Cooke & Graziano, 2003) and non-defensive (e.g., Occelli, O'Brien, Spence, & Zampini, 2010) contexts. Indeed, the ability to identify and locate objects in space by use of auditory information alone is critical to guiding perception-action capabilities when vision is obscured due to an obstacle, the object being located behind the body, or other loss of visual information (e.g., blindness). As such, the purely auditory task described in the current studies would provide an ecologically valid means of examining peripersonal space representations.

Larger Peripersonal Space Representations in Response to Threatening Targets

This work also contributes to a growing body of literature showing that humans consistently demonstrate expanded peripersonal space representations in response to threatening stimuli as compared to nonthreatening stimuli (de Haan et al., 2016; Taffou & Viaud-Delmon, 2014). Such expansion could prove adaptive by leading humans and other organisms to maintain a larger margin of safety between themselves and potentially deadly threats (Graziano & Cooke, 2006; Sambo & Iannetti, 2013) and, in turn, may enable earlier defensive responses (i.e., fight, flight). Given that we controlled for perceived loudness in Experiment 3, this finding cannot be accounted for by differences in this low-level property. As discussed above, participants maintained a larger peripersonal space representation in front of the body as compared to the rear throughout both defensive and non-defensive conditions. This finding suggests that peripersonal space is oriented so as to provide precise guidance of motor actions under both threatening and nonthreatening circumstances. Such precision may be adaptive in enabling proper flight responses (e.g., running directly away from a threat) as well as targeted attacks (e.g., hitting a target in vulnerable areas).

Trait Anxiety and Peripersonal Space

Though we found some evidence for a relation between trait anxiety and peripersonal space in our first experiment, we failed to replicate this finding in our subsequent experiments. The lack of a consistent relation between individual differences in anxiety and peripersonal space representations would seem to contrast with previous work in which greater trait anxiety was associated with larger peripersonal space representations as related to the face (Sambo & Iannetti, 2013). One possible explanation for the different findings is that the relation to trait anxiety may depend on which body part is primed. For instance, given that the face includes both highly pain sensitive (e.g., the lips) and soft, easily damaged tissues (e.g., the eyes), humans may be particularly sensitive to threats approaching this region. As such, trait anxiety may amplify this sensitivity such that performance on tasks priming facial peripersonal space is associated with trait anxiety. On the other hand, our task involves stimuli approaching the body as a whole and, though we did not directly test which body part was primed in the current study, may prime peripersonal space representations associated with the trunk. Given that this region contains less pain sensitive and less easily damaged tissue, humans may be less sensitive to stimuli approaching this region

Arm Length and Peripersonal Space

A similar explanation might account for why, though we found a relation between arm length and peripersonal space in Experiment 1, this effect largely failed to replicate in Experiments 2 and 3. Though previous work reports a relation between arm length and peripersonal space, with longer arms predicting larger peripersonal space representations, this study relied on the line bisection task (Longo & Lourenco, 2006), which may be limited to measuring peripersonal space as related to the arm. If the task used in the current study primes peripersonal space as related to the trunk, it may be that representations in this region are not sensitive to arm length. As indicated above, though, we did not directly test which body part was primed by the current task. Thus, this issue remains an open question for future research.

Conclusions

In conclusion, this study establishes a novel paradigm to examine peripersonal space representations around the body. When stimuli are controlled for low-level properties and perceived loudness, this auditory looming task allows researchers to examine spatial representations at all points around the body. Our findings revealed that participants consistently underestimated stimuli approaching from the front compared with those approaching from the rear, suggestive of larger peripersonal spaces in front of the body. Furthermore, we found that peripersonal space representations were modulated by threat such that more threatening stimuli were associated with larger peripersonal spaces. This work paves the way for examining how humans behave and survive in a 3D environment, shedding light on the undergirding cognitive and neural mechanisms involved in representing peripersonal space.

