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Peripersonal space: why so last-second?

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Abstract

A vast range of neurophysiological, neuropsychological and behavioral results in monkeys and humans have shown that the immediate surroundings of the body, also known as peripersonal space (PPS), are processed in a unique way. Three roles have been ascribed to PPS mechanisms: to react to threats, to avoid obstacles, and to act on objects. However, in many circumstances, one does not wait for objects or agents to enter PPS to plan these behaviors. Typically, one has more chances to survive if one starts running away from the lion when one sees it in the distance than if it is a few steps away. PPS makes sense in shortsighted creatures but we are not such creatures. The crucial question is thus two-fold: (i) why are these adaptive processes triggered only at the last second, or even milliseconds? And (ii) what is their exact contribution, especially for defensive and navigational behaviors? Here we propose that PPS mechanisms correspond to a plan B, useful in unpredictable situations or when other anticipatory mechanisms have failed. Furthermore, we argue that there are energetic, cognitive and behavioral costs to PPS mechanisms, which explain why this plan B is triggered only at the last second.

The theoretical frame of embodied cognition has proposed that the body shapes our cognitive abilities. Over the years, it has been applied – with more or less success – to various cognitive domains, including high-level capacities such as social cognition, language, and mathematics. However, if there is one area in which there is clear evidence that the body plays an essential role, it is in the perceptual domain. More precisely, a vast range of neurophysiological, neuropsychological and behavioral results in monkeys and humans have shown that the relatively close surroundings of the body, also known as peripersonal space (PPS), are processed in a unique way and that the extent of PPS depends on one's bodily abilities (Vignemont et al., 2021a). These findings provide conclusive evidence that the way we hear and see the outside world can depend on our bodily location and capacities. What remains unclear, however, is why the world is processed in a special way only at such a relatively short distance from the body.

Three distinct roles have been ascribed to PPS mechanisms¹:

- A defensive role, to react to threats;
- A navigational role, to avoid obstacles;
- An appetitive role, to act on objects.

However, in many circumstances, one does not wait for objects or agents to enter PPS to plan these behaviors. In particular, one has more chances to survive if one starts running away from the lion when one sees it in the distance than if one can almost feel its breath on one's face. Even if the lion is still two meters away, it is most probably too late. Or consider navigation in a packed environment, such as a classroom full of tables and chairs. Graziano and Cooke (2006) claim that this requires the PPS neural network to monitor the proximity of objects but we are not like old-fashioned robots with only short-distance receptors that wait until they are next to

¹ Though it has been suggested that peri-personal space is related to the social notion of personal space (e.g. Dureux et al, 2021; Bogdanova et al, 2021), here we shall leave the social dimension aside.

the table to get around it. We plan ahead our path computing the easiest and possibly most straightforward trajectory when entering the room because we have visual access to all the potential obstacles long before they are next to us. PPS mechanisms would make most sense in shortsighted creatures but human beings are not such creatures. Although PPS mechanisms may not be exclusively about what is immediately next to our limbs, they are still primarily concerned by the region of space that is relatively close to us and when it comes to action, space is time, the time to prepare for us to act and the time for us to perform the movement. The crucial question is thus two-fold: (i) why are these adaptive processes triggered mostly at the last second? And (ii) what is their exact contribution, especially for defensive and navigational behaviors? In order to answer those questions, we shall consider not only the benefits of PPS processes, but also their potential energetic, cognitive and behavioral costs. It is only if we consider the trade-off of PPS mechanisms that we can explain *when* they are worth it, and, in turn, *why* their emergence has been selected through evolution. In this paper, we shall first briefly review the distinctive signatures associated with PPS. We shall then argue that many other mechanisms appear more advantageous for self-protection and propose that PPS mechanisms only correspond to a plan B, especially useful in unpredictable environments. We shall conclude by explaining why this plan B is triggered so late.

1. The signatures of PPS

Since its original discovery by Rizzolatti and his colleagues (1981ab), there has been a booming of research on PPS, especially these last ten years. Our objective here is not to provide an exhaustive review of this ever-expanding literature, this has been done elsewhere (e.g. Noël et al., 2021), but rather to give the gist of the most significant trademarks of PPS processing across multisensory, unisensory, sensorimotor, and attentional dimensions. Beforehand, it should be

noted that the experimental paradigms can vary to such an extent that one may wonder whether they all investigate the same notion of PPS (Vignemont et al., 2021b). PPS is classically described in spatial terms, typically as approximately less than 50 cm from the hand and 1 meter for the trunk, but this metric definition has been questioned (Graziano, 2018; Bufacchi and Iannetti, 2018). The precise distance from the body can vary depending on the body part, the sensory modality, the context, and the species. Notwithstanding these differences, one can still assume that PPS primarily emphasizes objects and events in the relative proximity of the body.

(i) Multisensory dimension

Since the earliest studies, the multisensory property of PPS has been emphasized as an almost necessary definitional aspect. While perception is overall a multisensory affair (Choi et al, 2023; Driver & Spence, 2000), PPS involves a peculiar kind of interaction that occurs between external senses (vision and audition) and somatosensory senses (touch and nociception). These multisensory effects are anchored to the location of the various parts of the body, as signaled by proprioception. Pioneering work in macaques first reported multisensory neurons that responded to tactile stimuli presented on the animal's body, as well as to visual stimuli mostly – though not exclusively – when located in its close vicinity (Hyvärinen and Poranen 1974; Rizzolatti et al, 1981ab; Colby et al., 1993; Graziano et al, 1994). This inspired research in right brain-damaged patients suffering from tactile extinction. It was found that their awareness of contralesional tactile stimuli was lost when tactile stimuli were concurrently applied ipsilesionally, but also when visual or auditory stimuli were concurrently presented ipsilesionally, provided they were within a distance of roughly 30 cm from their body (di Pellegrino et al, 1997; Farnè & Ladavas, 2022; Farnè et al, 2005). Since then, a variety of multisensory studies have explored PPS extent, boundaries and malleability. While cross-modal congruency paradigms mostly focus on the behavioral costs resulting from visual/auditory distracting stimuli over tactile targets (Spence et al., 2004; but see Holmes et al., 2004 and for

review, Macaluso & Maravita, 2010), dynamic multisensory stimulation paradigms emphasize the benefits in reporting tactile targets when visual/auditory stimuli are concurrently presented at closer compared to farther distances (e.g. Canzoneri et al, 2012; Clery et al., 2017). Strikingly, this type of multisensory interaction follows the body and its parts when they move in space. Perceptual effects generated by multisensory processing in PPS are literally anchored to the body, which constitutes the origin of PPS reference frame (di Pellegrino & Ladavas, 2015; Serino 2019; Zanini et al, 2021).

Evidence thus converges in showing that both the neural activity and the behavioral responses to visual/auditory stimuli are enhanced when occurring near the body (Brozzoli et al., 2011; Noël et al., 2019; Patané et al, 2020; Patané et al., 2019). Though part of PPS mechanisms may be hard-wired (Graziano, 2018), it has been suggested that these multisensory effects could also be explained in terms of association learning mechanism. Repeated exposure of visual/auditory stimuli soon to be followed by tactile stimuli may have tuned some neurons to be activated for both. On this view, these contingencies have been probabilistically generalized to an extended space around the body in which they have higher probability to occur (Bertoni et al., 2021; Straka et al., 2022).

