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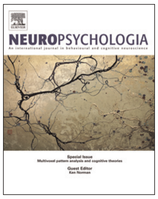

How many peripersonal spaces?

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ABSTRACT

Several studies in humans and non-human primates have explored and characterised the features of the cortical representation of the portion of space immediately surrounding the body – the peripersonal space. In this paper we ask the following question: is it legitimate to assume that there is a single representation of peripersonal space? This issue has rarely been addressed in the literature, leading to much confusion, especially when one compares results reported in social psychology and in cognitive neuroscience. Indeed, studies in both fields explore and refer to more or less the same portion of space, but the terminology used to describe it differs greatly. Therefore, the definition of this portion of space immediately surrounding the body has remained quite vague, allowing for many variations. Here, we propose a dual model of peripersonal space, based on a clear functional distinction between *bodily protection* and *goal-directed action*. We argue that the two functions of peripersonal space require distinct sensory and motor processes that obey different principles. Furthermore, we highlight that the effects of anxiety and tool use on peripersonal space provide empirical support to our distinction.

1. Introduction

It is now well accepted that the central nervous system represents differently and separately sensory stimuli happening on the body, in the space immediately surrounding the body, and in the space beyond reach, in which the individual navigates. Hence, objects and events are processed differentially depending on where they are located in the environment. Interestingly, there may be different ways for the location of objects and events to be represented in each of these three spatial domains – let us call them *bodily space*, *peripersonal space*, and *extrapersonal space*. This has already been shown for objects and events located in bodily space and extrapersonal space. Indeed, in bodily space sensory events can be represented in at least two different ways: in relation to action (i.e. body schema) or in relation to perception (i.e. body image). In extrapersonal space sensory events can be represented within an egocentric frame of reference (i.e. in relation to oneself), or within an allocentric frame of reference (i.e. in relation to other objects or events). An interesting question now is whether there are also distinct ways to represent object and events in the third spatial domain – the *peripersonal space* (hereafter PPS).

This has rarely been addressed in the literature, leading to much confusion, especially when combining results reported in social psychology and in cognitive neuroscience. Both fields refer to more or less the same spatial area, namely, the space immediately surrounding the body. However, the terminology used to describe it varies greatly (e.g. flight zone, personal space, peripersonal space, reaching space). Therefore, the definition of this portion of space remains vague, allowing for many variations. There are, for example, variations in its spatial extent: more or less close to the body, between few and 50 cm. There are also social differences: the space of preys, predators, and objects. There are, finally, functional differences: the space for protection, joint action, and goal-directed action. All these differences urge us to ask the following questions: is it legitimate to assume that there is a single type of PPS representation? If there are more, what distinguishes them?

Unfortunately, the available empirical evidence is not sufficient to answer. In that respect, this paper will be mainly exploratory and speculative. Our objective is only to lay the groundwork in the analysis of possibly distinct types of PPS. Further experimental evidence will be required to validate or invalidate the hypotheses we will make here. We will propose a dual model of PPS, with a clear functional distinction between *protection of the body* and *goal-directed action*. We will argue that the two functions of PPS require distinct processes that obey different principles. Furthermore, we will analyse the effect of anxiety and the effect of tool use on PPS, and suggest that they might offer some empirical support to our distinction.

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2. Definitional issues

In their seminal paper describing neurons activated both by tactile and visual stimuli presented in the space surrounding the body of a monkey, Rizzolatti et al. (1981) first coined the term “peripersonal space”. However, the idea that there is a special zone surrounding the body can already be found in the work of the Swiss biologist Heini Hediger (1955), the director of the Zurich zoo, who noted that animals display different behaviours depending on the proximity of other animals. Typically, when a potential predator is close to the animal, entering what is known as its *flight distance*, the animal flees or withdraws. But a tame animal will have a flight distance of zero. Even when the other animal belongs to the same species, there is a distance, what Hediger called the *personal distance*, at which the proximity of conspecifics becomes no longer tolerable.

Since Hediger and Rizzolatti, numerous studies in monkeys and humans, in both healthy and pathological states, have explored the functional features of this specific area close to the body (for review, see Brozzoli et al. (2012)). These features can be summarised as follows:

(i) Bodily reference frame: the PPS is anchored to specific body parts, and moves when the body parts move.
(ii) Multisensory vigilance: the perception of objects and events occurring in PPS triggers the allocation of multisensory attention.
(iii) Sensorimotor relevance: objects and events perceived in PPS are represented in terms of possible actions.
(iv) Plasticity: the boundaries of PPS are flexible.

