



Sensorimotor and social aspects of peripersonal space



About three decades ago, multisensory coding of the space surrounding the body was first described (Rizzolatti et al., 1981). Neurophysiological primate studies showed that information from different sensory modalities converge at single cell level within a set of interconnected multisensory fronto-parietal areas. Since then, this topic has gained increasing interest in the field of neurophysiology, neuropsychology, cognitive science and neuroimaging, with the number of publications per year doubling during the last decade.

Accumulating evidence suggests that multisensory coding of peripersonal space is important for a wide range of functions including bodily perception, the sensory guidance of goal-directed and defensive movements, and localization of the limbs in space. Furthermore, recent studies additionally provide evidence for the idea that peripersonal space has an important social function and is modulated by social and affective cues.

In this special issue we aimed to provide a state of the art overview of the current investigations and topics on peripersonal space. The idea is to advance this field of research by bringing together multidisciplinary findings about peripersonal space and offering a view of its functions and underlying neural mechanisms.

We received a wide range of contributions that varied in terms of topic (sensorimotor function, plasticity and development, social cognition), discipline (e.g. neuropsychology, cognitive science, neurophysiology) and methodology, including reviews, theory papers as well as original research reports. As such we consider the papers in this special issue to provide a good overview of the current state of research in multisensory coding of peripersonal space and to contain many interesting pointers for future studies.

1. Mechanisms of peripersonal space representation

Several contributions discuss or investigate the mechanisms underlying peripersonal space coding.

Di Pellegrino and Ladavas (2015), eminent researchers in the field of peripersonal space research, who have been researching this topic for over two decades, provide a review of the research done so far, including neurophysiological studies, investigations with neuropsychological patients and neuroimaging. They suggest that different highly plastic body-part centred representations of peripersonal space exist, arising through extensive multisensory interactions. These representations depend on interconnected parietal and frontal regions and are crucial for sensorimotor guidance of our actions. Furthermore, they play a role in interactions with people around us. Indeed the roles of peripersonal space coding for motor and social function are extensively researched

currently and several research papers in this issue report on them (see below).

In a second review, Cléry et al. (2015) describe neurophysiological evidence for peripersonal space coding. They also suggest that low level sensorimotor and multisensory processing supported by fronto-parietal interactions is central. They further propose that peripersonal space boundaries are highly plastic and are not only influenced by arm and hand centred actions and alterations in body schema, but also by the emotional and social context. Again, this is investigated in several contributions to this special issue.

Several authors provide a further theoretical specification or alternative accounts of the functional organisation of peripersonal space. De Vignemont and Iannetti (2015) argue that peripersonal space has so far been considered to involve a single representation, despite the multitude of functions it has been linked to. Moreover, various definitions have been used, adding to conceptual confusion (e.g. reaching space, defence space etc). Based on evidence from, for example, the effects of anxiety and tool use, they propose a dual model of peripersonal space representations based on a functional distinction between bodily protection and goal-directed action.

Others have focused on a reinterpretation of the spatial characteristics of peripersonal space coding. van der Stoep et al. (2015) review the literature on 3D multisensory interactions. They critically appraise the often reported distinction between multisensory coding in peripersonal and extrapersonal space and suggest that this distinction is not so much a consequence of differences in multisensory coding between the spaces, but rather due to one mechanism, namely, that multisensory interactions are increased when unsensory stimuli are spatially aligned. As tactile stimuli can only be perceived when applied to the body, visuotactile and audiotactile interactions inherently occur near the body and the peripersonal space boundary can therefore be explained by spatial alignment of different stimulus modalities with the body.

The near–far space distinction was investigated empirically in the study by Longo et al. (2015). They examined whether the typical leftward bias in near space (as compared to a rightward bias in far space (Longo and Lourenco, 2006), is related to right hemisphere dominance for spatial attention in near space. Recording EEG during a landmark task (e.g. judging whether a mark was to the left or right of the centre of the line), they indeed found a larger right-lateralized negativity over parieto-occipital cortex that was linked to spatial attention. The amplitude of this negativity was related to viewing distance, being larger when the stimulus was presented close to the observer. This finding suggests that the right hemispheric spatial attention system is particularly relevant for the representation of space near the body.