(ii) Unisensory dimension

Whatever the effect on tactile processing (either cost or benefit), proximity may also modify visual processing *per se*. The so-called near-hand effect, for example, consists in a purely visual detection advantage for near-hand compared to far-hand stimulus locations, in the absence of multisensory stimulation (Reed et al., 2006; Reed and Park, 2021). Shape discrimination also benefits from proximity, as shown by Blini and colleagues (2018) (Figure 1). Participants had to decide as fast and accurately as possible which shape they saw, when presented close (within PPS) or far (outside PPS). Importantly, retinal size correction was applied because in everyday

life far objects appear as smaller. However, despite the fact that equating the retinal size of close and far shapes made the latter appears bigger, participants were faster in discriminating shapes appearing smaller but close to them. This advantage was also observed when the shapes were embedded within a 2D Ponzo illusion of depth, indicating that even illusory proximity could profoundly affect fundamental aspects of visual perception.

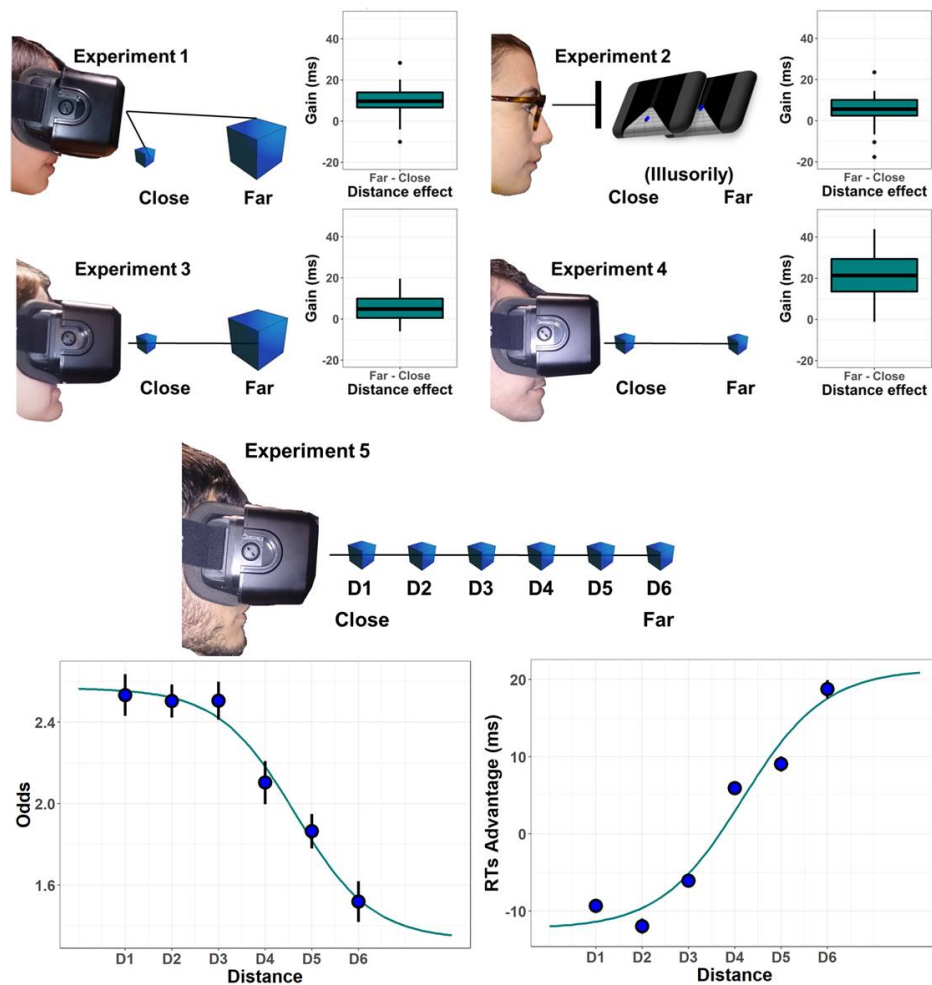


Figure 1. Results from the series of experiments (1 to 5) assessing unisensory visual shape discrimination near and far from the body (from Blini et al, 2018): box-and-whisker plots depict the mean facilitation in response time as a function of distance. Note the significant advantage for close over far shape presentation is present in a 3D virtual environment (Experiment 1), as well as in a 2D version (Experiment 2) when only monocular depth indices are available. The close advantage in shape discrimination is also present despite retinal correction makes far objects bigger (Experiment 3) and is further enhanced when shapes size respects the natural scaling with distance (Experiment 4). When shapes were presented at six different depths (In Experiment 5), sigmoidal curves for mean accuracy (left panel) and mean response time (RT) (right panel) predicted the advantage as a function of distance (from D1 for the closest to D6 for the farthest position). Error bars show standard errors of the mean. The y-axes

refer to the odds of providing a correct response (accuracy) and the relative RT advantage observed with respect to participant-specific mean performance. From Blini et al (2018).

Recent work extended these findings to social perception (Dureux et al, 2021; see for review Bogdanova et al, 2021). Participants had to discriminate male from female faces depicting happiness, anger or neutral emotions presented close or far (50 vs. 300 cm). They showed faster response times for close faces, with concurrent modulation of their physiological indexes (e.g., pupil dilation, heart rate variability). Overall, these findings clearly indicate that, notwithstanding their impact on somatosensory modalities, the processing of visual stimuli in the close vicinity to the observer's body is different at the unisensory level. In brief, close is better (Blini et al, 2021). However, one may wonder about the advantage for survival of such a perceptual boosting in one's bodily proximity.

(iii) Sensorimotor dimension

PPS processes take place at the crossroad between perceptual (visual, auditory, vestibular and somatosensory cortices) and motor dedicated regions, both in human and non-human primates. Neurons capable of PPS multisensory integration in monkeys have been identified in the ventral intraparietal region (VIP), parietal cortex 7b, as well as in the premotor cortex (PM) and the putamen. In these (and human-analog) sensorimotor regions, electrophysiological studies in non-human primates (Fogassi, et al., 1996; Colby et al., 1993; Graziano et al., 1994; Graziano & Gross, 1995; Rizzolatti et al., 1981ab) and neuroimaging work in healthy humans (Bremmer et al, 2001; Brozzoli et al, 2011; Serino et al., 2011) have identified populations of neurons exhibiting multisensory processing. Remarkably, the dual- and tri-modal neurons in these regions show tactile receptive fields on specific parts of the body and visual and/or auditory receptive fields spatially overlapping with and anchored to them. While their extension in depth can sometimes reach a few meters, they typically protrude only a few centimeters in the space around the body. They can thus provide detailed joint maps of the limbs and the space around

them to plan effective actions within a body-centered frame: the proximity of the hand to a visual object evokes responses from this PPS network, whereas moving the hand farther away reduces such an activity (Brozzoli et al., 2011).

Thus, both anatomically and functionally, these multisensory systems seem to be the ideal candidate to link perception and action (Brozzoli et al, 2012). When acting, one faces the challenge of transforming object-, body- and environment-related signals into a common reference frame, while factoring the high number of different starting positions of the hand, and its constant motion, possibly unseen. The PPS machinery, with its hand-centered coding of the surrounding space, offers the advantage of achieving this goal in a quite straightforward fashion, as shown by Brozzoli and coll. (2009). Participants had to respond to touches delivered to their hand while it was immobile, or about to start a reach-to-grasp movement towards a 47 cm far object. Visual distractors displayed on the object were found to evoke stronger multisensory effects when the hand barely started moving, as compared to when movement was not yet initiated. Thus, despite being at the same distance from the hand, visual stimuli become more effective to alter tactile processing in agentive situations (see also Berger et al, 2019; 2020). More recent work along these lines revealed that actual movements were not even required for multisensory enhancement: the mere planning of an upcoming hand action was sufficient to tune the sensitivity of tactile perception to visual interference, further supporting the notion that PPS regions may serve as sensorimotor interfaces to control acquisitive actions (Patanè et al, 2019).