Based on these functional features, the PPS has been defined as follows:

> “Peripersonal space contains the objects with which one can interact in the here and now, specifies our private area during social interactions and encompasses the obstacles or dangers to which the organism must pay attention in order to preserve its integrity” Coello et al. (2012, p. S131)

This summary reveals the complexity of PPS, and perhaps, the confusion that surrounds this notion. Indeed, it assumes that a single PPS can subserve diverse functions. But is this assumption justified? An urgent question is indeed to what extent those functions require distinct types of PPS representations. We will first isolate the two major functions highlighted in this definition of PPS: (i) to take advantage of opportunities within the PPS (e.g., to grasp food and useful objects) and (ii) to protect the body from potential threats occurring within the PPS (e.g., to avoid a bee flying towards the face). We will then discuss the implications that the functional distinction between goal-directed and protective actions has on way the brain represents PPS. More specifically, two alternative hypotheses must be teased apart: one and the same peripersonal representation subserving both goal-directed and protective actions versus two distinct peripersonal representations, one for each of these two functions.

In several cognitive domains it has been observed that differences in function correspond to differences in information processing. The most well known functional distinction is between the two anatomical pathways of visual processing for perception and for action: the ventral pathway for visual judgement and the dorsal pathway for sensorimotor control (Milner and Goodale, 1995). Another example of the application of such Perception-Action model can be found in the case of body representation. Indeed, some taxonomies propose that there are at least two types of body representations, some dedicated to action (i.e. body schema) and others to perceptual judgments (i.e. body image, which includes body structural description and body semantic) (Schwoebel and Coslett, 2005; de Vignemont, 2010; Dijkerman and de Haan, 2007; Paillard, 1999). We do not suggest that one can simply apply the Perception-Action model to PPS. Both functions of PPS are action-oriented, whether for object grasping or for body protection. Hence, the representations of PPS are sensorimotor regardless of the purpose of the final motor output. Nevertheless, the Perception-Action model can be taken as an example that functional differences can have strong implications for the way the world is represented. How the brain uses the available sensory information can partly determine how it encodes it. It is thus appropriate to ask how many peripersonal representations exist. Here we will consider two explanatory models, which we call the *Swiss army-knife model* and the *Specialist model* (Fig. 1).

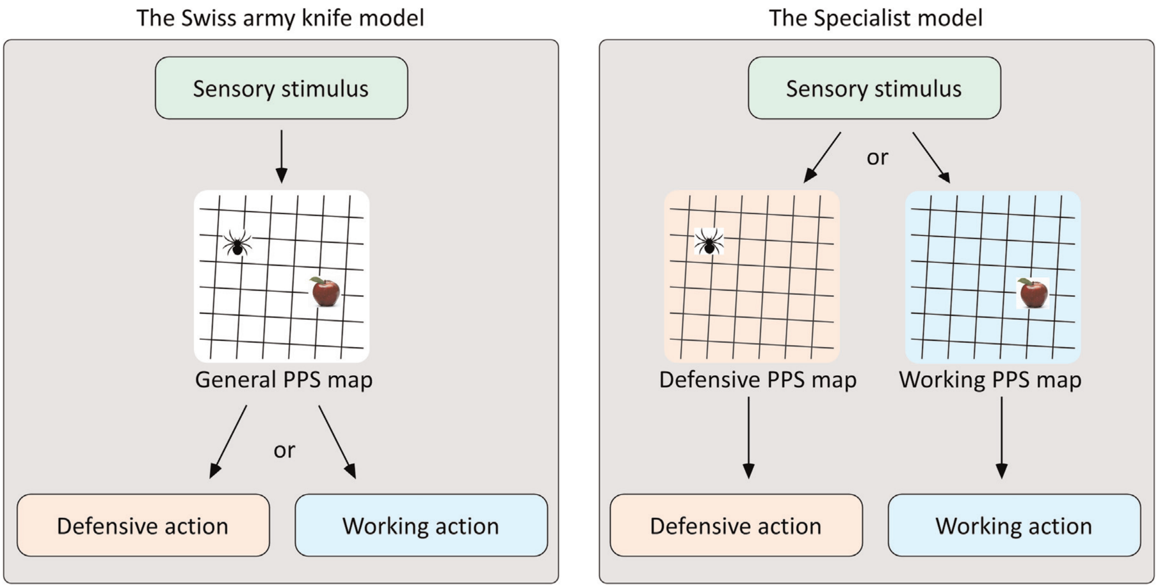

Fig. 1. Two models of peripersonal space.