One paper focuses on yet another possible mechanism for peripersonal space coding: visuotactile prediction. Predictive coding is a topic which is gaining increasing attention in cognitive neuroscience, with respect to both perceptual recognition and motor control (Friston, 2009; Summerfield and de Lange, 2014; Wolpert and Flanagan, 2001), and recently also for body representations and interoception (Apps and Tsakiris, 2013; Seth, 2013; Ishida et al., 2010). Kandula et al. (2015) suggest that visuotactile coding of peripersonal space is predictive, that is, visual information about the approaching object is used to predict the somatosensory consequences of contact with the object. This prediction allows fast and efficient selection of the appropriate action. The study of Kandula et al. (2015) provides empirical support for this idea by showing that participants respond faster to a tactile stimulus when it occurs at the place and time anticipated based on visual information about an approaching hand.

2. Body-part centred coding

One core characteristic of peripersonal space also mentioned by di Pellegrino and Ladavas (2015) is body-part centred coding. This requires combining visual, proprioceptive and tactile input. The study by Badde et al. (2015) assesses how proprioceptive and tactile information is combined and whether coding of tactile stimuli in a body-part centred reference frame is fixed or flexible. They used the well-established temporal order judgement task in combination with crossed and uncrossed arm postures (Yamamoto and Kitazawa, 2001). Badde et al. (2015) observed that coding of tactile stimuli in a body part centred anatomical reference frame is not fixed and can be influenced by the characteristics of a secondary task and by top-down factors. While this study only investigated coding of tactile stimuli, the idea of differential weighting of reference frames depending on task context and top-down influences may also apply to visuotactile coding of peripersonal space.

3. Functions of peripersonal space: motor action

One of the crucial aspects of peripersonal space coding is the link with motor action. Ample evidence exists of their close association (Brozzoli et al., 2010; Graziano and Cooke, 2006; Makin et al., 2009). This special issue contains several papers that assess how motor action and peripersonal space representations interact. These interactions have been studied in two ways. Several papers report on how motor action influences peripersonal space coding, while others show that stimuli within peripersonal space modulate activity within the motor system.

With respect to the former, Noel et al. (2015) show that during walking peripersonal space boundaries are expanded compared with standing still. As peripersonal space so far has been investigated only in relation to arm movements, this is a nice addition showing that similar mechanisms are used for different types of action. Also on the topic of how motor action influences peripersonal space, Bassolino et al. (2015) investigated how the use of the arm affected distance perception and body representations. Their study showed that restraining the use of one arm for 10 h resulted in a contraction of peripersonal space on that side. Interestingly, overusing the other arm did not result in an expansion of peripersonal space on that side, but did show an enlargement of the perceived length of that arm (which was not affected for the arm that was not used). Thus in addition to showing effects of motor activity on peripersonal space coding, this study also provides evidence for dissociable effects of motor activity on peripersonal space and certain aspects of body

representation. Interestingly, reaching movements do not need to be made with a real hand for it to have an effect on distance perception in peripersonal space. Linkenauger et al. (2015) showed that reaching with the virtual arm of a first person perspective avatar also influences distance perception, although participants required some experience with virtual reaches before the effect was evident. Just having a short or long virtual arm was not sufficient to influence distance perception.

Other studies also investigated the links between motor action, peripersonal space and body representation. Garbarini et al. (2015) tested neurological patients with a pathological embodiment of foreign limbs. Interestingly, they observed that reaching with tools with the foreign embodied hand (which belonged to one of the experimenters) resulted in a perceived elongation of their own arm. The findings suggest a tight coupling between body ownership, motor intention and spatial maps. Using a myoelectric-controlled robotic hand in a study with healthy participants, Romano et al. (2015) observed that synchrony between movements made by the unseen own hand and the robot hand resulted in a proprioceptive drift in felt position of the own hand towards the robot hand, even though participants did not experience ownership over this hand.