Direct transformations of spatial coordinates may be useful for the motor control of voluntary acquisitive actions, but they might be even mandatory for fast defensive actions. As we will further develop, for PPS mechanisms being phylogenetically advantageous in protecting the body from threats and damages, they need to process upcoming stimuli quickly. Evidence supporting this quick processing of nearby events comes from a study using single

pulse Transcranial Magnetic Stimulation (spTMS) over the motor cortex, whereby participants performed a simple button-press motor response while seeing a ball that suddenly fell just above their responding hand, or far from it (Figure 2). Applying TMS over the contralateral primary motor cortex, we found that this potentially threatening visual stimulus suppressed corticospinal excitability as early as 70ms following its appearance, which we interpreted as the sign of proactive suppression of an automatic avoidance-related response. This inhibition reversed to facilitation when the two motor behaviors (the avoidance and the task-related responses) were uncoupled (see also Serino et al, 2009). Importantly, in both cases the modulation of the motor excitability varied with the distance of the ball from the hand, being maximal at the shortest one, and it was independent from the retinal position of the visual stimulus, thus showing the PPS typical hand-centered pattern. Such a fast modulation of M1 may be granted by a short and rapid pathway from the retina to the motor cortex (Lyon et al, 2010), which could update hand-relevant visual information for the dynamic control of hand–object interactions. As suggested elsewhere (Makin et al, 2010), such a mechanism might be useful to either catch or avoid objects in a suddenly changing environment, when alternative pre-planned options would fail.

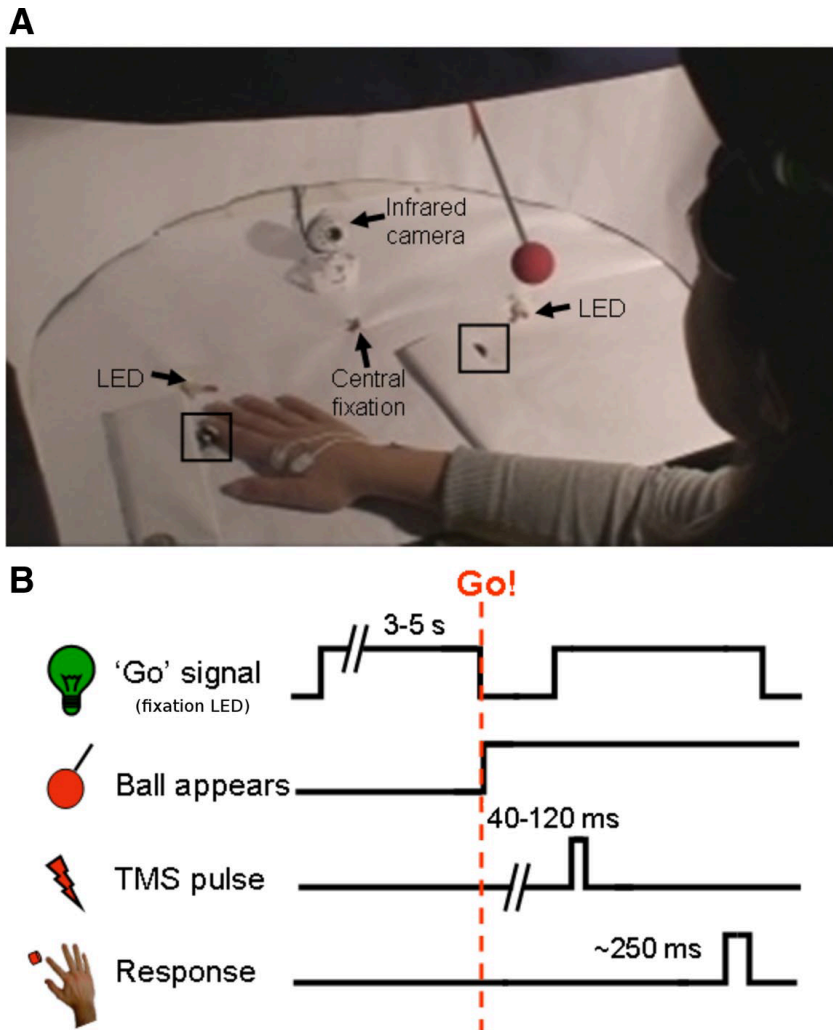


Figure 2. Experimental setup (A) and time course (B) of the spTMS study. Participants held their right hand either to the left (as shown in A) or to the right of a central LED which served as fixation point. They had to respond to a transient (130 ms) offset of the fixation LED by abducting their right index finger to push a button (black square) while ignoring the distractor ball (red sphere). The distractor ball appeared simultaneously with the go signal, approaching either the left or right (shown in A) side of fixation. Between 40 and 120 ms after the appearance of the distractor ball, a single pulse of TMS was delivered to the hand area of the left hemisphere primary motor cortex, eliciting a MEP in the right FDI muscle. From Makin et al (2009).

(iv) Attentional dimension

At this point, one may wonder whether one can provide a unified explanation for the different effects found in PPS beside their mere spatial overlap in relative proximity. For instance, it has been initially suggested that sensory enhancement in PPS possibly results from attention-dependent facilitation (Ladavas et al, 1998). However, growing evidence shows that it reflects a distinct process, though attention and PPS processes are likely to co-occur and thus difficult

to take apart. In the falling-ball TMS study by Makin and colleagues (2012), in order to control for *overt* attention, we asked participants to look at led-cued positions congruent or incongruent with the hand position, so that the proximity effect of the ball could be defined in reference either to the hand (near the hand, fixation to the opposite side), or to the eyes (near ocular fixation, hand on the opposite side). Similarly, to control for *covert* attention, we asked participants to fixate centrally and to orient attention at different led-cued positions. In both control experiments, the rapid inhibition of corticospinal excitability was predominantly hand-centered, depending upon the distance of the ball from the hand, regardless of the locations of both visual fixation and covert spatial attention. These findings call for a genuine PPS-related effect independent from spatial attentional effect.

Zanini and colleagues (2021) recently brought additional evidence for the separation between PPS- and attention-dependent effects on behavioral performance. In a series of experiments designed to distinguish PPS from the (often conflated) Arm Reaching Space (ARS), they found that PPS was smaller than ARS. They further found that multisensory facilitation closely followed hand location for PPS, but not for ARS. Most importantly, when participants' attention was diverted elsewhere (they had to perform a visual gap detection task at a location equidistant from the locations where near and far stimuli were respectively projected), participants still showed better multisensory performance for near stimuli. This finding corroborates the distinction between PPS- and attention-dependent modulation of perception.

This dissociation rules out attention as the unifying driving mechanism for increased multisensory facilitation and for improved visual processing in PPS. Instead, we explain the various effects found in PPS by the primary function of PPS mechanisms, namely, their motor function. As described by Maravita and coll. (2003, p. 531), PPS is the space “within which it [the body] can act”. All bodily movements necessarily unfold in the space that immediately

surrounds one's limbs. One may then propose that both unimodal and multimodal effects have been selected because of their respective importance for action. On the one hand, mapping external objects in body part coordinates allows for direct sensorimotor transformations. On the other hand, faster and more accurate shape recognition facilitates action preparation. Hence, the two types of sensory signatures do not merely coincide in the same region of space; they share the same functional role.