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3. Two models of peripersonal space

3.1. The Swiss army-knife model

According to the Swiss army-knife model, there is a single cortical map representing the PPS. This map subserves the two functions, in the same way as a Swiss army knife can be used either to protect oneself or to open a bottle. Similarly, a single peripersonal representation can result in different actions depending on the context. In this model, both an apple that one wants to eat and a spider approaching the body are mapped on the same peripersonal representation, although the two stimuli trigger different responses depending on their contextual meaning. The precise mapping of the location of the apple then activates reaching and grasping movements, whereas the mapping of the location of the spider approaching the body (or being already on the body) activates defensive motor responses. In this Swiss army-knife model, the context differs and determines the final motor outcome, but the stimulus is always mapped on the same peripersonal representation, regardless of its contextual meaning (Fig. 1, left panel).

3.2. The Specialist model

By contrast, in the Specialist model, peripersonal representations are functionally defined. Unlike a multifunctional Swiss army knife, a specialist has a unique expertise to which he or she is fully dedicated. In such a function-specific model, one should then distinguish at least two types of peripersonal representations: the representation of PPS involved in the protection of the body, called the *protective* (or *defensive*) *space* (Sambo and Iannetti, 2013), and the representation of PPS involved in goal-directed action, called the *working space* (Rizzolatti et al., 1997). It should be noted that the PPS may have more than the two described functions, and thus there would possibly be more peripersonal representations; however, for the purpose of this opinion paper we shall focus on the two representations for which there is stronger experimental evidence. In the Specialist model, the meaning of the stimulus defines onto which peripersonal representation the stimulus is mapped (Fig. 1, right panel). It should also be noted that to posit distinct action-specific peripersonal representations does not preclude multiple representations of the same stimulus on the two maps, as well as interactions between them. For example, it has been shown that the perception of what can be reached is modulated by the potential threat raised by the object (Coello et al., 2012).

Finally, the Specialist model does not assume that protective and working spaces evolved independently. Arguably, although the protective space is likely to be the most ancestral, part of its sensorimotor processes could have been later co-opted for the working space (Brozzoli et al., 2012). This is in line with the "massive redeployment" hypothesis proposed by Anderson (2007, 2010) and by Dehaene and Cohen (2007), among others. On this view, some brain regions that were originally shaped by natural selection for a specific cognitive function are recycled to support other cognitive functions. The hypothesis that brain regions are recycled makes sense from an evolutionary perspective, as it is more parsimonious than developing new neural systems. But if resources can be shared between two functions, then it may be thought that those two functions are subserved by a single mechanism, like in the Swiss army-knife model. However, the fact that the working space might have exploited/recycled part of the resources dedicated to the protective space does not invalidate the Specialist model. Indeed, the functional distinction between working and protective space holds as long as they are not identical. Let us imagine that the shape or the extension of the protective space is disrupted by wearing a helmet or having a small defensive screen close to the body (Sambo et al., 2012b). This modulation is not expected to alter the working space and the consequent goal-oriented processes (e.g. an object can still be reached when wearing a helmet). Therefore, only protective space will be modified. Sharing part of the neural resources is thus fully compatible with specialized cognitive abilities that can be specifically altered or impaired (Carruthers, 2006; Jungé and Dennett, 2010).

Herein, we shall consider and discuss arguments for and against the two models and suggest experiments that might help clarifying which PPS model is correct. Unfortunately, there has been no attempt to devise experiments aiming to test whether the two PPS are differentially represented in the brain. In addition, deficits of PPS are rare in patients with brain lesion, and still seldom explicitly looked for. We are only aware of a single study showing that neglect can be modulated by the fearful value of the perceived object (Vuilleumier and Schwartz, 2001). This study, however, does not provide information in favour of either the Swiss army-knife model or the Specialist model. Finally, despite fundamental conceptual differences between the two functions, it is difficult to operationalise the distinction between them at the experimental level. Indeed, both types of sensorimotor functions recruit multisensory attention, which has been used as the main signature of the extent of the PPS. Multisensory attention is typically assessed with the cross-modal congruency task, in which participants are asked to perform a speeded discrimination of the location of a vibro-tactile stimulus presented either on the index finger or on the thumb, while trying to ignore visual distractors presented simultaneously at either congruent or incongruent positions. Crucially, incongruent visual distractors interfere with the tactile discrimination (i.e. participants are both slower and less accurate) only when visual stimuli are close to the body (Spence et al., 2004). But what does such a cross-modal congruency effect reveal precisely, the extent of the working space or the extent of the protective space? Most probably, it is relevant for both. Therefore, the cross-modal congruency task, at least in this form, cannot help in determining whether there are one or two types of PPS. A few studies investigated whether the meaning of the visual stimulus (neutral versus dangerous) alters the distance from the body at which the cross-modal congruency effect is modulated (Coello et al., 2012; Lloyd et al., 2006; Anelli et al., 2013; Poliakoff et al., 2007). For example, Poliakoff et al. (2007) showed that the cross-modal congruency effect was enhanced if the visual stimulus near the hand was a snake rather than a neutral object. Also relevant is the study by Lloyd et al. (2006), who described an increase in activation in posterior parietal areas when a threatening object (a syringe) was seen approaching the hand rather a non-threatening object (Q-tip). They concluded:

