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Close is better

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Visual perception in peripersonal space

Elvio Blini, Alessandro Farnè, Claudio Brozzoli, and Fadila Hadj-Bouziane

3.1 Highlights

• The neuroscientific approach to PPS originates from lines of research devoted to the study of the properties of multisensory neurons.
• The dominant multisensory context largely influenced the use of tasks that are multisensory in nature.
• Studies on spatial attention concurrently reported proximity-related advantages in purely unisensory (visual) tasks.
• Brain activations observed in purely visual paradigms tightly overlap with multisensory areas coding for PPS.
• Seeing PPS as a multisensory-only interface may be limiting, and its role may be broader than previously thought.

3.2 Peripersonal space: the multisensory origins

The intuition that the space closely surrounding our body is somehow special has a rather C3.P6 long history (Hall, 1966; Hediger, 1950). For example, Hall (1966) sketched several rough boundaries which, from a social perspective, are functional to different types of interaction (e.g. intimate, up to 45 cm; personal, up to 1.2 m; social, up to 3.6 m; or public; see de Vignemont, 2018). However, it is probably the seminal study of Rizzolatti et al. (1981) that shaped and gave impulse to the vast literature about the newly termed 'peripersonal space' (PPS; also see Hyvärinen & Poranen, 1974). Rizzolatti and colleagues recorded, in macaque monkeys, the responses of neurons located in the periarcuate cortex—part of the frontal lobe that receives input from associative sensory areas. They found a substantial proportion of neurons that were reliably coding for visual stimuli appearing in PPS, defined operationally as the space immediately surrounding the body (e.g. 10 to 30 cm). Strikingly, the vast majority of these visual neurons had bimodal (visual and somatosensory) receptive fields that were in register with the corresponding somatosensory area (e.g. neurons responding to visual stimuli close to the mouth had a tactile counterpart on the mouth), an observation that has been confirmed and extended afterwards to other brain regions (e.g. putamen, ventral intraparietal area, premotor cortex; Colby, Duhamel & Goldberg, 1993; Fogassi et al., 1996; Graziano & Cooke, 2006; Graziano & Gross, 1993). This seminal finding gave rise to a first neuroscientific approach to studying PPS, with a dominant multisensory perspective, as well as a framework to guide cognitive models.

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The original account of Rizzolatti et al. (1981) advocated that the role of these bimodal neurons may essentially be action-oriented (also see Murata et al., 1997). PPS is the only region of space in which we can act on, reach, or manipulate objects directly: a tight link between visual and somatosensory input is particularly expected in PPS, because it may contribute to the efficiency of our goal-directed actions, on the one hand, and it may be shaped by the continuous experience of simultaneous multisensory stimulations, on the other hand. Arguably, studies exploring the effect of tool-use training (Iriki, Tanaka, & Iwamura, 1996; Maravita & Iriki, 2004), which can expand the region of space upon which we can purposefully act, were largely inspired by this formulation. In the seminal study of Iriki et al. (1996), macaque monkeys were trained to reach objects with a rake while the activity of multisensory neurons in the postcentral gyrus was recorded. The authors found that, during tool use, the visual receptive field of these neurons was enlarged up to covering the tip of the rake (Iriki et al., 1996). Tool use has been exploited ever since to probe the plasticity of PPS representation and body schema (Berti & Frassinetti, 2000; Cardinali et al., 2009; Farnè & Làdavas, 2000; Maravita et al., 2002; Sposito et al., 2012), a closely related—yet different—representation of the body for actions (Cardinali, Brozzoli, & Farnè, 2009).

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Defensive actions are particularly important responses that can be accomplished in PPS (Graziano & Cooke, 2006). Escape from a predator or a threatening stimulus has a much more pronounced motivational priority than the needs for food or mating, yet the sight of a threat is not generally sufficient to activate defensive responses: the threat must also violate some safety boundary around the body, termed 'flight distance' (Hediger, 1950), and be perceived as intrusive (Graziano & Cooke, 2006). PPS has also been conceptualized as a system evolved to be highly specialized in coding and maintaining this safety boundary (Graziano & Cooke, 2006), a task for which multisensory interactions are paramount. Think, for example, about looming objects: potentially harmful objects approaching enhance automatically the tactile sensitivity of the body part (and nearby body parts) upon which contact is expected to happen (Cléry et al., 2015; Colby, Duhamel, & Goldberg, 1993; Neppi-Mòdona et al., 2004). Stressing the defensive function of PPS does not contradict the first, actionrelated formulation. This account has provided instead fertile ground for studies extending the notion of PPS plasticity to include interpersonal distance regulation depending on emotion- or stress-related stimuli. For example, Ruggiero et al. (2017) presented to healthy participants visual avatars depicting different facial expressions with emotional valence (e.g. happy vs angry) approaching them in an immersive virtual reality environment. They asked participants to press a button as soon as the distance of the visual avatars was felt as uncomfortable, thus delineating a comfort distance or zone. Participants showed enlarged comfort zones for the avatars signalling anger (Ruggiero et al., 2017). The magnitude of this enlargement can be predicted on the basis of individuals' autonomic responses (Cartaud et al., 2018) and is modulated by personality traits such as the level of anxiety (Sambo & Iannetti, 2013). Overall, this picture is coherent with the notion that the presence of threatening cues within the close space surrounding us prompts avoidance behaviours (Ruggiero et al., 2017; also see Ferri et al., 2015; Teneggi et al., 2013). As such, PPS may help us move efficiently towards (to reach) or away from (to avoid) elements of our close environment. Separating the two functions of PPS into action- or defence-related is therefore probably artificial (de Vignemont & Iannetti, 2015). A more general take could assume a flexible organization of PPS that would depend on current task and environmental constraints (e.g. Bufacchi & Iannetti, 2018). It is worth stressing, however, that both formulations firmly build on, and were originally put

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forward to accommodate for, the multisensory and distance-tuned properties of neurons ascribed to PPS coding.