2. A defensive conception of PPS

The original reports on PPS-related regions (e.g., VIP) described that multisensory neurons were especially sensitive for stimulus displacements. This has been taken as evidence that their function is more reactive (responding to changes in the environment) than active (initiating changes in the environment). More specifically, it has been argued that one of the major functions of PPS mechanisms is “to maintain a margin of safety around the body and to coordinate actions that defend the body surface.” (Graziano and Cooke, 2006, p. 2622). The protective role of PPS is said to generalize to anything to which is ascribed a negative value, from predators to mere obstacles on one's path. One may also argue that it extends to threats surrounding other individuals in light of the activity of PPS mechanisms when objects approach other bodies (Ishida et al., 2010; Brozzoli et al., 2013), or vice-versa (Patanè et al, 2020). Although most evidence comes from the stimulation of visuo-tactile neurons, it is in the auditory modality that the defensive conception of PPS appears as the most plausible. For sighted individuals, auditory information provides limited information for instrumental actions such as reaching or grasping. By contrast, it is an efficient alarm system that gives reliable cues about the presence and the proximity of threats (as long as they are noisy), even in the dark and in the rear space that the animal cannot see.

Two main series of results support the defensive conception. First, at the motor level it has been found that the activation of PPS mechanisms triggers defensive responses that are body-part specific (Cooke et al., 2003; Cooke and Graziano, 2003, 2004; Sambo and Iannetti 2013; Makin et al., 2009; Avenanti et al., 2012; Finisguerra et al., 2015). Secondly, at the sensory level the negative value of stimuli has been shown to significantly modify the extent of PPS, especially if participants display anxiety (Ferri et al., 2015; Taffou & Viaud-Delmon, 2014; Taffou et al., 2021; Lourenco et al., 2011; Sambo and Iannetti 2013; de Haan et al. 2016; Spaccasassi and Maravita, 2020). These findings suggest that PPS mechanisms are sensitive to whatever has been appraised as potential threats by the amygdala (Clery et al., 2021) in order to monitor them and to react to them, even though we shall note some limitations to this conception.

The most convincing evidence comes from Michael Graziano's research in monkeys. With his team, he found that electrical stimulation of the regions embedding multisensory neurons in the precentral gyrus and in the VIP elicited defensive movements spatially tuned to body parts similar to those induced by a puff of air directed at the animals (Cooke et al., 2003; Cooke and Graziano, 2003, 2004). For instance, monkeys rapidly lifted their hand into the space near the side of their head as if to block an impending impact when the stimulation was applied on the region that contained face-centered tactile neurons or they brought their hand behind their back when it was applied on the region that contained hand-centered neurons. In humans, it has also been found that the perception of threats in PPS can trigger defensive responses. The eye-blink reflex can be elicited by a strong stimulation of the median nerve at the wrist (the hand-blink reflex, HBR) and this reflex is substantially enhanced with the proximity of the hand to the eyes (Sambo and Iannetti 2013). It has also been found that a 300 ms burst of white noise near the hand reduces corticospinal excitability, which resembles that found during the presentation of noxious stimuli, unexpected events and potential threats (Makin et al., 2009; Avenanti et al.,

2012). In addition, the amplitude of motor evoked potentials evoked by TMS was enhanced when a sound was heard within a distance of 60 cm from the hand with respect to sounds occurring further away (Finisguerra et al., 2015).

Unfortunately, these are the only studies that investigate the defensive function of PPS at the motor level. Although PPS has been described as a ‘motor space’ from the beginning (Rizzolatti, 1997), little has been done to directly investigate its purely motor effects.² Instead, most studies focus on its multisensory dimension. The question then is no longer whether PPS mechanisms contribute to defensive movements, but whether they contribute to threat monitoring. Interestingly, the presentation of visual stimuli in PPS can interfere not only with tactile processing, but also with nociceptive processing (Dong et al., 1994; de Paepe et al., 2016). Even for tactile processing, it has been shown that it is differentially affected depending on the affective value of the surrounding stimuli. Auditory-tactile facilitation effects are found for stimuli at larger distances when participants hear looming towards them the sound of screaming individuals or of fearful animals, or abstractly unpleasant sounds (Ferri et al., 2015; Taffou & Viaud-Delmon, 2014; Taffou et al., 2021). These effects are enhanced if participants feel anxious or display anxiety trait (Lourenco et al., 2011; Sambo and Iannetti 2013; Taffou & Viaud-Delmon, 2014; de Haan et al. 2016; Spaccasassi and Maravita, 2020). For instance, seeing approaching spiders induces visuo-tactile facilitation effects earlier in participants with high levels of arachnophobic fear (de Haan et al. 2016). Although brain regions can modulate indirectly these responses, these findings are consistent with the hypothesis that PPS mechanisms are used to monitor what has been appraised as immediate threats by the amygdala. On this view, if the extent of PPS ‘stretches’ farther away in threatening contexts, it is to give

² Here we leave aside here studies on the ARS, which is different from PPS itself, as argued earlier.

more time for the animal to react. However, one may ask, is it not already too late to hear or see the predator coming if it is already close to us?

3. Plan B hypothesis

The defensive conception of PPS has been inspired by Hediger's (1950) work on the direct link between spatial processing and defensive animal behaviors (e.g. Graziano and Cooke, 2006; Vignemont and Iannetti, 2015). However, what Hediger and later research have shown is that there is a spatio-temporal gradient of defensive responses, some of them starting very early on, long before the threat enters PPS and long before there is any emergency. According to the *threat imminence continuum* hypothesis, there are at least three phases, each associated with distinct affective, motor, and neural signatures (Fanselow and Lester, 1988; Mobbs et al., 2020). In *pre-encounter threat stage*, predators may be around but they are not yet detected. The animal is vigilant and act with caution. It displays 'anticipatory anxiety'. In *post-encounter threat stage*, predators have been detected but they are not attacking. The animal now displays 'encounter anxiety' and initiates stereotypical behaviours like freeze or flight. When the threat becomes closer in time and space and the attack is a few seconds away, the animal shows fear response. It typically engages into flight, freeze or fight depending on the context. Finally, in the *circa-strike threat phase*, when the predator attacks, the animal typically displays panic responses and tries to defend itself (Mobbs et al., 2020). Likewise, humans react differently depending on the imminence of danger. In one study, participants were in a two-dimensional maze in which they had to avoid a "virtual predator" that had the capacity to chase, capture, and cause pain of high or low electrical shock. As the virtual predator grew closer, brain activity shifted from the ventromedial prefrontal cortex, associated with decision making, to midbrain

structures involved in defensive responses and pain anticipation, especially for high-pain predators (Mobbs et al., 2007).

In this continuum, it seems that PPS arrives at the very end only. Although it has been suggested that PPS corresponds to the *flight zone* (distance at which the animal starts fleeing) (Graziano and Cooke, 2006), this zone extends far beyond the majority of receptive fields of PPS-related neurons. Although some of the neurons in PPS regions have receptive fields that extend out a few meters, most have a strong preference for near space, whereas the flight zone can be as large as 130 m for a giraffe or 10 m for a howler monkey (Hediger, 1950). Others have recently proposed that PPS is more closely related to *freezing*, which consists in reduced mobility, tense body posture, and bradycardia (Serino et al. 2021; Ellena et al., 2022). However, the main functions of freezing are for the animal to evade detection, scan its environment and prepare its actions. It must thus occur again before the predator enters the PPS. For instance, in rats, freezing is near maximal when the predator is 100-300 cm distant from the animal, and declines abruptly at about 50 cm, when the attack becomes imminent (Eilam, 2005). At this final step, the animal is gradually overtaken by the predator and it is generally left with little choice but attack with emergency characteristics. Hediger (1950) then talks of *critical distance*, which is a space not only for fleeing, but also for fighting. This may be possibly the closest equivalent to PPS. Interestingly, if this is the case, then it means that the direction of defensive responses in PPS can be towards the predator, and not systematically away from it.