Concluding Thoughts

As described in this dissertation, research has long documented both neural and cognitive distinctions between the space near the body, known as peripersonal space, and the space farther away, known as extrapersonal space (e.g., Brain, 1941; Hall, 1968; Previc, 1998; Rizzolatti et al., 1981). These representations provide a multimodal (e.g., Canzoneri et al., 2012; Graziano & Gross, 1995), “body-part-centered” (e.g., Graziano & Gross, 1998; Lourenco & Longo, 2009; Sambo et al., 2012) mapping of the space surrounding the body that is used for guiding perception-action processes relative to the objects close to the body. How humans and other primates represent the space around them appears to respond flexibly to situational demands, expanding when given a tool that extends one’s reach (e.g., Canzoneri, Ubalidi, et al., 2013; Iriki et al., 1996; Longo &

Lourenco, 2006) or when approached by a threat that needs to be kept far from the body (e.g., de Haan et al., 2016; Taffou & Viaud-Delmon, 2014) as well as contracting when experiencing motor restriction (Lourenco & Longo, 2009) or encountering obstacles (Morgado et al., 2013). Such representations appear necessary not only for guiding non-defensive behaviors relative to innocuous objects (e.g., coffee cups) but also to potentially deadly threats (e.g., angry tigers) (de Vignemont & Iannetti, 2015).

The current dissertation contributes to this literature in two primary ways. The first contribution is to synthesize both historical and current findings regarding the nature of peripersonal space while highlighting gaps, notably unanswered questions about the relation between peripersonal space and personal space as well as the body schema, individual differences in the flexibility of peripersonal space representations, and how peripersonal space is represented around the body. In this vein, the second major contribution of this dissertation is to provide empirical insight into peripersonal space representations in front of as compared to behind the body in response to both threatening and nonthreatening stimuli. The findings described herein depict larger representations of peripersonal space in front of the body relative to the rear in relation to both threatening and nonthreatening stimuli, suggesting that the defensive and non-defensive functions of peripersonal space may rely on a single representational system. Furthermore, these studies provide further evidence of the expansion of peripersonal space representations in reaction to threatening stimuli. As such, this dissertation provides a roadmap for future research as well as a novel paradigm with which to examine peripersonal space.

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Supplemental Experiments

Supplemental Experiment 1

The goal of this experiment was to examine whether the stimuli used in Experiment 2 of the main manuscript differed in perceived loudness. Participants were asked to rate how loud the front and rear versions of the threatening (i.e., car horn) and nonthreatening (i.e., low-pass filtered car horn) sounds appeared to them.

Methods

Participants

Thirteen undergraduate students (10 female) between the ages of 18 and 21 years participated for course credit. All participants reported having normal hearing.

Apparatus and Stimuli

Auditory stimuli. Stimuli in this experiment were 1 s sound clips extracted from the end of the car horn and low-pass filtered car horn (control sound) used in Experiment 2. This manipulation ensured that the sound clips did not differ in length and that all participants were judging the loudness of each sound at its loudest point. Given time constraints, the 5000 ms sound file from the TTC used in Experiment 2 was excluded. Files were created for all other TTCs (3000 ms, 4000 ms, 6000 ms, and 7000 ms). This produced four different sound files from each direction for each sound type, resulting in 16 sound files (2 Directions × 2 Sounds × 4 Speeds). All sounds were recorded as having an absolute loudness of 65 dB, using a decibel meter (RadioShack).

Perceived loudness ratings. Perceived loudness was rated on a 0 to 100 scale. Participants were told that 0 represented silence and that 100 was equivalent to a 75 dB, 400 Hz tone that was played as an example for them prior to the rating task (10 dB louder than the maximum loudness of the looming stimuli). These guidelines were used to ensure that participants' responses were anchored to the same reference point and followed the procedure used by Siegel and Steffanucci (2011).