> "The main functional components of this network are body-part-centred encoding of the space surrounding the hand […], discriminating the motivational relevance of objects in that space (here, whether the probe was noxious or innocuous), and elaborating the motivational-affective sensorimotor representation of the stimulus in terms of appropriate motor responses." Lloyd et al. (2006, p. 211)

However, a crucial confound in both studies is the different saliency of the stimuli. Indeed, a snake is not only more threatening, but also more salient than a neutral object. Therefore, it is not possible to rule out the possibility that the saliency of the stimulus, rather than its threat value, was the factor determining the observed effect. To address this issue, a key experimental design requirement is that stimuli of equal saliency, but with different threat value, should be used. To conclude, more empirical

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evidence is required to decide whether there are one or two distinct types of peripersonal representation. In this paper we offer some beginning of an answer to this question.

4. The motor signatures of PPS

In the motor domain the distinction between the two types of PPS is reasonably clear. Each function corresponds to a specific set of actions: goal-oriented actions and protective actions. Let us imagine that you are cooking. You can then hold the knife to cut the carrots (goal-directed action) or you can withdraw your hand from the hot handle of the pot (defensive action). There is, however, a vast repertoire of protective behaviours, such as squinting, ducking, withdrawing from the direction of the potential threat, navigational veering during locomotion to avoid obstacles, protecting a body part with another one, and so forth (Bracha, 2004; Dosey and Meisels, 1969; Graziano and Cooke, 2006). Some of these defensive behaviours require avoiding the object that is potentially hazardous. For example, human participants lean away from a visible object (Bonnet et al., 2010), and, when walking through a doorway tilt their shoulders to protect their body from hitting the doorframe (Warren Jr. and Whang, 1987). Other defensive behaviours require no action at all, like freezing or playing dead. For example, an intense sound near the hand can cause a defensive-like freeze response in humans (Avenanti et al., 2012), resembling that observed during the presentation of noxious stimuli or potential threats (Cantello et al., 2000; Furubayashi et al., 2000). Makin et al. (2009) found that motor excitability is reduced as a function of the distance between an approaching ball and the hand – an effect that most probably reflects the proactive inhibition of avoidance responses elicited by the approaching object. Another category of defensive behaviours involves goal-directed actions. For example, using a spoon instead of a finger to stir a hot soup clearly avoids body damage. One can also grasp the spider on the arm to defend oneself. Therefore, the defence of the body may require the use of objects. The two sets of actions – goal-directed and defensive – can thus sometimes overlap. However, most goal-directed actions are not defensive, and defensive actions do not often require goal-directed actions. What therefore matters is the *purpose* for which the movement is performed.

Because of this functional dichotomy, the two kinds of PPS give priority to different body parts in the allocation of attentional and motor resources. The working space is heavily biased towards the hand, and it can sometimes be referred to as the “grasping space” (Brain, 1941) or the “reaching space”[1] (i.e. how far one can reach without moving the torso), although this does not mean that it is exclusively hand-centred. By contrast, an object entering the protective space can be a threat for any part of the body. Thus, although a fine mapping of the shape of the protective space has not been achieved, we expect the protective space to surround the whole body. If there are body territories whose defence needs to be prioritised, then the face matters more than the hand – as suggested by the fact that one automatically protects the face with the hands, and that close to the face there is an “ultra-near” area within which stimuli elicit particularly enhanced defensive responses (Sambo and Iannetti, 2013).