One may reply that monkeys react with squinting or ducking behaviors after electrical stimulations of PPS neurons, and not with aggressive behaviours (Graziano and Cooke, 2003), but it is hard to predict what they would do in more ecological conditions when facing a predator that cannot be outrun, especially if it is already within PPS. Still, it remains to be tested whether fighting responses do involve PPS mechanisms. Our claim is only that when a predator is close, the best response is not necessarily flying away and thus, contrary to what is sometimes

assumed (e.g. Buffacchi and Iannetti, 2018), the negative value of the surrounding stimulus should not be equated with avoidance behavior.

In our contemporary western society, we rarely encounter predators but there are still many sources of danger. There again, we generally do not wait for the last second to act. Consider the case of *looming perception*. There are predictive mechanisms that allow computing the time to collision at an early stage, before the looming stimulus enters the immediate surroundings of one's body (Clery et al., 2017). This allows time to plan one's response (interception or avoidance). Consider also the defensive function of the *colliculus*, which displays multisensory processing with interesting basic integration principles properties. According to the 'inverse efficiency' principle, visual-auditory neurons typically display a stronger (super- or sub-additive) integration of sensory inputs when the latter are weak. For example, seeing a barking dog at a distance (when both visual and auditory signals are weak) makes neurons fire more strongly than when the dog is close (Stein & Stanford, 2008). In a nutshell, collicular multisensory integration properties are best suited to detect threat well in advance compared to PPS processing (Figure 3).

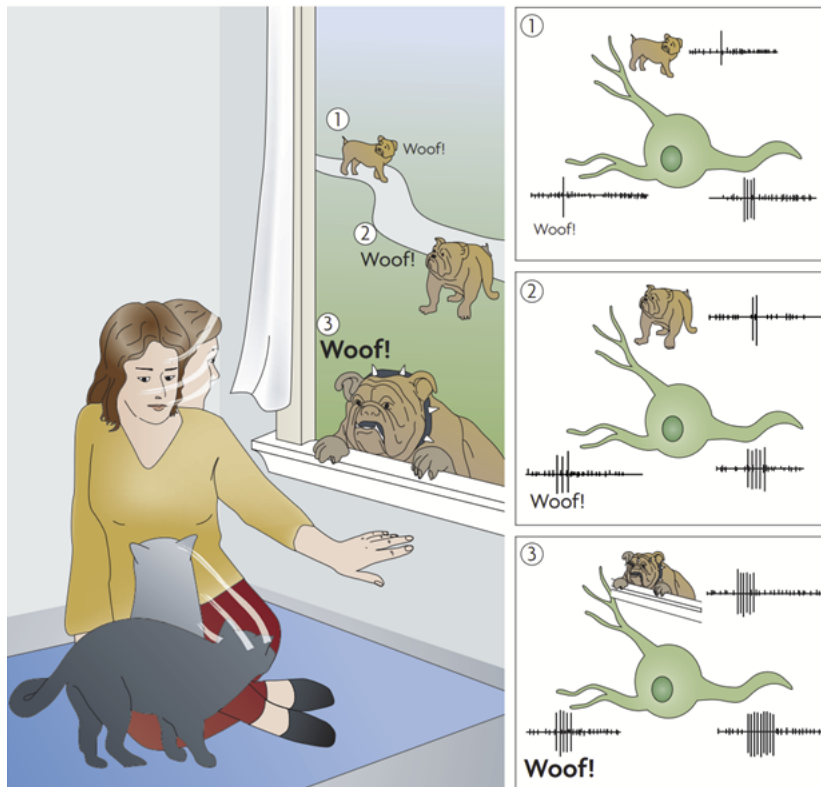


Figure 3. Multisensory integration at the level of the single neuron in the colliculus allows for anticipated detection of threats. The approach of the dog is signaled by audition and vision. 1. When the dog is far and the sensory inputs are weak, multisensory integration is super-additive: the neuronal response is stronger than the sum of each unisensory response. 2. As the dog approaches, unisensory responses become more vigorous, whereas integrated responses get smaller. The computation now becomes additive. 3. When the dog is close, the computation is sub-additive. All enhancements increase the probability of orientation, but the benefits of multisensory integration are proportionately the greatest when cross-modal cues are the weakest, i.e., when the threat is the farthest. From Stein & Stanford (2009).

We thus have a range of mechanisms specifically designed to protect our body. For these mechanisms to be the most efficient they need to be activated before the last second. Some may be tempted to enlarge the notion of PPS so that it is no longer specific to the immediate surroundings of the body and so that it encompasses these other mechanisms. On this view, PPS is characterized as a graded action field triggered by the ascription of values at various distances from the body (Buffachi and Iannetti, 2018). Such an enlarged notion of PPS can secure its major significance for self-preservation, but at the cost of losing the physiological and behavioural specificity of PPS. Furthermore, even within an enlarged conception, one might still fix limits to PPS. Arguably, it is doubtful that seeing a predator 20 m away and initiating a flight response depend on PPS mechanisms. As argued in their original paper on

PPS, “proximity of the stimulus to the animal was really the condition responsible for the neuron responses” (Rizzolatti et al., 1981b, p. 149). Rizzolatti and his colleagues meant by proximity 1 meter away, but even one stretches it farther, it still remains that the majority of PPS neurons are sensitive to what is *relatively close* to the subject.

The challenge is thus to understand how PPS mechanisms may still contribute to bodily protection despite being triggered so late. One may indeed wonder what role is left for them to play given the richness of these other defensive mechanisms and the necessity for them to be activated as early as possible. Here we propose what we call the *Plan B Hypothesis*, according to which PPS mechanisms for self-defence are required only when all the other mechanisms have failed, which unfortunately often happens in unpredictable environments. They thus may have originally been selected for two reasons: for bad surprises and as a last resort.

We have seen that we have long range sensory systems that allow us to detect threats and obstacles at large distance and that we further have a number of anticipatory mechanisms that allow us to plan our actions accordingly. Although some neurons in PPS regions can contribute to longer range processing, eye-centred mechanisms can outweigh PPS hand-centered mechanisms under predictable conditions. Indeed, they are likely to provide more accurate visuospatial information about the relative positions of the object and the hand. However, there are limits to what one can predict, especially under unstable environmental conditions. By definition, last-minute changes cannot be anticipated. They thus require last-minute mechanisms, namely, PPS mechanisms. These mechanisms are specialized in the rapid updating of relevant visual information during response selection and online control of action, which are useful when the position of a target object unexpectedly changes (Makin et al., 2012). This is especially true when one is surrounded by other agents. Objects obey basic principles in physics that allow us to predict their trajectory, but agents’ movements are more complex to anticipate. If you need to walk in the subway at rush hour, instead of a room full of furniture,

you cannot predict well in advance the other passengers' paths. Monitoring your immediate environment is then important in order to react quickly to sudden, unpredictable changes. Predictions can also fail for lack of sensory information. We may not be short-sighted but it does not mean that we have an exhaustive sensory access to all our surroundings. A snake may have been hidden from our sight till our steps get us close to it and it suddenly jumps on us. As recalled above, humans are much quicker at recognizing shapes in close than in far space (Blini et al, 2018). This efficiency is directly useful when something suddenly pops out next to one's body and one needs to identify it to determine whether it is a threat or not. To recap, the unexpected explains why it is beneficial for the organism to have enhanced visual processing in PPS. Finally, even when one is able to accurately predict the threat in advance, one's responses may be insufficient to fully neutralize it. PPS mechanisms can then be seen as the final stage in a series of attempts to stop the danger, a last resort.