Procedure

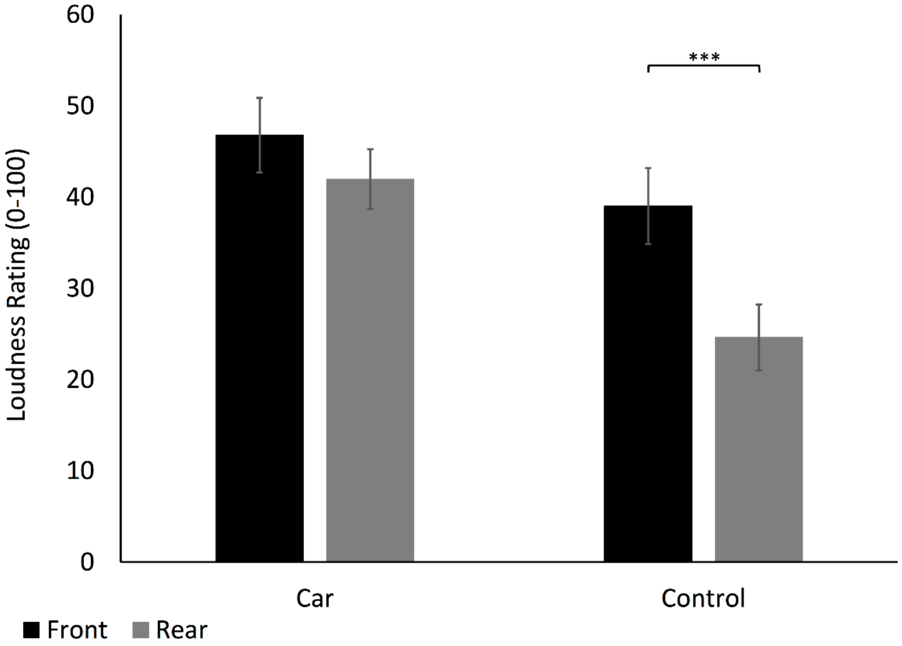
Participants sat between the two speakers used in Experiments 1 and 2 of the main manuscript, which were placed exactly 1 m in front of and behind participants. Participants were seated in an office chair with a small desk placed in front of them for writing. They were asked to keep their back firmly against the back of the chair throughout the task to ensure that they did not lean forward and change their distance to the speakers. The experimenter monitored their posture throughout the trials to ensure compliance and asked participants to readjust their posture if they deviated from their upright position.

Prior to beginning the task, the participant was told that they would hear sounds from either in front of or behind the body. Once the participant indicated that they were ready, the experimenter played the sound assigned to that trial, and the participant rated the sound. If necessary, the participant could request to hear the sound again so that they could be sure of their rating. Each sound was presented once (randomized order) for a total of 16 trials.

Results

To examine whether perceived loudness differed by sound type and sound direction, we conducted a 2 × 2 repeated measures ANOVA, with sound type (car horn, control sound) and direction (front, rear) as independent variables and participants' mean ratings of perceived loudness as the dependent variable. This analysis yielded significant main effects of sound type, $F(1, 12) = 16.58$, $p = .002$, $\eta_p^2 = .52$, and direction, $F(1, 12) =$

40.66, $p < .001$, $\eta_p^2 = .77$, as well as a significant interaction between these two factors, $F(1,12) = 12.21$, $p = .004$, $\eta_p^2 = .50$. Pairwise comparisons (Bonferonni corrected) revealed that the control sound was perceived as significantly louder in the front than the rear, $M_{diff} = 14.50$, $SE_{diff} = 2.04$, 95% CI (9.94, 18.85), $t(12) = 7.04$, $p < .001$, $d = 1.16$, but there was no significant difference in perceived loudness for front and rear for the car horn, $M_{diff} = 4.83$, $SE_{diff} = 2.03$, 95% CI (0.41, 9.25), $t(12) = 2.38$, $p = .139$, $d = .32$ (see Supplemental Figure 1). In addition, the car horn was perceived as louder than the control sound for both the front, $M_{diff} = 7.78$, $SE_{diff} = 2.57$, 95% CI (2.18, 13.38), $t(12) = 3.03$, $p = .043$, $d = .55$, and the rear, $M_{diff} = 17.35$, $SE_{diff} = 4.02$, 95% CI (8.58, 26.11), $t(12) = 4.31$, $p = .004$, $d = 1.30$, but this effect was exaggerated in the rear.