One may also claim that it is not only the repertoire of motor responses and their spatial organisation that can differ between the protective space and the working space, but also their automaticity, at least to some extent. One way to distinguish the two types of sensorimotor representation is indeed to assume that the working space is more often associated to voluntary movements, and the protective space to automatic movements. This is not to say that the evaluation of the level of threat is entirely automatic. Nor it is to say that goal-directed action can never be automatic, and bodily defence never voluntary.

Although most movements within working space are voluntary, some, like those triggered by environmental affordances, can be automatic. Gibson's (1979) original hypothesis of affordance has been reinforced by the discovery of neurons activated when the monkeys observe graspable objects (Jeannerod et al., 1995). In humans, automatic motor activations were described during the observation of manipulable objects (Chao and Martin, 2000; Grafton et al., 1997). Costantini et al. (2010) explicitly showed that the influence of affordances on the motor system was tightly linked to their location in PPS. They found that the spatial alignment of the object with the body affected the subsequent motor response only if the object was within the working space. For instance, subjects were quicker in using the left hand than the right hand to grasp the handle of a mug that was aligned with the left hand. Furthermore, the working space is automatically and constantly updated while the grasping action unfolds (Brozzoli et al., 2009).

By contrast, the majority of movements within the protective space are largely automatic. However, this does not preclude influence from high-level cognitive factors. Indeed, although some defensive responses are largely stereotyped (e.g. the blink reflex and the limb withdrawal reflex) (Cruccu and Deuschl, 2000; Sandrini et al., 2005) and mediated by subcortical pathways that enable rapid reaction to potentially noxious stimuli, they can undergo a significant top-down modulation. For example, directing attention away from the stimulus can reduce the magnitude of the lower limb withdrawal reflex (R3) by approximately 50% (Willer et al., 1979). More importantly, related to the topic of this article, is the observation that such defensive reflex responses can be finely modulated by the position of the stimulus within the PPS, and, in particular, in relation to the area of the body for which the reflex response provides protection (Sambo et al., 2012a, 2012b). For example, the blink reflex elicited by a strong stimulation of the median nerve of the wrist (the hand-blink reflex, HBR) is modulated by the distance between the hand and the eye, i.e. by where the stimulus is mapped within the PPS (Sambo and Iannetti, 2013). Although the HBR is an entirely subcortical response (Miwa et al., 1998), when the stimulated hand is placed closer to the eye the reflex magnitude is dramatically increased. This effect is a consequence of the fact that the brainstem circuits mediating the HBR undergo a tonic and selective top-down modulation from higher order cortical areas responsible for encoding the location of somatosensory stimuli (Sambo et al., 2012b). This observation shows that the nervous system is able to adjust its output in a very specific and fine-grained manner, even at the level of seemingly stereotyped defensive reflex responses. Interestingly, the magnitude of such top-down modulation is dependent on the cognitive expectation about the stimulus (Sambo et al., 2012a). Indeed, the HBR enhancement by hand–face proximity is suppressed when a thin wooden screen is placed between the participants' face and their hand. Thus, protective objects can reshape and reduce the extension of the protective space.

It is thus hardly controversial that the motor outcome changes depending on the function. But does the function of PPS also make a difference at the sensory level? In other words, does it make a sensory difference whether one sees a threatening or a non-threatening object entering PPS? Unfortunately, this has been rarely directly investigated, with a few exceptions. But if sensory stimuli occurring within the PPS were differentially represented depending on their meaning (e.g. whether they are a threat or an object to reach), then this would provide substantial support to the Specialist model.

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[1] According to some authors the reaching space goes beyond the PPS (Cardinali et al., 2009).

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5. The sensory signatures of peripersonal space

When first described by Rizzolatti et al. (1981), the PPS was characterised purely in sensory terms. A large number of studies in non-human primates later found bimodal neurons in several cortical and subcortical structures (putamen, parietal and frontal areas). These neurons respond to somatosensory and visual stimuli, or to somatosensory and auditory stimuli, but only when the visual or auditory stimuli are spatially close to the somatosensory receptive field. Thus, these visual and auditory receptive fields are anchored to the body. Several studies show similar multimodal representations of the PPS in humans, which result in the interaction between non-somatosensory stimuli near the body and somatosensory processing (Sambo and Forster, 2009). In particular, it has been found that there is a multisensory system of detection and reaction to salient events occurring in the proximity of the body, which is activated by stimuli within the PPS, regardless of whether they are nociceptive, visual or auditory (Iannetti and Mouraux, 2010). This system is not activated by just any kind of novel stimulus (Ronga et al., 2013). Rather, it appears to be specific to stimuli that are of direct significance for the subject, e.g. stimuli which reflect an increase of sensory input in the environment. Question is whether they include not only threats but also any object one upon which one wants to act.