4. A cost-benefit analysis of PPS

At this point, one may wonder why wait so late to trigger the plan B. Wouldn't it be more beneficial if PPS mechanisms operate when the threat is not yet in relative proximity? One might intuitively assume that an animal in which PPS mechanisms are activated when the potential threat is still relatively far away would have more chance to survive but this would be without factoring the *cost* of these mechanisms. Most studies have focused on their benefits, but rarely on their detrimental aspects. Yet, they do have a price, and it may not be worth it to trigger PPS mechanisms earlier. Here we can draw a comparison with optimal flight initiation distance (FID), which is computed on the basis of cost-benefit analysis. It has been proposed that optimal FID occurs at the distance when the cost of not fleeing and the cost of fleeing are equal (Ydenberg and Dill, 1986). It depends not only on predation risk, but also on the costs of

fleeing, which include the energy it requires, but also the loss of opportunities, like eating or mating. The fact is that not all components of fitness can be maximized simultaneously (Möller, 2021). For instance, short FID is associated with high fecundity, but low survival prospects, whereas long FID is associated with low fecundity but high survival prospects.

We may then ask whether an earlier PPS would be worth the costs. Within the recent trend of predictive coding theories, predictions are said to be pervasive across all the layers of the brain architecture, as if they could be generated for free. However, if they do have a psychological reality, instead of being merely a computational model of what happens in the brain, then they must have a neural, and thus energetic cost. Neural computations do not come for free, and this applies to PPS computations too. The cost is also cognitive. For instance, when participants are asked to localize a target among distractors, they are slower when the visual display is close than when it is far (Abrams et al. 2008). In this respect, PPS mechanisms seem to fit well the ‘better safe than sorry’ tenet. Hence, visual search can be less efficient in PPS than in far space because more thorough. Relatedly, ongoing work investigated whether perceptual learning could vary according to the proximity of visual stimuli. As in Blini et al. (2018), we used the Ponzo illusion to manipulate the perceived distance. Participants performed a visual search task in which they reported whether a specific target object orientation (e.g., triangle pointing downward) was present among distractors. Performance was assessed before and after practicing the visual search task (30 minutes/day for 5 days) at either close or far distance. Results showed that the performance improved only when trained in far space, and not in near space (Zafarana et al, 2023). Arguably, learning is more effective thanks to a greater deployment of attention, which may not be worth its cost in the immediate vicinity of one’s body. Indeed, when an object appears in PPS, investing too much attention is both inefficient and risky. There is not enough time left, from its identification to the appropriate reaction, and

there is the risk of increasing the likelihood of failure because of slower, attentional demanding processes.

Finally, we need to question the actual usefulness of the gains given by PPS processing if it were activated farther away from the body. Consider first its multisensory signature. Objects seen or heard in PPS are encoded in a somatotopic frame of reference relative to the specific body part that they may impact. One way to interpret these results is that the brain generates *somatosensory predictions* on the basis of what is seen or heard. Though it is perceived as being still outside of the body, one anticipates its contact with the body. Somatosensory encoding of external events allows for more spatially tuned responses. You do not react in the same way if you see a bee next to your head or next to your hand. When the bee is still relatively far away, however, the exact end point of its trajectory is still too uncertain for making it worth computing it. Furthermore, your response needs not be as specific. At this stage the bee is only flying in your direction, and you can simply move away. What matters is only its relation to your whole body, and not to any specific part of it. In the end, keeping the PPS machinery always ‘on’ in these conditions would come at a large cost for little-to-no advantage. Finally, predicting a forthcoming contact makes sense when the object is close-by because its probability is at its highest. It suffices for either the object or the subject to move slightly to make it happen. By contrast, when the object is further away, the uncertainty is too high because many things can intervene preventing the contact, or making the contact happen in a previously unforeseen location on your body. We argue here that fine-grained spatial tuning enabled by the somatotopic organization of PPS mechanisms increases the likelihood of survival when the threat is close, but it is not required when it is farther away. Consider now the sensorimotor signature of PPS. In close space, perception can directly be transformed into action: this is efficient insofar as there is no need for intermediary decision-making process. However, if one

can afford the time to think things through, because the threat is still remote for instance, it seems that it is better to be smarter, even though slower.

5. Conclusion: Picking up berries

PPS mechanisms may be a plan B when it comes to self-defense, but is there no other purpose for which it is the plan A? Is it only a sparing wheel, and nothing else? Here it should be reminded that self-defence in the animal kingdom primarily requires the detection of the predator but its localization can remain only approximate. All that is needed for escape is a rough sense of the direction of danger (Sillar et al., 2016). It is in the case of attack that the animal requires fine-grained spatial information. In many species, however, the same mechanisms are involved in both escape and predation: “the neural and muscular machinery that evolved for escape purposes has also been usurped (or perhaps co-evolved) within the same species for the purpose of attack” (Sillar et al., 2016, p. xv). This is true of PPS mechanisms too, especially in the visual modality, which is our primary source of information to act on the world. One may tentatively suggest that depending on the external context and one’s inner states, whether there is food around and whether one wants to get it for instance, PPS neurons may switch to a different mode/function, which then becomes more prepotent. Here we would like to explore the hypothesis that PPS visual mechanisms could be the plan A for fine tuning appetitive movements. This hypothesis does not entail that the defensive function of PPS mechanisms is only secondary, and the appetitive function primary. The contrast that we draw instead is that PPS mechanisms are only required in some circumstances for self-defense, but that they might be more systematically required for appetitive action planning. More precisely, our working hypothesis is that in many circumstances the precise trajectory of the hand and the arm is computed only when the target of the movement is in the immediate surrounding of the

effector. Imagine being in front of a bush full of raspberries. You form the intention to pick them up long before you are next to it but it is only when you are very close that you program the precise hand motion to get to the fruit that seems to be ripe enough. There is no need to plan it before. Further work, however, needs to be done to explore both theoretically and experimentally this plan A hypothesis, which remains highly speculative at this stage.

References

- Abrams, R. A., Davoli, C. C., Du, F., Knapp, W. H., & Paull, D. (2008). Altered vision near the hands. *Cognition*, *107*(3), 1035-1047.
- Berger, M., Neumann, P., Gail, A. (2019). Peri-hand space expands beyond reach in the context of walk-and-reach movements. *Sci Rep.* *9*(1):3013.
- Berger, M., Agha, N.S., Gail, A. (2020). Wireless recording from unrestrained monkeys reveals motor goal encoding beyond immediate reach in frontoparietal cortex. *Elife*, *9*:e51322.
- Bertoni, T., Magosso, E., & Serino, A. (2021). From statistical regularities in multisensory inputs to peripersonal space representation and body ownership: Insights from a neural network model. *European Journal of Neuroscience*, *53*(2), 611-636.
- Blini, E., Desoche, C., Salemme, R., Kabil, A., Hadj-Bouziane, F., & Farnè, A. (2018). Mind the depth: Visual perception of shapes is better in peripersonal space. *Psychological science*, *29*(11), 1868-1877.
- Blini, E., Farnè, A., Brozzoli, C., & Hadj-Bouziane, F. (2021). Close is better: Visual perception in peripersonal space. In de Vignemont, F., Serino, A., Wong, H.W., Farnè, A. (eds), *The World at Our Fingertips: A Multidisciplinary Exploration of Peripersonal Space*. Oxford: Oxford University Press.