***$p < .001$

Supplemental Figure 1. Participants' mean ratings of perceived loudness for the car horn and control sound from each direction. Error bars are ± SEM.

Discussion

The results of this first supplemental experiment demonstrate that with stimuli identical in absolute loudness (i.e., 65 dB), the car horn was perceived as equally loud in front of the body as compared to the rear. However, the control sound, a low pass filtered version of the car horn, was perceived as louder in the front than the rear. Furthermore, the car horn sound was perceived as louder than the control sound, an effect that was exaggerated behind the body. One possible reason for these effects could be due to differences in the threat-level presented by each stimulus. The control sound, being less threatening, could prime a non-defensive representation of peripersonal space, with a larger representation in front of the body. As such, a sound presented in front of the body would be perceived as closer, leading participants to judge it to be louder than a sound presented in the rear. Similarly, the threatening car sound could prime the defensive function of peripersonal space, leading to a redistribution of attention around the body, making the sounds appear equally as close in front of and behind the body. As such, participants would judge the sounds as equally as loud for both directions.

However, an alternative explanation is that participants' performance was a reflection of the low-level property of loudness, which was unrelated to the threat value of the stimuli or participants' peripersonal space representations. As such, participants' decreased underestimation for the rear in the nonthreatening condition of Experiment 2 may simply be due to the sound appearing quieter, thus leading them to allow the sound to approach "closer" to the body. Given this possibility, we thus ensured that perceived loudness was matched for all stimuli in Experiment 3.

Supplemental Experiment 2

The goal of Supplement Experiment 2 was to identify candidates for new auditory looming stimuli to be used in Experiment 3 of the main manuscript that were equivalent in perceived loudness, across both direction (i.e., front, rear) and stimulus categories (i.e., threatening, nonthreatening), and included both biologically produced sounds and sounds produced by artifacts.

Methods

Participants

Twenty-two undergraduate students (16 female) between the ages of 18 and 21 years participated for course credit. All reported having normal hearing.

Apparatus and Stimuli

Auditory stimuli. To identify target sounds, we first developed lists of threatening and nonthreatening sounds from both biological sources (i.e., animals) and artifacts. We then searched for available online auditory recordings, either freely available through sites such as YouTube (www.youtube.com) or for purchase through Soundsnap (www.soundsnap.com). Sounds were selected based on their clarity (e.g., including minimal background noise) and the ease with which they could be continuously looped, a prerequisite for creating auditory looming files of varying lengths.

This search yielded 10 candidate sounds, including 7 from biological sources (a growling tiger, a bee buzzing, a rattlesnake, a snake hissing, a humming bird, an eastern screech owl [*Megascops asio*], and a cow mooing), and three from artifacts (a car horn [from Experiments 1 and 2], a semi-truck horn, and a cruise ship horn). In addition, Taffou and Viaud-Delmon (2014) generously agreed to provide the sounds from their study, examining the effect of threat on peripersonal space (i.e., dog growling, a sheep bleating). We also included four manufactured stimuli from artificial sources. We utilized the low-pass filtered version of the car horn (control sound 1) from Experiment 2, which preserved frequencies from 200 to 400 Hz, and created two new low-pass filtered versions of the car horn using new parameters: one preserving frequencies from 300 to 700 Hz with a smoothing factor of 75 (control sound 2) and the other preserving frequencies of 500 to 850 Hz with a smoothing factor of 100 (control sound 3; Praat; Boersma, 2001). The two new control sounds included a wider range of frequencies to increase the chance that they would be perceived as equally loud in front of as compared to behind the body. Importantly, pilot testing revealed that participants still could not recognize these sounds as car horns, despite including a wider range of frequencies. Finally, we created a 470 Hz tone using Adobe Audition 3.0. All sounds were manipulated to be 3 s in length, and they were adjusted such that each was 60 dB. In total, we tested 16 candidate sounds.