It would not be surprising, at this point, to note that most of the tasks devised to probe PPS-related processing involve bimodal sensory stimulations. One common scenario involves the presentation of one to-be-discriminated tactile stimulus coupled with an irrelevant visual or auditory one, delivered in either an overlapping, close, or distant position in space (Brozzoli et al., 2009; Canzoneri, Magosso, & Serino, 2012; Maravita, Spence, & Driver, 2003; Spence, Pavani, & Driver, 2004; Teneggi et al., 2013). These tasks have shown that, when both stimuli are overlapping in space and time, stronger multisensory interaction occurs: neural and behavioural responses are therefore enhanced, resulting in advantages (Makin et al., 2012). This effect is maximal near the body (i.e. where touch is delivered) and decreases as a function of the distance at which the irrelevant stimulus is presented. Psychophysical modelling of this decay allows one to estimate a rough point of 'indifference', in which multisensory interaction no longer occurs, and thus to functionally identify two seemingly different regions of space (Canzoneri et al., 2012; Noel et al., 2015; Teneggi et al., 2013). For example, Canzoneri et al. (2012) measured response times for tactile discrimination of stimuli presented with a concurrent dynamic sound (i.e. perceived to be looming or receding, and at different distances from the delivered touch). The results showed an audiotactile interaction effect, stronger with approaching sounds, that was maximal close to the stimulated hand. Psychophysical modelling further suggested that a sigmoidal function could adequately capture this decay, and the inflection point of the curve (the aforementioned 'indifference point') was taken as a proxy for the putative limit and extension of PPS. This approach was proven fertile and capable of highlighting the peculiar plasticity of PPS. For example, it was exploited to show that sounds associated—by either physical or semantic properties—with negative emotions or contents are capable of pushing the PPS boundaries farther away (Ferri et al., 2015), in agreement with the PPS role in maintaining a safety zone around the body.

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The wide use of multisensory tasks to probe PPS processing is paradigmatic of its conception as the region of space in which multisensory interactions occur. This is certainly the case for the integration of touch with other sensory stimulations, because touch clearly cannot happen in extrapersonal space. Indeed, PPS is inherently multisensory. However, this does not preclude the existence of unimodal advantages tied to PPS-specific processing. This chapter will review recent evidence for the existence of such unisensory (visual) advantages. However, before tackling this emerging field, we deem useful a brief overview of the literature concerning the distribution of spatial attention in depth.

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3.3 Peripersonal space and attention: the inextricable link?

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 It is hard, perhaps impossible, to tease apart whether depth-specific neural and behavioural modulations result from enhanced attentional processing close to the body or rather to a dedicated system for PPS (perceptual) processing (but see Makin et al., 2009; Reed et al., 2013, for dissociations between effects depending on mere hand proximity and orienting of attention). This literature, however, allows us to access and appreciate several findings that, far from denying a privileged role of PPS in perception, may increase our understanding of PPS-specific unisensory advantages.

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Spatial and hemispheric asymmetries hold a special place within the literature on human perceptual and attentional systems. General consensus has been reached on the notion that

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attention is not uniformly distributed along the three orthogonal axes (Gawryszewski et al., 1987; Shelton, Bowers, & Heilman, 1990). However, the majority of experiments has been carried exploiting two-dimensional screens, thereby neglecting the sagittal (near-to-far) plane (but see Couyoumdjian, Nocera, & Ferlazzo, 2003; Losier & Klein, 2004; Plewan & Rinkenauer, 2017).

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As notable exceptions, few studies exploited cued detection tasks with stimuli appearing at different distances (Couyoumdjian et al., 2003; Gawryszewski et al., 1987; Losier & Klein, 2004). The first notion drawn from these studies is that spatial attention can be displaced along the sagittal plane just like it can be displaced along the horizontal and vertical planes (Couyoumdjian et al., 2003; Gawryszewski et al., 1987; Losier & Klein, 2004), as seen by cueing validity effects (i.e. better performance when cues and targets appear in the same region of space, and decreased performance when positions are incongruent). Second, participants are faster in responding to stimuli appearing close to their body, in PPS, suggesting that more attentional resources are allocated there (Gawryszewski et al., 1987; Plewan & Rinkenauer, 2017). A more specific manifestation of this phenomenon has been described for the space close to the hands (Reed, Grubb, & Steele, 2006). Reed et al. (2006) used a purely visual covert attention paradigm, a cued detection task like the ones described earlier in this paragraph, in which the only experimental manipulation was the position of the participants' hand (either close to left- or right-sided targets); thus, also in this case, the task had no explicit cross-modal component, being confined to the visual modality. Visual stimuli were detected faster when appearing closer to the perceived position of the hands (nearhand effect). This applied also when visual input was lacking-namely, when the hand was occluded, the proprioceptive input appeared sufficient for this effect to emerge (but see, for contrasting evidence on the role of hand proprioception, Blini et al., 2018; Di Pellegrino & Frassinetti, 2000; Làdavas et al., 2000). Hand position alone could, indeed, modulate both early and late attention-sensitive components of brain activity in a subsequent experiment exploiting event-related potentials (Reed et al., 2013). Behavioural results were later extended with different tasks (e.g. visual search, inhibition of return, attentional blink), all consistently showing that visual and attentional abilities are altered near the hands (Abrams et al. 2008).