- Bogdanova, O. V., Bogdanov, V. B., Dureux, A., Farne, A., & Hadj-Bouziane, F. (2021). The Peripersonal Space in a social world. *Cortex*, *142*, 28-46.
- Bremmer, F., Schlack, A., Duhamel, J. R., Graf, W., & Fink, G. R. (2001). Space coding in primate posterior parietal cortex. *Neuroimage*, *14*(1), S46-S51.
- Brozzoli, C., Makin, T. R., Cardinali, L., Holmes, N. P., and Farnè, A. (2012). Peripersonal space: a multisensory interface for body–object interactions. In M. M. Murray and M. T. Wallace (eds). *The Neural Bases of Multisensory Processes*. Boca Raton, FL: CRC Press.
- Brozzoli C, Pavani F, Urquizar C, Cardinali L, Farnè A. Grasping actions remap peripersonal space. *Neuroreport*. 2009 Jul 1;20(10):913-7.
- Brozzoli C, Gentile G, Petkova VI, Ehrsson HH. fMRI adaptation reveals a cortical mechanism for the coding of space near the hand. *J Neurosci*. 2011 Jun 15;31(24):9023-31.
- Brozzoli C, Gentile G, Bergouignan L, Ehrsson HH. A shared representation of the space near oneself and others in the human premotor cortex. *Curr Biol*. 2013 Sep 23;23(18):1764-8.
- Bufacchi, R. J., & Iannetti, G. D. (2018). An action field theory of peripersonal space. *Trends in cognitive sciences*, *22*(12), 1076-1090.
- Canzoneri, E., Magosso, E., Serino, A. (2012). Dynamic sounds capture the boundaries of peripersonal space representation in humans. *PLoS One*; *7*(9): e44306.
- Choi, I., Demir, I., Oh, S., & Lee, S. H. (2023). Multisensory integration in the mammalian brain: diversity and flexibility in health and disease. *Philosophical Transactions of the Royal Society B*, *378*(1886), 20220338.
- Cléry, J., Guipponi, O., Odouard, S., Pinède, S., Wardak, C., & Ben Hamed, S. (2017). The prediction of impact of a looming stimulus onto the body is subserved by multisensory integration mechanisms. *Journal of Neuroscience*, *37*(44), 10656-10670.
- Cléry, J., Ben Hamed, S. (2021). Functional networks for peripersonal space coding and prediction of impact to the body. In *The world at our fingertips: A multidisciplinary*

investigation of peripersonal space, edited by F. de Vignemont, A. Serino, H.Y. Wong, A. Farnè, Oxford: Oxford University Press.

- Colby, C.L., Duhamel, J.R., Goldberg, M.E. (1993). Ventral Intraparietal Area of the Macaques: Anatomic Location and Visual Response Properties. *J Neurophysiol*, 69/3: 902-914.
- Cooke, D. F., & Graziano, M. S. (2003). Defensive movements evoked by air puff in monkeys. *Journal of Neurophysiology*, 90(5), 3317-3329.
- Cooke, D. F., & Graziano, M. S. (2004). Super-flinchers and nerves of steel: defensive movements altered by chemical manipulation of a cortical motor area. *Neuron*, 43(4), 585-593.
- Cooke, D. F., Taylor, C. S., Moore, T., & Graziano, M. S. (2003). Complex movements evoked by microstimulation of the ventral intraparietal area. *Proceedings of the National Academy of Sciences*, 100(10), 6163-6168.
- de Haan, A. M., Smit, M., Van der Stigchel, S., & Dijkerman, H. C. (2016). Approaching threat modulates visuotactile interactions in peripersonal space. *Experimental Brain Research*, 234, 1875-1884.
- De Paepe, A. L., Crombez, G., & Legrain, V. (2016). What's coming near? The influence of dynamical visual stimuli on nociceptive processing. *PLoS One*, 11(5), e0155864.
- di Pellegrino, G., Ladavas, E. & Farnè, A. (1997). Seeing where your hands are. *Nature*, 21;388(6644): 730.
- di Pellegrino, G., & Ladavas, E. (2015). Peripersonal space in the brain. *Neuropsychologia*, 66, 126-133.
- Dong, W.K, Chudler, E.H., Sugiyama, K., Roberts, V.J., Hayashi, T. (1994). Somatosensory, multisensory, and task related neurons in cortical area 7b (PF) of unanesthetized monkeys. *J Neurophysiol*; 72:542–64.

- Driver, J., & Spence, C. (2000). Multisensory perception: beyond modularity and convergence. *Current biology*, *10*(20), R731-R735.
- Dureux, A., Blini, E., Grandi, L. C., Bogdanova, O., Desoche, C., Farnè, A., & Hadj-Bouziane, F. (2021). Close facial emotions enhance physiological responses and facilitate perceptual discrimination. *Cortex*, *138*, 40-58.
- Eilam, D. (2005). Die hard: a blend of freezing and fleeing as a dynamic defense—implications for the control of defensive behavior. *Neuroscience & Biobehavioral Reviews*, *29*(8), 1181-1191.
- Ellena, G., Bertoni, T., Durand-Ruel, M., Thoresen, J., Sandi, C., & Serino, A. (2022). Acute stress affects peripersonal space representation in cortisol stress responders. *Psychoneuroendocrinology*, *142*, 105790.
- Fanselow, M. and Lester, L.S. (198). A functional behavioristic approach to aversively motivated behavior: Predatory imminence as a determinant of the topography of defensive behavior. In R.C. Bolles & M.D. Beecher (eds.), *Evolution and Learning*. pp. 185-211. Hillsdale, N. J.: Erlbaum.
- Farnè, A., & Làdavas, E. (2002). Auditory peripersonal space in humans. *Journal of cognitive neuroscience*, *14*(7), 1030-1043.
- Farnè, A., Demattè, M. L., & Làdavas, E. (2005). Neuropsychological evidence of modular organization of the near peripersonal space. *Neurology*, *65*(11), 1754-1758.
- Ferri, F., Tajadura-Jiménez, A., Väljamäe, A., Vastano, R., & Costantini, M. (2015). Emotion-inducing approaching sounds shape the boundaries of multisensory peripersonal space. *Neuropsychologia*, *70*, 468-475.
- Finisguerra, A., Canzoneri, E., Serino, A., Pozzo, T., & Bassolino, M. (2015). Moving sounds within the peripersonal space modulate the motor system. *Neuropsychologia*, *70*, 421-428.

- Fogassi, L., Gallese, V., Fadiga, L., Luppino, G., Matelli, M., & Rizzolatti, G. (1996). Coding of peripersonal space in inferior premotor cortex (area F4). *Journal of neurophysiology*, 76(1), 141-157.
- Graziano, M.S. (2018). *The space between us*. New York: Oxford University Press.
- Graziano, M. S., Yap, G. S., & Gross, C. G. (1994). Coding of visual space by premotor neurons. *Science*, 266(5187), 1054-1057.
- Graziano, M. S., & Gross, C. G. (1995). The representation of extrapersonal space: A possible role for bimodal, visual-tactile neurons.
- Graziano, M. S., and Cooke, D. F. (2006). Parieto-frontal interactions, personal space, and defensive behavior. *Neuropsychologia*, 44(6), 845-859.
- Hediger, H. (1950). *Wild animals in captivity*. London: Butterworths Scientific Publications.
- Holmes, N. P., Calvert, G. A., & Spence, C. (2004). Extending or projecting peripersonal space with tools? Multisensory interactions highlight only the distal and proximal ends of tools. *Neuroscience letters*, 372(1-2), 62-67.
- Hyvärinen, J., & Poranen, A. (1974). Function of the parietal associative area 7 as revealed from cellular discharges in alert monkeys. *Brain*, 97(4), 673-692.
- Ishida, H., Nakajima, K., Inase, M., & Murata, A. (2010). Shared mapping of own and others' bodies in visuotactile bimodal area of monkey parietal cortex. *Journal of Cognitive Neuroscience*, 22(1), 83-96.
- Làdavas, E., Pellegrino, G. D., Farnè, A., & Zeloni, G. (1998). Neuropsychological evidence of an integrated visuotactile representation of peripersonal space in humans. *Journal of Cognitive Neuroscience*, 10(5), 581-589.
- Lourenco, S. F., Longo, M. R., & Pathman, T. (2011). Near space and its relation to claustrophobic fear. *Cognition*, 119(3), 448-453.