So far the differences between the working space and the protective space at sensory level have not been explored explicitly. Yet it is interesting to note that some bimodal parietal neurons respond maximally to threatening visual stimuli *approaching* their somatosensory receptive field (Dong et al., 1994). Furthermore, although dedicated experiments have yet to be done, one can predict that the protective function primarily requires *rapid* detection of what can be conceived as a threat. This involves the recognition of the danger of the stimulus prior to the detailed processing of its fine features. For example, it is more important to detect quickly that there may be a snake over there (and in case of doubt, assuming that there is something dangerous), than to be able to appreciate its exact length. By contrast, the goal-oriented function primarily requires recognition of the *fine-grained* features of the object (for example its detailed shape and its exact location), to guide precisely the movement towards it. In this case sensory processing can afford to take more time to achieve the finest feature discrimination, since individuals do not always need to perform goal-oriented movements as soon as the object enters their working space. This hypothesis is partly supported by the evidence that salient sensory information reaches multimodal cortical areas responsible for its detection directly from the thalamus, without being first processed in primary and secondary sensory-specific areas (Liang et al., 2013). Such direct thalamocortical transmission of multimodal salient information occurs in parallel to the processing of finer stimulus attributes, which are transmitted in a modality-specific stream from the thalamus to the relevant primary sensory areas, and provides a fast and efficient way for the early detection of salient events and, thereby, trigger immediate and appropriate behaviour (Liang et al., 2013). Although this finding does not provide compelling evidence in favour of the Specialist model, it is entirely compatible with it. The Specialist model indeed predicts that when an object appears in PPS, one should be better at localising it when one intends to grasp it, and faster at detecting it when one needs to withdraw from it.

Another sensory difference between the working space and the protective space might concern the multisensory effects within the PPS. For example, visuo-tactile interactions can be interpreted to engage the perceptual system that anticipates the contact of an object (initially detected by vision) with the body (Hyvarinen and Poranen, 1974). The expectation created by the visual information influences the actual somatosensory experience when the stimulus comes into contact with the body. What is interesting is that such expectation can happen in two ways. Either the perceptual system expects the body to move towards the object or the perceptual system expects the object to move towards one's body – this is typically the case in front of a predator or an environmental threat. These two interpretations reflect the duality of touch, both *touchant* and *touché*. The *touchant* experience gives primacy to the object that is touched whereas the *touché* experience gives primacy to the body that is touched. One may then suggest that the working function involves more of the former and the protective function involves more of the latter.

6. Modulation of PPS

Another strategy to dissociate the working space and the protective space is to consider what influences their respective extension. One of the main features of the PPS is indeed its plasticity. If we could demonstrate that one experimental manipulation alters the protective space, but not the working space (or alters it but not to the same extent), and vice versa, then this would provide support for the Specialist model. There are at least two promising lines of research: the effect of anxiety and the effect of tool use.

6.1. *The effect of anxiety on PPS*

Numerous studies in social psychology have reported how intrusion of personal space and the feeling of crowding can induce anxiety (Hediger, 1955; Hayduk, 1983; Evans and Howard, 1973). Another interesting – though often ignored – aspect, is how anxiety can affect the representation of PPS. We would put forward the argument that anxiety has opposing effects on the two PPS: specifically, it decreases the extension of the working space and it increases the extension of the protective space.

Let us first consider the working space. It has been shown that at higher heights, individual judgments of reaching capability are lower (Nieuwenhuys et al., 2008). This is most likely because of the threatening consequences of overestimating reach in dangerous contexts. Noteworthy is the study by Graydon et al. (2012), where they asked subjects to judge if they could reach for a poker chip that was on a table at various locations. There was no danger in case they made a mistake. Yet, when anxiety was induced experimentally, participants underestimated their perceived reach, as well as their ability to grasp various blocks. Therefore, anxiety seems to reduce the perceived range of possible movements, and, consequently, of the working space.