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It is interesting to notice that the accounts proposed to frame these results also call into cause the role of attention in maximizing action efficiency or in monitoring the nearby space for defensive purposes (Abrams et al., 2008). The maintenance of a defensive space, indeed, would necessarily involve monitoring of the nearby environment, a mental representation of it, and ultimately attentional resources to be constantly deployed (Graziano & Cooke, 2006). The question as to whether such a-constantly active-monitoring is biologically and evolutionarily plausible remains open, because this could come at very high costs for already limited resources. In addition, the monitoring of looming objects, with respect to receding ones, would be privileged because more likely to result in an impact with the body (Cléry et al., 2015; Neppi-Mòdona et al., 2004). Looming objects are indeed known to strongly capture visuospatial attention in human (Franconeri & Simons, 2003; Lin, Murray, & Boynton, 2009) and non-human primates (Ghazanfar, Neuhoff, & Logothetis, 2002; Schiff, Caviness, & Gibson, 1962), and cause increased multisensory interaction (Canzoneri et al., 2012; Maier et al., 2004), typically attributed to PPS-specific processing. Similarly, threatening stimuli or cues strongly capture and hold attention (Armony & Dolan, 2002; Koster et al., 2004). It could thus be argued that this specificity may explain, at least in part, the effects reported over PPS signatures (i.e. extended PPS limits, Ferri et al., 2015; but see Makin et al., 2009, for evidence of a dissociation). Another possibility would be that the domain-general

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mechanism of spatial attention, and cross-modal attention in particular (e.g. Eimer, Velzen, & Driver, 2002), may exploit the neural circuits specialized for PPS, as initially suggested (Làdavas et al., 1998). Disentangling these—potentially not mutually exclusive—alternatives may be difficult, especially with purely behavioural paradigms. Yet, better identifying the specific roles played by attention versus PPS perception is likely to provide valuable contributions to our understanding of the mechanisms that today are indistinguishably gathered within the PPS label. At any rate, phenomena like the near-hand effects typically represent instances in which advantages for stimuli presented close to the body occur in purely unisensory tasks.

3.4 Neural bases of peripersonal multi- (and uni-) sensory processing

The functional linkage between PPS and actions, supported by neurophysiological and ana-C3.P15 tomical evidence from primate work (see for review, Makin et al., 2012), prompted the idea that visual processing in PPS would mainly rely on the dorsal visual stream, optimized for action, whereas visual processing beyond it would mainly rely on the ventral stream, optimized for perception (Milner & Goodale, 2008; Previc, 1990). Because the dorsal stream recruits more extensively parietal networks and magnocellular neurons—that are highly specialized in responding to rapid changes in the visual scene in spite of their low resolution—this is also well fitting with the PPS role in monitoring a zone around the body. One could argue that, at least in some conditions, it would be better to ward off an insect close to us before knowing whether it is a wasp or a ladybird. This notion has been supported by behavioural studies showing faster detection times for stimuli occurring close to the body or the hands (Gawryszewski et al., 1987; Plewan & Rinkenauer, 2017; Reed et al., 2006; but see Makin et al., 2015). Furthermore, studies have shown that performance on tasks requiring speeded temporal-gap detection improves in the near-hand space (Goodhew et al., 2013; Gozli, West, & Pratt, 2012), whereas performance in spatial-gap tasks is hampered (Gozli et al., 2012). This has been discussed as coherent with a general magnocellular advantage for PPS processing (Bush & Vecera, 2014; Goodhew et al., 2015, for a review).

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However, on the other side of the coin, on the bases of this account, performance benefits in fine-grained discrimination tasks could be predicted to occur beyond PPS, where the ventral pathway would play a more important role. Parvocellular neurons-with their small and contrast-sensitive receptive fields—appear indeed ideal matches to contribute to object identification, especially because, in everyday life, the size of an object (retinal size) scales with distance. In other words, we would be better at discriminating wasps from ladybirds when the insect was far; in this case, we could afford time to prepare an optimal response, shaped according to the significance of the threat (we would need a fast, automatic response when too late, the insect being already close). However, this view has recently been challenged, because visual discrimination appears to actually also improve in PPS (Blini et al., 2018). Although this classic account is well supported by neuropsychological and neurophysiological evidence, the dichotomy between ventral and dorsal pathways is not meant to be strict (Milner & Goodale, 2008). Accumulating evidence specifically points to the fact that the dorsal stream contains object representations that are to some extent independent of those in the ventral stream, and capable of contributing to human perception (Freud, Ganel et al., 2017; Freud, Plaut, & Behrmann, 2016; Quinlan & Culham, 2007; Wang et al., 2016). One recent study, for example, has shown that fundamental properties of shapes can ()

be reliably decoded from posterior parietal regions, whose activation profile appears correlated with recognition performance (Freud, Culham et al., 2017), suggesting a functional role in shape identification. Candidate areas appear to be a set of subcortical (e.g. putamen, Graziano & Gross, 1993) and fronto-parietal cortical areas (i.e. inferior parietal and premotor, Brozzoli, Gentile, & Ehrsson, 2012; Brozzoli et al., 2011; di Pellegrino & Làdavas, 2015; Fogassi et al., 1996; Graziano & Cooke, 2006; Lloyd, Morrison, & Roberts, 2006) associated with PPS processing. For example, Brozzoli et al. (2011) presented, to healthy participants lying supine inside a magnetic resonance imaging (MRI) scanner, 3D objects either close (3 cm) or far (100 cm) from their outstretched hand (or in the same physical/ visual position but while their hand was resting unseen on the torso). The authors capitalized on a robust property of neuronal responses measurable using functional MRI, which is neural adaptation: neural activity is reduced when a stimulus feature is repeated, but only for a subpopulation of neurons that is selective for the repeated feature itself (Grill-Spector, Henson, & Martin, 2006). The authors found evidence of neural adaptation only when visual stimuli appeared close to the outstretched hand, but not when the stimuli appeared in the same spatial position while the hand was placed on the torso (Brozzoli et al., 2011). Thus, in agreement with neurophysiological investigations in monkeys, they confirmed in humans that a set of interconnected premotor and posterior parietal regions specifically encodes the position of visual objects close to the body, in hand-centred coordinates. It is interesting to note that the set of areas described by Brozzoli et al. (2011) tightly overlapped with regions reported to respond to multisensory stimulations occurring in PPS (Brozzoli et al., 2012; Gentile, Petkova, & Ehrsson, 2010; Lloyd et al., 2006; Macaluso & Driver, 2005; Makin, Holmes, & Zohary, 2007), and yet were obtained via purely visual stimulation. This supports the idea that, although PPS is inherently multisensory, enhanced perceptual processing in it can be expected to occur for unimodal (e.g. visual) stimuli as well.