- Lyon, D.C., Nassi, J.J., Callaway, E.M. (2010) A disynaptic relay from superior colliculus to dorsal stream visual cortex in macaque monkey. *Neuron* 65:270–279
- Macaluso, E., & Maravita, A. (2010). The representation of space near the body through touch and vision. *Neuropsychologia*, 48(3), 782-795.
- Makin, T. R., Holmes, N. P., Brozzoli, C., & Farnè, A. (2012). Keeping the world at hand: rapid visuomotor processing for hand–object interactions. *Experimental brain research*, 219, 421-428.
- Maravita, A., Spence, C., & Driver, J. (2003). Multisensory integration and the body schema: Close to hand and within reach. *Current Biology*, 13(13), R531–R539
- Mobbs, D., Petrovic, P., Marchant, J. L., Hassabis, D., Weiskopf, N., Seymour, B., ... & Frith, C. D. (2007). When fear is near: threat imminence elicits prefrontal-periaqueductal gray shifts in humans. *Science*, 317(5841), 1079-1083.
- Mobbs, D., Headley, D. B., Ding, W., & Dayan, P. (2020). Space, time, and fear: survival computations along defensive circuits. *Trends in cognitive sciences*, 24(3), 228-241.
- Møller, A.P. (2021). Risk-taking behaviour as a central concept in evolutionary biology. In *The World at Our Fingertips: A Multidisciplinary Exploration of Peripersonal Space*, edited by F. de Vignemont, A. Serino, H.W. Wong, A. Farnè. Oxford: Oxford University Press.
- Noel, J. P., Serino, A., & Wallace, M. T. (2019). Increased neural strength and reliability to audiovisual stimuli at the boundary of peripersonal space. *Journal of cognitive neuroscience*, 31(8), 1155-1172.
- Noel, J. P., Bertoni, T., & Serino, A. (2021). Peri-personal space as an interface for self-environment interaction. In *The World at Our Fingertips: A Multidisciplinary Exploration of Peripersonal Space*, edited by F. de Vignemont, A. Serino, H.W. Wong, A. Farnè. Oxford: Oxford University Press.

- Patané, I., Cardinali, L., Salemme, R., Pavani, F., Farnè, A., & Brozzoli, C. (2019). Action planning modulates peripersonal space. *Journal of Cognitive Neuroscience*, *31*(8), 1141-1154.
- Patané, I., Brozzoli, C., Koun, E., Frassinetti, F., & Farnè, A. (2020). Me, you, and our object: Peripersonal space recruitment during executed and observed actions depends on object ownership. *Journal of experimental psychology: general*, *150*(7), 1410.
- Reed, C. L., Grubb, J. D., & Steele, C. (2006). Hands up: attentional prioritization of space near the hand. *Journal of Experimental Psychology: Human Perception and Performance*, *32*(1), 166.
- Reed, C. L., & Park, G. D. (2021). Functional actions of hands and tools influence attention in peripersonal space. In *The World at Our Fingertips: A Multidisciplinary Exploration of Peripersonal Space*, edited by F. de Vignemont, A. Serino, H.W. Wong, A. Farnè. Oxford: Oxford University Press, 101-116.
- Rizzolatti, G., Scandolara, C., Matelli, M., & Gentilucci, M. (1981a). Afferent properties of periarculate neurons in macaque monkeys. I. Somatosensory responses. *Behavioural brain research*, *2*(2), 125-146.
- Rizzolatti, G., Scandolara, C., Matelli, M., and Gentilucci, M. (1981b). Afferent properties of periarculate neurons in macaque monkeys. II. Visual responses. *Behavioural Brain Research*, *2*(2), 147-63.
- Rizzolatti, G., Fadiga, L., Fogassi, L., and Gallese, V. (1997). The space around us. *Science*, *277*(5323), 190-1.
- Sambo, C. F., & Iannetti, G. D. (2013). Better safe than sorry? The safety margin surrounding the body is increased by anxiety. *Journal of Neuroscience*, *33*(35), 14225-14230.

- Serino, A., Canzoneri, E., & Avenanti, A. (2011). Fronto-parietal areas necessary for a multisensory representation of peripersonal space in humans: an rTMS study. *Journal of cognitive neuroscience*, *23*(10), 2956-2967.
- Serino, A. (2019). Peripersonal space (PPS) as a multisensory interface between the individual and the environment, defining the space of the self. *Neuroscience & Biobehavioral Reviews*, *99*, 138-159.
- Serino, A., Annella, L., & Avenanti, A. (2009). Motor properties of peripersonal space in humans. *PLoS One*, *11*;4(8):e6582.
- Serino, S., Trabanelli, S., Jandus, C., Fellrath, J., Grivaz, P., Paladino, M. P., & Serino, A. (2021). Sharpening of peripersonal space during the COVID-19 pandemic. *Current Biology*, *31*(14), R889-R890.
- Sillar, K. T., Picton, L. D., & Heitler, W. J. (2016). *The neuroethology of predation and escape*. John Wiley & Sons.
- Spaccasassi, C., & Maravita, A. (2020). Peripersonal space is diversely sensitive to a temporary vs permanent state of anxiety. *Cognition*, *195*, 104133.
- Spence, C., Pavani, F., & Driver, J. (2004). Spatial constraints on visual-tactile cross-modal distractor congruency effects. *Cognitive, Affective, & Behavioral Neuroscience*, *4*(2), 148-169.
- Stein, B. E., & Stanford, T. R. (2008). Multisensory integration: current issues from the perspective of the single neuron. *Nat Rev Neurosci*, *9*(4): 255-66.
- Straka, Z., Noel, J. P., & Hoffmann, M. (2022). A normative model of peripersonal space encoding as performing impact prediction. *PLOS Computational Biology*, *18*(9), e1010464.
- Taffou, M., & Viaud-Delmon, I. (2014). Cynophobic fear adaptively extends peri-personal space. *Frontiers in psychiatry*, *5*, 122.

- Taffou, M., Suied, C., & Viaud-Delmon, I. (2021). Auditory roughness elicits defense reactions. *Scientific Reports*, *11*(1), 956.
- de Vignemont, F., & Iannetti, G. D. (2015). How many peripersonal spaces?. *Neuropsychologia*, *70*, 327-334.
- de Vignemont, F., Serino, A., Wong, H.W., Farnè, A. (eds) (2021a). *The World at Our Fingertips: A Multidisciplinary Exploration of Peripersonal Space*. Oxford: Oxford University Press.
- de Vignemont, F., Serino, A., Wong, H.W., Farnè, A. (2021b). Peripersonal space: a special way of representing space. In *The world at our fingertips: A multidisciplinary investigation of peripersonal space*, edited by F. de Vignemont, A. Serino, H.Y. Wong, A. Farnè, Oxford: Oxford University Press.
- Ydenberg, R. C., & Dill, L. M. (1986). The economics of fleeing from predators. In *Advances in the Study of Behavior* (Vol. 16, pp. 229-249). Academic Press.
- Zafarana, A., Farnè, A., & Tamè, L. (2023). Visual perceptual learning is effective in the illusory far but not in the near space. *Psychonomic Bulletin & Review*, 1-10.
- Zanini, A., Salemme, R., Farnè, A., & Brozzoli, C. (2021). Associative learning in peripersonal space: fear responses are acquired in hand-centered coordinates. *Journal of Neurophysiology*, *126*(3), 864-874.