By contrast, evidence both in social psychology and cognitive neuroscience shows that anxiety increases the protective space. For instance, a significant increase in interpersonal distance in a two-person conversation (which is a proxy of protective space size) was observed in anxiety-inducing situations (Brady and Walker, 1978). Furthermore, Dosey and Meisels (1969) observed that stress makes individual stay further away from each other, although the explicit measures used in these studies are questionable (for a review, see Hayduk, 1983; (Evans and Howard, 1973)). More promising are recent experimental results that use implicit physiological measures, like the enhancement of the hand-blink reflex (HBR) when the hand is close to the eye (Sambo et al., 2012a, 2012b). Single-subject analysis revealed clear inter-individual differences in the extension of the protective space, strongly and positively related to the variability in trait anxiety (Sambo and Iannetti, 2013). Although it is important to note that the absolute values of the extension of the protective space are expected to vary as a function of the threat context in which they are measured (e.g. sitting in the safe environment of a

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psychophysics laboratory is less threatening than walking in a dangerous street of London late in the night), it is important to highlight that within-subject *changes* in protective space extension correlate with the anxiety in an opposite fashion than observed for the working space.

The effect of anxiety on protective space has been also explored by measuring spatial biases in visual bisection task: when bisecting horizontal lines close to the body, individuals show a slight leftward bias that, however, shifts rightward when the line is presented in far space (Longo and Lourenco, 2006). Lourenco et al. (2011) examined whether this bias is modulated by claustrophobia, a condition characterised by intense anxiety in relation to enclosed spaces and physically restrictive situations. They found that more claustrophobic subjects showed a more gradual rightward shift over distance, a finding interpreted as evidence that these individuals had a larger representation of their protective space. In another study found that individuals wearing wrist weights showed a less gradual rightward shift in the bias, a finding that suggests a reduction of the working space. They concluded that these two opposite sets of results (PPS extension in claustrophobia and PPS reduction in effortful situations) reflect the two distinct functions of PPS, which here we have related to the protective space and the working space (Lourenco et al., 2011).

Anxiety makes individuals likely to underestimate their capabilities, which has opposite effects depending on the behaviours related to the different types of PPS. Indeed, it induces a reduction of the working space (as described in Lourenco and Longo (2009)), together with an extension of the protective space (because the individual feels less able to react to threats). Anxiety can also lead individuals to overestimate potential threats, thus reinforcing the extension of the protective space. This dissociation brings clear support to the Specialist model.

6.2. Effect of tool use on PPS

Let us now consider another dissociation, determined by tool use. By tool, we do not mean any kind of object. Rather, we refer to the now classic definition given by Beck (1980). The use of a tool allows actively manipulating (and not simply holding) an unattached external object. Interestingly, tool use can temporarily alter the representation not only of the body (Cardinali et al., 2009), but also of the PPS. For example, in a seminal study Iriki et al. (1996) trained monkeys to use a rake to reach food placed outside their reaching space. Some neurons that before training did not display a response to the food presented outside the reaching space, after training started to respond to the same visual stimulus. A few minutes after the monkey did not use the rake the visual receptive fields shrank back to their original size. Similarly, in stroke patients, visual stimuli presented in extrapersonal space induced stronger cross-modal extinction after the use of a tool to retrieve distant objects. Far visual stimuli induced more severe extinction immediately after tool use (Berti and Frassinetti, 2000; Farne et al., 2005; Farne and Ladavas, 2000; Maravita and Iriki, 2004). Along the same lines, healthy participants had a cross-modal congruency effect when the visual stimuli were presented close to the tip of a tool (Maravita et al., 2002; Holmes et al., 2007; Bassolino et al., 2010; Canzoneri et al., 2013).

The exact interpretation of those results merits discussion. For example, Holmes (2012) suggests distinguishing between three possibilities of PPS modulation: (i) extension, when the PPS surrounds the hand and the whole tool; (ii) projection, when the PPS surrounds exclusively the tip of the tool; and (iii) addition, when the PPS surrounds the hand and the tip of the tool, but not the intermediate area. The difficulty in settling which possibility is correct is that most studies have exclusively tested the allocation of multisensory attention to the tip of the tool (for an exception, see Park et al. (2013)). Although interesting, this debate is not necessarily directly relevant for the topic of this article. Rather, we question whether tool use alters only protective space, only working space, or both.

It is important to note that the tools used in these experiments (e.g. a rake or a grabber) are primarily designed to perform goal-directed actions like reaching and grasping. Therefore, it is not surprising that their use affects the size of working space. When describing their results on tool use, most authors actually refer to the reaching space (Farne et al., 2007; Iriki et al., 1996; Maravita and Iriki, 2004; Serino et al., 2007). Furthermore, we often use similar tools in potentially hazardous situations, provided there is no risk to the body. If a tool is damaged, we may feel annoyed (or even really upset). But we never feel hurt. If tools had to be protect tools as bodies, the range of an individual's actions would be dramatically limited.