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3.5 Visual discrimination advantages in peripersonal space

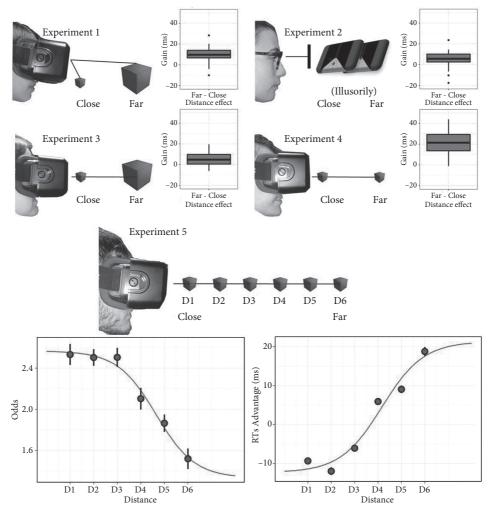
Purely visual advantages occurring in PPS, in contrast to multisensory ones, have been seldom reported (for a recent review, see de Vignemont, 2018), or have been framed in attentional terms.. The aforementioned near-hand effects for target detection, for example, actually consist of purely visual advantages, which occur without direct multisensory stimulation and depend on a *static* proprioceptive feedback. Notwithstanding the difficulty in disentangling attentional and perceptual processing (but see Makin et al., 2009; Reed et al., 2013), a recent study attempted to investigate how shape perception—classically considered a function of the ventral visual pathway (Goodale & Milner, 1992)—is affected by proximity (Blini et al., 2018).

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Blini et al. (2018) presented, to healthy participants, 3D shapes in the context of an immersive virtual reality environment (Figure 3.1). The task was adapted from that used by O'Connor et al. (2014), originally employed to test spatial sensitivity to reward. The geometrical shapes were presented either close (50 cm) or far (300 cm) from participants, thus within reach (in PPS) or not; the task consisted in a speeded discrimination of the presented shape (i.e. cube or sphere). As physical size scales, in everyday life, with depth (that is, farther shapes appear smaller), and this has arguably a profound impact on visual capacities (experiment 4), retinal size correction was applied. By equating the retinal size of close and far shapes, the latter appear illusorily bigger (because depth cues are accounted for by the visual system to estimate objects' size). Despite this striking visual illusion, participants

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Figure 3.1 In the study of Blini et al. (2018), the authors sought to assess perceptual discrimination abilities across different depths. Geometrical shapes were presented close (50 cm) or far (300 cm) from participants, in a 3D virtual environment (VE) or in the context of a visual illusion of depth (experiment 2); in this context, participants saw 2D images depicting perspective cues that created an illusory perception of depth. In experiments 1 (3D VE) and 2 (2D Ponzo-like illusion), closer shapes appeared in the bottom part of the participants' visual field (below a fixation cross), and farther ones in the upper visual field; in experiments 3, 4, and 5, all shapes were presented at the same height of the fixation cross. In experiments 1, 2, and 3, retinal size was kept constant for close and far stimuli, whereas in experiments 4 and 5 it was naturally scaled with distance. The authors consistently found an advantage in discriminating shapes when these were presented close as compared to far-difference depicted in the boxplots. Furthermore, a sigmoid trend could capture the spatial distribution of this, purely unimodal, advantage (experiment 5). Reproduced from Blini et al. Mind the Depth: Visual Perception of Shapes Is Better in Peripersonal Space. Psychol Sci. 2018 Nov;29(11):1868-1877. doi: 10.1177/0956797618795679. Epub 2018 Oct 4. Licensed under a Creative Commons-License 4.0 International

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were consistently faster in discriminating shapes appearing close to them (experiment 1, see Figure 3.1). Moreover, this effect could not be explained by upper/lower visual field confounds (i.e. in everyday life, close objects more commonly appear at the bottom of the visual field, which could therefore be privileged, Previc, 1990), or vergence eye-movements. First, the effect persisted when both shapes appeared at the same height—that of the fixation cross-to avoid any upper/lower visual field confound (experiment 3). Second, the effect persisted when the authors exploited a mere illusion of depth to avoid any vergence eyemovements confound (i.e. Ponzo illusion, experiment 2). In the illusion, perspectives cues (i.e. converging lines) were used as a background for two elements displayed at different heights, one of which therefore appeared illusorily farther away in space. Thus, this context stripped the task of many important depth indices, including vergence eye-movements, except for perspective cues. Interestingly, when Blini et al. (2018) probed the spatial distribution of this performance benefit, termed 'distance effect', by presenting shapes at six equispaced distances from the participants, they found that a sigmoid trend could adequately account for behavioural performances in terms of both accuracy and response times. As discussed in section 3.2, the sigmoidal trend has been considered a hallmark signature of PPS (multisensory) processing. Having described such a pattern for a purely unisensory (visual) task has one important theoretical implication: defining PPS as the region of space in which multisensory interaction occurs, and explaining PPS-related performance benefits in terms of multisensory convergence, is probably limiting in not properly accounting for what appears to be a more fundamental role of PPS circuitry in perception. Thus, researchers conducting multisensory studies should not neglect the fact that unimodal stimulations alone (at least in the visual modality) could capture behavioural signatures of PPS processing, and should be cautious before ascribing them to multisensory convergence.

3.6 Close is better

Recent proposals have questioned the view of PPS as a unitary construct, but rather declined several peripersonal space(s) according to their functional role (i.e. body protection vs goaldirected action), and therefore sensory and motor requirements (de Vignemont & Iannetti, 2015). The lowest common denominators of these PPS constructs appear, however, to encompass two elements: the body-which, by definition, is involved in any action towards an object or defensive behaviour—and the distance of a stimulus from it (i.e. proximity, in its parametric and continuous meaning). Recent frameworks have also stressed the taskdependent nature of PPS signatures, depending on 'the behavioural relevance of actions aiming to create or avoid contact between objects and the body' (Bufacchi & Iannetti, 2018). The latter definition can account for the manifold variables tapping onto PPS plasticity. The magnitude of PPS functional measurements would additionally vary according to several factors, listed under the umbrella concept of behavioural relevance—and, again, hardly distinguishable from enhanced attentional processing. However, proximity to the body by itself attributes saliency to a cue (Spaccasassi, Romano, & Maravita, 2019). Interestingly, behavioural sensitivity to reward decreases in the far space (O'Connor et al., 2014) as if the intrinsic or learned value of stimuli presented close to the body is automatically increased and gains in salience (Spaccasassi et al., 2019).