Threat Rating. Participants rated each sound on a scale from 1 to 7, with 1 representing “not at all threatening” and 7 representing “as threatening as possible.”

Perceived Loudness Ratings. Participants rated sounds on perceived loudness from 0 to 100, following the procedure from Supplement Experiment 1.

Procedure

Participants began this experiment by completing the threat rating task. They sat at a desktop computer and listened to each of the sounds over headphones. For each sound, a label would appear describing the sound, and participants could play the target sound by pressing a play button on screen. Participants then provided their rating of how threatening they perceived each sound. Sounds were presented in a random order, and participants could listen to each sound as many times as they liked before continuing. Sounds were presented in a random order and each sound was presented twice, resulting in 32 total trials, which were averaged for a mean rating of each sound.

After rating each sound on perceived threat, participants then rated each sound on perceived loudness, following the procedure from Supplemental Experiment 1. However, rather than rating 1 s clips of each sound, participants heard the full 3 s clip of each sound, which was done to provide participants adequate time to judge the loudness of the sound. If necessary, participants could request to repeat the sound so that they were confident in their rating. Sounds were presented in a random order, and each sound was presented once from each direction, resulting in 32 total trials.

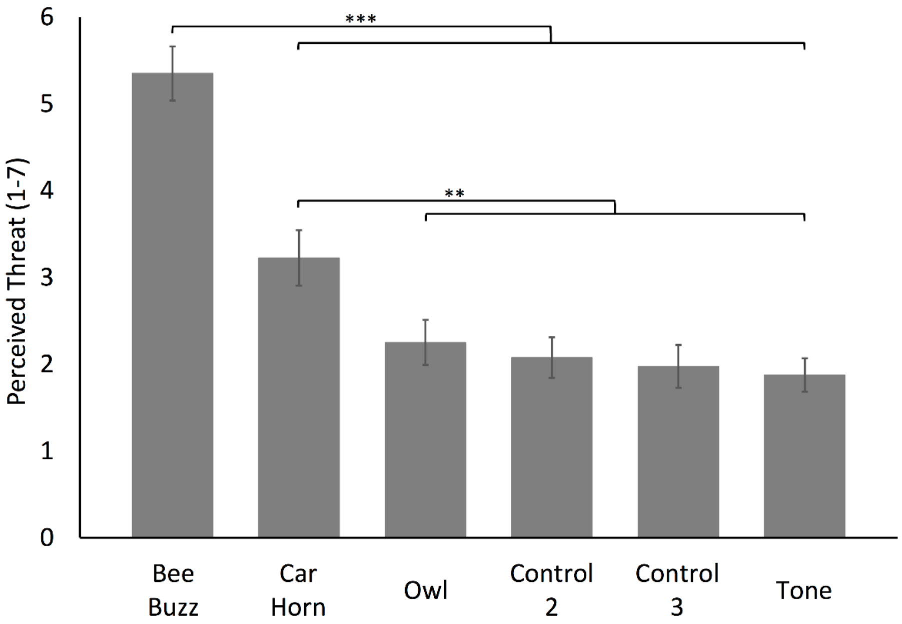
Results

The first step of our analyses was to examine which sounds differed in front and rear loudness perception (i.e., were perceived as louder from one direction or the other). We conducted a 2 × 16 repeated measures ANOVA with direction (front, rear) and sound type (growling tiger, bee buzz, rattlesnake, snake hissing, humming bird, eastern screech owl, cow mooing, car horn, semi-truck horn, cruise ship horn, dog growling, sheep bleating, control sound 1, control sound 2, control sound 3, 470 Hz tone) as independent variables, and participants' ratings of perceived loudness as the dependent variable. This analysis revealed significant main effects of direction, $F(1, 19) = 96.66$, $p < .001$, $\eta_p^2 = .84$, and sound type, $F(15, 285) = 16.36$, $p < .001$, $\eta_p^2 = .46$, as well as a significant interaction between these two factors, $F(15, 285) = 6.23$, $p < .001$, $\eta_p^2 = .25$. Pairwise comparisons revealed that the tiger, dog, hummingbird, snake hissing, rattlesnake, sheep, cruise ship horn, semi-truck horn, and control sound 1 all differed in perceived loudness for the front and rear such that front sound was perceived as significantly louder than the rear sound (see Supplemental Table 1). These sounds were removed from subsequent analyses. Of the remaining sounds, the cow moo was removed because a number of participants remarked that it did not sound like a cow. This left six sound files for analysis: the bee buzzing, car horn, eastern screech owl, control sound 2, control sound 3, and the artificial 470 Hz tone.