> “Tools are frequently used in ways that we would never employ our hands. For instance, we will readily use a stick to stoke the hot embers of a campfire, or stir a pot of boiling soup with a wooden spoon. In these circumstances, the target of the actions may be located well within reach, but a tool is chosen as a substitute for the upper limb in order to avoid harm.” (Povinelli et al., 2010, p. 243)

Povinelli et al. (2010) found that chimpanzees removed the cover of a box with a tool when they perceived the content to be potentially hazardous, and with their hand when they believed the box contained food. If the tools were to be protected, they could not play such an important role in hazardous contexts. Some tools, like the shields under which policemen hide, have even been designed to protect the body. Although tools do need to be taken care of (as the shield would be of little use if broken), tool protection does not follow the same rules as bodily protection because of differences in materials and functions. For instance, some tools can tolerate extremely high temperature while other tools can fall from a cliff with little damage. Furthermore, their protection is hierarchically lower than the protection of the body. Hence, we do protect tools (Rossetti et al., in this issue) but not in the same way and to the same extent as our body. Consequently, although experimental evidence is lacking, it is reasonable to assume that the protective space does not surround tools.

7. Conclusion: a risk of infinite multiplication?

We have argued in favour of a dual representation of PPS and spelled out the distinction in functional terms. In one case, the *protective space* is a privileged interface for avoiding potential threats for the body. In the other case, the *working space* is a privileged interface for the body to act on nearby objects. The question that arises is whether there are more than two functions. As noted by the social psychologist Hall (1966, p. 10): “Each animal is surrounded by a series of bubbles or irregularly shaped balloons that serve to maintain proper spacing between individuals”. But how many bubbles? And what is their respective function?

Hall distinguishes between intimate space, in which you can feel the warmth of another person's body (up to 45 cm), personal space, in which you can directly interact with the other (up to 1.2 m), social space, in which you can work or meet together (up to 3.6 m), and public space, in which you have no involvement with other people. Hediger (1955) also distinguishes different distances, which subserve different functions: the flight distance (distance of the predator at which one must flee), the critical distance (distance of the predator at which one must fight), the personal distance (distance at which the presence of conspecifics is tolerable)

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and the social distance (distance at which one needs to be to belong to the group).

As plausible as these various notions may appear, there is a risk of infinite multiplication of PPS. One may then wonder at what level functional distinctions must operate. For example, does one need to take into account fine-grained differences among various types of protective movements? We would argue no. This is not to deny differences between flight, fight and freeze responses. But we do not believe that the different nature of these responses is essential enough to require distinct peripersonal representations. For example, anxiety is likely to affect similarly the flight distance and the critical distance. But we can also consider more important functional differences. Here we will focus on a third plausible function of PPS joint action, which encompasses a wide range of behaviours, from mating to, carrying a heavy box with another individual. It is indeed important not only to avoid some animals (when they are judged potentially dangerous), but also to get close to other individuals, and synchronise bodily movements. For example, when two individuals carry together a heavy box, they need to coordinate their movements and adjust to what the other does. What type of peripersonal representation does such a joint action involve? We suggest that it does not require a specific kind of PPS, distinct from the working and the protective space. Joint action, which often consists in synchronous, coordinated, goal-directed movements, is clearly related to the working space. The only difference is that in joint action more than one individual act on objects together. Accordingly, recent findings indicate that acting with another individual partly obeys the same principles as bimanual activity (Tsai et al., 2011). In some circumstances joint action may also have protective value. This can take at least two forms. First, during any goal-directed movements, individuals often need to navigate among obstacles. In joint action this task is more complex, because one individual needs to consider the obstacles that may affect the other person. Second, joint action involves trust. If the other person interrupts performing the task or fails it (e.g. the other voluntarily or accidentally drops the side of the heavy box that you are both carrying), this may not represent an aggression that the protective space allows avoiding, but can have potentially harmful consequences. Therefore, the other person's movements within one's own PPS have a specific saliency, and they are probably mapped within the protective space. But the working space and the protective space are sufficient, and there is no need for a further type of peripersonal representation specifically dedicated to joint action.

To conclude, the Specialist model does not lead to an infinite multiplication of PPS. It is parsimonious and plausible to assume the existence of only two types of PPS, which are clearly identified at functional, sensory, and motor levels. However, empirical evidence is necessary to validate this dual model hypothesis conception.

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