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One could therefore put forward the general prediction that *everything* would be enhanced when close to the body, as long as the task at hand offers sufficient sensitivity and it is, indeed, enhanced by increased attentional or PPS-specific processing. The latter two

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requirements are not trivial. First, behavioural effects can often reveal themselves as being very fragile and necessitating of well-powered and rigorous designs (Dosso & Kingstone, 2018, for the near-hand effects). Second, one may debate whether the increased attentional salience of body parts invariantly leads to improved behavioural performance on one task. There are, indeed, instances in which hands proximity seems to *hamper* the task 'at hand'. Abrams et al. (2008), for example, reported that people shifted their attention between items more slowly when their hands were near the display, in comparison with when their hands were placed farther apart. At odds with most previous near-hand effect studies, here both hands served as spatial attentional wands, thus possibly increasing the cost of shifting attention by modulating either the engagement or disengagement attentional components. Leveraging a classic inhibition of return paradigm, the same study indeed associated hands proximity to delayed attentional disengagement for cued locations (also see Qi et al., 2019). This can actually reflect a more thorough visual assessment of the region of space around the hands (i.e. visual enhancement, not hampering), which was supported by higher accuracy in target discrimination in the visual search task when hands were near to, as compared to far from, the display. There are, indeed, situations in which a more thorough assessment of the space around the hands or the body is critical—namely, when goal-oriented actions (including reactive/defensive ones) must be performed. In this case, sensory processing of objects presented in PPS may be effectively enhanced for the sake of guiding the motor system toward an optimal response (e.g. de Vignemont, 2018). Thus, this can be reconciled with views that stress the need of a purpose for PPS to serve in order to effectively enhance performance within PPS. In this chapter, we have focused on visual advantages, although such advantages may potentially extend to other modalities (e.g. audition, see Brungart, 1999; Brungart, Durlach, & Rabinowitz, 1999), or other dimensions of stimuli such as their perceived duration (Qi et al., 2019), provided the aforementioned conditions are met. More research is needed in this regard.

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The system for PPS coding is ancient and subtended by a large neural network, already optimized for monitoring the space close to the body, as well as the distance of stimuli from it. Two scenarios are possible, and not mutually exclusive: the PPS-specific system may easily be exploited by domain-general mechanisms for saliency attribution (i.e. spatial attention) to promote the processing of relevant stimuli; the specialized PPS processing may bias spatial attention toward the region of space in which it excels. At any rate, as reviewed earlier, the role of PPS processing extends, as a consequence, from multisensory interaction to more basic features of (unisensory) perception, including visual shape discrimination. Its contribution appears, therefore, much broader than previously thought. In essence, while facing a potentially annoying insect, there may be no need to surrender to a speed/accuracy trade-off in visual discrimination as a function of depth: PPS-specialized processing could provide performance benefits for both processes (fast reaction and proper identification of the threat) concurrently. For a defensive system to work efficiently (i.e. by being quick without bugging constantly for stimuli not deserving protection from), such an extra perceptual boost appears indeed very convenient (Makin et al., 2015, 2009).

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Abrams, R. A., Davoli, C. C., Du, F., Knapp III, W. H., & Paull, D. (2008). Altered vision near the hands. *Cognition*, 107(3), 1035–1047. https://doi.org/10.1016/j.cognition.2007.09.006

References

- C3.P23 Armony, J. L., & Dolan, R. J. (2002). Modulation of spatial attention by fear-conditioned stimuli: an event-related fMRI study. *Neuropsychologia*, 40(7), 817–826. https://doi.org/10.1016/ S0028-3932(01)00178-6
- C_{3-P24} Berti, A., & Frassinetti, F. (2000). When far becomes near: remapping of space by tool use. *Journal of Cognitive Neuroscience*, 12(3), 415–420.
- C3.P25 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. https://doi.org/10.1177/0956797618795679
- C3.P26 Brozzoli, C., Gentile, G., & Ehrsson, H. H. (2012). That's near my hand! Parietal and premotor coding of hand-centered space contributes to localization and self-attribution of the hand. *Journal of Neuroscience*, 32(42), 14573–14582. https://doi.org/10.1523/JNEUROSCI.2660-12.2012
- C3.P27 Brozzoli, C., Gentile, G., Petkova, V. I., & Ehrsson, H. H. (2011). fMRI adaptation reveals a cortical mechanism for the coding of space near the hand. *Journal of Neuroscience*, *31*(24), 9023–9031. https://doi.org/10.1523/JNEUROSCI.1172-11.2011
- C3.P28 Brozzoli, C., Pavani, F., Urquizar, C., Cardinali, L., & Farnè, A. (2009). Grasping actions remap peripersonal space. *NeuroReport*, 20(10), 913–917. https://doi.org/10.1097/ WNR.0b013e32832c0b9b
- C_{3.P29} Brungart, D. S. (1999). Auditory localization of nearby sources. III. Stimulus effects. *Journal of the Acoustical Society of America*, *106*(6), 3589–3602. https://doi.org/10.1121/1.428212
- C_{3.P30} Brungart, D. S., Durlach, N. I., & Rabinowitz, W. M. (1999). Auditory localization of nearby sources. II. Localization of a broadband source. *Journal of the Acoustical Society of America*, 106(4), 1956–1968. https://doi.org/10.1121/1.427943
- C_{3.P31} Bufacchi, R. J., & Iannetti, G. D. (2018). An action field theory of peripersonal space. *Trends in Cognitive Sciences*, 22(12), 1076–1090. https://doi.org/10.1016/j.tics.2018.09.004
- C3.P32 Bush, W. S., & Vecera, S. P. (2014). Differential effect of one versus two hands on visual processing. Cognition, 133(1), 232–237. https://doi.org/10.1016/j.cognition.2014.06.014
- C_{3.P33} Canzoneri, E., Magosso, E., & Serino, A. (2012). Dynamic sounds capture the boundaries of peripersonal space representation in humans. *PLoS ONE*, 7(9), e44306. https://doi.org/10.1371/ journal.pone.0044306
- C3.P34 Cardinali, L., Brozzoli, C., & Farnè, A. (2009). Peripersonal space and body schema: two labels for the same concept? *Brain Topography*, 21(3–4), 252–260. https://doi.org/10.1007/s10548-009-0092-7
- C3.P35 Cardinali, L., Frassinetti, F., Brozzoli, C., Urquizar, C., Roy, A. C., & Farnè, A. (2009). Tool-use induces morphological updating of the body schema. *Current Biology*, 19(12), R478–R479. https://doi.org/ 10.1016/j.cub.2009.05.009
- C3.P36 Cartaud, A., Ruggiero, G., Ott, L., Iachini, T., & Coello, Y. (2018). Physiological response to facial expressions in peripersonal space determines interpersonal distance in a social interaction context. *Frontiers in Psychology*, 9. https://doi.org/10.3389/fpsyg.2018.00657
- C3.P37 Cléry, J., Guipponi, O., Odouard, S., Wardak, C., & Hamed, S. B. (2015). Impact prediction by looming visual stimuli enhances tactile detection. *Journal of Neuroscience*, 35(10), 4179–4189. https://doi.org/10.1523/JNEUROSCI.3031-14.2015
- C3.P38 Colby, C. L., Duhamel, J. R., & Goldberg, M. E. (1993). Ventral intraparietal area of the macaque: anatomic location and visual response properties. *Journal of Neurophysiology*, 69(3), 902–914.
- C3.P39 Couyoumdjian, A., Nocera, F. D., & Ferlazzo, F. (2003). Functional representation of 3d space in endogenous attention shifts. *Quarterly Journal of Experimental Psychology Section A*, 56(1), 155–183. https://doi.org/10.1080/02724980244000215