Stimulus	**Mean Difference (*SD*)**	***t*-value**
Growling Tiger	10.00 (15.04)	3.12**
Growling Dog	14.10 (21.97)	3.01**
Bee Buzzing	7.27 (16.95)	2.01
Rattlesnake	-26.72 (19.11)	-6.45***
Snake Hissing	14.18 (20.28)	3.28**
Humming Bird	14.68 (21.03)	3.28**
Screech Owl	7.96 (20.16)	1.85
Cow Mooing	2.55 (12.62)	0.95
Sheep Bleating	17.77 (17.20)	4.85***
Car Horn	-2.05 (12.79)	-0.75
Semi-Truck Horn	8.73 (11.63)	3.52**
Cruise Ship Horn	7.82 (17.03)	2.15*
Control Sound 1	35.91 (17.70)	9.51***
Control Sound 2	6.86 (22.39)	1.44
Control Sound 3	-6.59 (27.92)	-1.11
470 Hz tone	0.32 (18.40)	0.08

* $p < .05$
** $p < .01$
***$p < .001$
Supplemental Table 1. Mean difference of perceived loudness (front – rear) between front and rear sounds for each stimulus (*SD* in parentheses).

To examine how the remaining six sounds differed in their level of perceived threat, we conducted a one-way repeated measures ANOVA with sound type as the independent variable and participants' threat ratings as the dependent variable. Two participants failed to complete this section of the experiment. This analysis revealed a significant effect of sound type, $F(5, 95) = 31.89$, $p < .001$, $\eta_p^2 = .63$. Pairwise comparisons revealed that the bee buzzing was perceived as significantly more threatening than all other sounds (all p's < .001; d's = 1.04 – 1.97), and the car horn was perceived as more threatening than all remaining sounds (all p's < .01, d's = .65 – .92) (see Supplemental Figure 2). The remaining sounds (eastern screech owl, LP2, LP3, and artificial 470Hz tone) did not differ significantly in their ratings of perceived threat (all p's > .24).



***p* < .01
****p* < .001
Supplemental Figure 2. Participants' mean ratings of perceived threat for each stimulus. Error bars are ± SEM

Discussion

Based on these analyses, we selected the bee buzz as our threatening animal sound and the car horn as our threatening artifact-made sound. For our nonthreatening animal sound, we selected the eastern screech owl, and for our nonthreatening artifact-made sound, we chose control sound 2 (300 – 700 Hz, smoothing factor: 75). We decided against the 470 Hz tone given that it was completely artificial and shared no low-level properties associated with a real-world object. Control sound 2 was chosen over control sound 3 given that it preserved a wider range of frequencies from the original car horn sound and was still unrecognizable as such.