()

()

blini, farnè, brozzoli, and hadj-bouziane 57

- C3.P40 de Vignemont, Frédérique. (2018). Peripersonal perception in action. Synthese. https://doi.org/ 10.1007/s11229-018-01962-4
- C_{3.P41} de Vignemont, F., & Iannetti, G. D. (2015). How many peripersonal spaces? *Neuropsychologia*, 70, 327–334. https://doi.org/10.1016/j.neuropsychologia.2014.11.018
- C_{3.P42} di Pellegrino, G., & Frassinetti, F. (2000). Direct evidence from parietal extinction of enhancement of visual attention near a visible hand. *Current Biology*, 10(22), 1475–1477. https://doi.org/10.1016/S0960-9822(00)00809-5
- C_{3.P43} di Pellegrino, G., & Làdavas, E. (2015). Peripersonal space in the brain. *Neuropsychologia*, 66(Supplement C), 126–133. https://doi.org/10.1016/j.neuropsychologia.2014.11.011
- C3.P44 Dosso, J. A., & Kingstone, A. (2018). The fragility of the near-hand effect. Collabra: Psychology, 4(1), 27. https://doi.org/10.1525/collabra.167
- C3.P45 Eimer, M., Velzen, J. van, & Driver, J. (2002). Cross-modal interactions between audition, touch, and vision in endogenous spatial attention: ERP evidence on preparatory states and sensory modulations. *Journal of Cognitive Neuroscience*, 14(2), 254–271. https://doi.org/10.1162/089892902317236885
- C3.P46 Farnè, A., & Làdavas, E. (2000). Dynamic size-change of hand peripersonal space following tool use. NeuroReport, 11(8), 1645.
- C_{3.P47} Ferri, F., Panadura-Jiménez, A., Väljamäe, A., Vastano, R., & Costantini, M. (2015). Emotion-inducing approaching sounds shape the boundaries of multisensory peripersonal space. *Neuropsychologia*, 70(Supplement C), 468–475. https://doi.org/10.1016/j.neuropsychologia.2015.03.001
- C3.P48 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.
- C3.P49 Franconeri, S. L., & Simons, D. J. (2003). Moving and looming stimuli capture attention. Perception & Psychophysics, 65(7), 999–1010. https://doi.org/10.3758/BF03194829
- C_{3.P50} Freud, E., Culham, J. C., Plaut, D. C., & Behrmann, M. (2017). The large-scale organization of shape processing in the ventral and dorsal pathways. *ELife*, 6. https://doi.org/10.7554/eLife.27576
- C3.P51
 Freud, E., Ganel, T., Shelef, I., Hammer, M. D., Avidan, G., & Behrmann, M. (2017). Three-dimensional representations of objects in dorsal cortex are dissociable from those in ventral cortex. *Cerebral Cortex*, 27(1), 422–434. https://doi.org/10.1093/cercor/bhv229
- C₃P₅₂ Freud, E., Plaut, D. C., & Behrmann, M. (2016). 'What' is happening in the dorsal visual pathway. *Trends in Cognitive Sciences*, 20(10), 773–784. https://doi.org/10.1016/j.tics.2016.08.003
- C3.P53 Gawryszewski, L. de G., Riggio, L., Rizzolatti, G., & Umiltá, C. (1987). Movements of attention in the three spatial dimensions and the meaning of 'neutral' cues. *Neuropsychologia*, 25(1), 19–29. https://doi.org/10.1016/0028-3932(87)90040-6
- C_{3.P54} Gentile, G., Petkova, V. I., & Ehrsson, H. H. (2010). Integration of visual and tactile signals from the hand in the human brain: an fMRI study. *Journal of Neurophysiology*, *105*(2), 910–922. https://doi. org/10.1152/jn.00840.2010
- C3.P55 Ghazanfar, A. A., Neuhoff, J. G., & Logothetis, N. K. (2002). Auditory looming perception in rhesus monkeys. *Proceedings of the National Academy of Sciences*, 99(24), 15755–15757. https://doi.org/ 10.1073/pnas.242469699
- C3.P56 Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 15(1), 20–25. https://doi.org/10.1016/0166-2236(92)90344-8

()

- C3.P57 Goodhew, S. C., Edwards, M., Ferber, S., & Pratt, J. (2015). Altered visual perception near the hands: a critical review of attentional and neurophysiological models. *Neuroscience & Biobehavioral Reviews*, 55, 223–233. https://doi.org/10.1016/j.neubiorev.2015.05.006
- C_{3.P58} Goodhew, S. C., Gozli, D. G., Ferber, S., & Pratt, J. (2013). Reduced temporal fusion in near-hand space. *Psychological Science*, *24*(6), 891–900. https://doi.org/10.1177/0956797612463402
- C3.P59 Gozli, D. G., West, G. L., & Pratt, J. (2012). Hand position alters vision by biasing processing through different visual pathways. *Cognition*, 124(2), 244–250. https://doi.org/10.1016/ j.cognition.2012.04.008
- C3.P60 Graziano, M. S. A., & Cooke, D. F. (2006). Parieto-frontal interactions, personal space, and defensive behavior. *Neuropsychologia*, 44(6), 845–859. https://doi.org/10.1016/j.neuropsycholo gia.2005.09.009
- C3.P61 Graziano, M. S. A., & Gross, C. G. (1993). A bimodal map of space: somatosensory receptive fields in the macaque putamen with corresponding visual receptive fields. *Experimental Brain Research*, 97(1), 96–109. https://doi.org/10.1007/BF00228820
- C3.P62 Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: neural models of stimulus-specific effects. *Trends in Cognitive Sciences*, 10(1), 14–23. https://doi.org/10.1016/ j.tics.2005.11.006
- C_{3.P63} Hall, E. T. (1966). *The hidden dimension*. New York: Doubleday & Co.
- c_{3.P64} Hediger, H. (1950). *Wild animals in captivity*. London: Butterworths Scientific Publications.
- C_{3.P65} 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. https://doi.org/10.1093/brain/97.4.673
- C_{3.P66} Iriki, A., Tanaka, M., & Iwamura, Y. (1996). Coding of modified body schema during tool use by macaque postcentral neurones. *NeuroReport*, 7(14), 2325–2330.
- C3.P67 Koster, E. H. W., Crombez, G., Van Damme, S., Verschuere, B., & De Houwer, J. (2004). Does imminent threat capture and hold attention? *Emotion*, 4(3), 312–317. https://doi.org/10.1037/1528-3542.4.3.312
- C3.P68 Làdavas, E., Farnè, A., Zeloni, G., & di Pellegrino, G. P. (2000). Seeing or not seeing where your hands are. *Experimental Brain Research*, *131*(4), 458–467. https://doi.org/10.1007/s002219900264
- C3.P69 Làdavas, Elisabetta, di Pellegrino, G., 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. https://doi.org/10.1162/089892998562988
- C3.P70 Lin, J. Y., Murray, S. O., & Boynton, G. M. (2009). Capture of attention to threatening stimuli without perceptual awareness. *Current Biology*, 19(13), 1118–1122. https://doi.org/10.1016/ j.cub.2009.05.021
- C3.P71 Lloyd, D., Morrison, I., & Roberts, N. (2006). Role for human posterior parietal cortex in visual processing of aversive objects in peripersonal space. *Journal of Neurophysiology*, 95(1), 205–214. https://doi.org/10.1152/jn.00614.2005
- C3.P72 Losier, B. J., & Klein, R. M. (2004). Covert orienting within peripersonal and extrapersonal space: young adults. *Cognitive Brain Research*, 19(3), 269–274. https://doi.org/10.1016/j.cogbrainres.2004.01.002
- C_{3.P73} Macaluso, E., & Driver, J. (2005). Multisensory spatial interactions: a window onto functional integration in the human brain. *Trends in Neurosciences*, 28(5), 264–271. https://doi.org/10.1016/j.tins.2005.03.008

()

BLINI, FARNÈ, BROZZOLI, AND HADJ-BOUZIANE 59

- C3.P74 Maier, J. X., Neuhoff, J. G., Logothetis, N. K., & Ghazanfar, A. A. (2004). Multisensory integration of looming signals by rhesus monkeys. *Neuron*, 43(2), 177–181. https://doi.org/10.1016/ j.neuron.2004.06.027
- C3.P75 Makin, T. R., Brozzoli, C., Cardinali, L., Holmes, N. P., & Farnè, A. (2015). Left or right? Rapid visuomotor coding of hand laterality during motor decisions. *Cortex*, 64, 289–292. https://doi.org/ 10.1016/j.cortex.2014.12.004
- C3.P76 Makin, T. R., Holmes, N. P., Brozzoli, C., & Farnè, A. (2012). Keeping the world at hand: rapid visuo-motor processing for hand-object interactions. *Experimental Brain Research*, 219(4), 421–428. https://doi.org/10.1007/s00221-012-3089-5
- C3.P77 Makin, T. R., Holmes, N. P., Brozzoli, C., Rossetti, Y., & Farnè, A. (2009). Coding of visual space during motor preparation: approaching objects rapidly modulate corticospinal excitability in hand-centered coordinates. *Journal of Neuroscience*, 29(38), 11841–11851. https://doi.org/10.1523/JNEUROSCI.2955-09.2009
- C3.P78 Makin, T. R., Holmes, N. P., & Zohary, E. (2007). Is that near my hand? Multisensory representation of peripersonal space in human intraparietal sulcus. *Journal of Neuroscience*, 27(4), 731–740. https:// doi.org/10.1523/JNEUROSCI.3653-06.2007
- C3.P79 Maravita, A., & Iriki, A. (2004). Tools for the body (schema). *Trends in Cognitive Sciences*, 8(2), 79–86. https://doi.org/10.1016/j.tics.2003.12.008
- C3.P80 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. https://doi.org/10.1016/S0960-9822(03)00449-4
- C3.P81 Maravita, A., Spence, C., Kennett, S., & Driver, J. (2002). Tool-use changes multimodal spatial interactions between vision and touch in normal humans. *Cognition*, 83(2), B25–B34. https://doi.org/ 10.1016/S0010-0277(02)00003-3
- C3.P82 Milner, A. D., & Goodale, M. A. (2008). Two visual systems re-viewed. *Neuropsychologia*, 46(3), 774– 785. https://doi.org/10.1016/j.neuropsychologia.2007.10.005
- C3.P83 Murata, A., Fadiga, L., Fogassi, L., Gallese, V., Raos, V., & Rizzolatti, G. (1997). Object representation in the ventral premotor cortex (area F5) of the monkey. *Journal of Neurophysiology*, 78(4), 2226–2230.
- C3.P84 Neppi-Mòdona, M., Auclair, D., Sirigu, A., & Duhamel, J.-R. (2004). Spatial coding of the predicted impact location of a looming object. *Current Biology*, 14(13), 1174–1180. https://doi.org/10.1016/ j.cub.2004.06.047
- C3.P85 Noel, J.-P., Grivaz, P., Marmaroli, P., Lissek, H., Blanke, O., & Serino, A. (2015). Full body action remapping of peripersonal space: the case of walking. *Neuropsychologia*, 70, 375–384. https://doi.org/ 10.1016/j.neuropsychologia.2014.08.030
- C3.P86 O'Connor, D. A., Meade, B., Carter, O., Rossiter, S., & Hester, R. (2014). Behavioral sensitivity to reward is reduced for far objects. *Psychological Science*, *25*(1), 271–277. https://doi.org/10.1177/ 0956797613503663
- C3.P87 Plewan, T., & Rinkenauer, G. (2017). Simple reaction time and size–distance integration in virtual 3D space. *Psychological Research*, *81*(3), 653–663. https://doi.org/10.1007/s00426-016-0769-y
- C3.P88 Previc, F. H. (1990). Functional specialization in the lower and upper visual fields in humans: its ecological origins and neurophysiological implications. *Behavioral and Brain Sciences*, *13*(3), 519–542.
- C3.P89 Qi, Y., Wang, X., He, X., & Du, F. (2019). Prolonged subjective duration near the hands: effects of hand proximity on temporal reproduction. *Psychonomic Bulletin & Review*. https://doi.org/10.3758/s13423-019-01614-9

()

C3.P90	Quinlan, D. J., & Culham, J. C. (2007). fMRI reveals a preference for near viewing in the human parieto- occipital cortex. <i>NeuroImage</i> , <i>36</i> (1), 167–187. https://doi.org/10.1016/j.neuroimage.2007.02.029
C3.P91	Reed, C. L., Leland, D. S., Brekke, B., & Hartley, A. A. (2013). Attention's grasp: early and late hand proximity effects on visual evoked potentials. <i>Frontiers in Psychology</i> , <i>4</i> , 420–420. https://doi.org/ 10.3389/fpsyg.2013.00420
C3.P92	Reed, Catherine L., Grubb, J. D., & Steele, C. (2006). Hands up: attentional prioritization of space near the hand. <i>Journal of Experimental Psychology: Human Perception and Performance</i> , <i>32</i> (1), 166. https://doi.org/10.1037/0096-1523.32.1.166
C3.P93	Rizzolatti, G., Scandolara, C., Matelli, M., & Gentilucci, M. (1981). Afferent properties of periarcuate neurons in macaque monkeys. II. Visual responses. <i>Behavioural Brain Research</i> , 2(2), 147–163. https://doi.org/10.1016/0166-4328(81)90053-X
C3.P94	Ruggiero, G., Frassinetti, F., Coello, Y., Rapuano, M., di Cola, A. S., & Iachini, T. (2017). The effect of facial expressions on peripersonal and interpersonal spaces. <i>Psychological Research</i> , <i>81</i> (6), 1232–1240. https://doi.org/10.1007/s00426-016-0806-x
C3.P95	Sambo, C. F., & Iannetti, G. D. (2013). Better safe than sorry? The safety margin surrounding the body is increased by anxiety. <i>Journal of Neuroscience</i> , <i>33</i> (35), 14225–14230. https://doi.org/10.1523/JNEUROSCI.0706-13.2013
C3.P96	Schiff, W., Caviness, J. A., & Gibson, J. J. (1962). Persistent fear responses in rhesus monkeys to the optical stimulus of 'looming'. <i>Science</i> , <i>136</i> (3520), 982–983. https://doi.org/10.1126/science.136.3520.982
C3.P97	Shelton, P. A., Bowers, D., & Heilman, K. M. (1990). Peripersonal and vertical neglect. <i>Brain</i> , <i>113</i> (1), 191–205. https://doi.org/10.1093/brain/113.1.191
C3.P98	Spaccasassi, C., Romano, D., & Maravita, A. (2019). Everything is worth when it is close to my body: how spatial proximity and stimulus valence affect visuo-tactile integration. <i>Acta Psychologica</i> , <i>192</i> , 42–51. https://doi.org/10.1016/j.actpsy.2018.10.013
C3.P99	Spence, C., Pavani, F., & Driver, J. (2004). Spatial constraints on visual-tactile cross-modal distractor congruency effects. <i>Cognitive, Affective, & Behavioral Neuroscience,</i> 4(2), 148–169. https://doi.org/10.3758/CABN.4.2.148
C3.P100	Sposito, A., Bolognini, N., Vallar, G., & Maravita, A. (2012). Extension of perceived arm length fol- lowing tool-use: clues to plasticity of body metrics. <i>Neuropsychologia</i> , 50(9), 2187–2194. https:// doi.org/10.1016/j.neuropsychologia.2012.05.022
C3.P101	Teneggi, C., Canzoneri, E., di Pellegrino, G., & Serino, A. (2013). Social modulation of peripersonal space boundaries. <i>Current Biology</i> , <i>23</i> (5), 406–411. https://doi.org/10.1016/j.cub.2013.01.043
C3.P102	Wang, A., Li, Y., Zhang, M., & Chen, Q. (2016). The role of parieto-occipital junction in the interaction between dorsal and ventral streams in disparity-defined near and far space processing. <i>PLoS ONE</i> , <i>11</i> (3), e0151838. https://doi.org/10.1371/journal.pone.0151838

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