Finisguerra et al. (2015) investigated the reverse relation, that is, they assessed how stimuli in peripersonal space modulate the motor system. Using moving sounds at different distances, they showed that only sounds within a 60 cm distance from the hand affect activation of the motor system, as measured through TMS induced MEPs.

A final study on the topic of motor representations and peripersonal space is that by Sclafani et al. (2015). They investigated the development of motor strategies for reaching for objects in peripersonal and extrapersonal space in young monkeys. Their results showed that during the first weeks of life, infant monkeys can already perceive objects at varying distances and use this information to obtain these objects. The monkeys progressively improved their motor strategies and grasping behaviour between 2–4 weeks of age. This developmental trajectory seems to parallel changes in body schema and hence also in space perception. Again this is consistent with the idea of a tight coupling between peripersonal space representations and the motor system with each affecting the other.

4. Functions of peripersonal space: social and affective factors

While studies of peripersonal space have traditionally investigated the link with motor behaviour, more recently attention has been focused on the importance of peripersonal space for social interactions. This recent interest is also reflected in the number of papers (7) on this topic in the current special issue.

A distinction can be made between studies of the role of peripersonal space during social interaction and those investigating how affective information influences peripersonal space coding.

With respect to social interactions and peripersonal space an important topic is that of self-other distinction and shared peripersonal space. A review by Ishida et al. (2015) focuses on this topic. Based on monkey neurophysiology as well as human fMRI studies, they report shared self-other body representation coding in multiple brain areas including visuotactile neurons in parietal cortex (Ishida et al., 2010), secondary somatosensory cortex (Keysers et al., 2004) and in insular cortex associated with affective touch and interoception. Based on these findings, they suggest a novel hierarchical predictive model that allows a distinction between self and other bodily experiences. This model is consistent with and builds upon evidence that suggests a shared social

peripersonal space (Heed et al., 2010; Teneggi et al., 2013). Interestingly, another paper in this issue by Maister et al. (2015) investigated whether increased multisensory integration near another person could be seen as an extension of peripersonal space to incorporate the other person, or whether it involved remapping of peripersonal space to the other person without including the space between the two people. The data clearly are consistent with the latter idea.

While remapping of peripersonal space occurs when the person is known and/or cooperative, the study by Szpak et al. (2015) shows that attentional withdrawal takes place when a stranger enters another's peripersonal space. Furthermore, this study reports that this is only the case for participants who showed discomfort when the stranger stood close to them.

In addition to the modulation peripersonal space by socially unpleasant situations, non-social affective cues can also influence coding of peripersonal space. Ferri et al. (2015) showed an enlargement of peripersonal space as measured by RT's to tactile stimuli when unpleasant approaching sounds were presented. This finding is consistent with the idea of a protective safety zone around the body, as proposed previously (Graziano and Cooke, 2006; Sambo and Iannetti, 2013). The mechanisms underlying the link between affective processes and a defensive safety zone around the body were further investigated by Åhs et al. (2015). In a series of experiments they used fear-potentiated startle in a 3D virtual reality environment to link spatial distance to affective processing. They showed that (a) fear potentiated startle is larger for nearby stimuli compared to distant stimuli (b) the defensive space is increased for stimuli that have become associated with negative consequences (i.e. shocks) (c) extinction of such associations is decreased if they were learned when presented close to the participants, and (d) proximity of the stimulus may have opposing effects on fear potentiated startle depending on whether it is linked to active avoidance or reward. Overall these experiments show that the relation between the position of stimuli near the observer, defensive space and affective processing is flexible and can be influenced by top-down processes. Finally, Rossetti et al. (2015) found that peripersonal space boundaries for unpleasant (painful) stimuli are extended even further after tool use. Specifically, they reported that skin conductance responses (SCR) in anticipation to painful stimuli were larger when the painful stimuli were presented near the body without tool use experience, but increased for painful stimuli further away from the body after tool use.

5. Conclusions

Investigations of peripersonal space coding have come a long way since the discovery of multisensory coding of the space near the body in the nineteen eighties. The relevance of peripersonal space for several fields of study, including, social and affective neuroscience, embodied cognition and visuomotor control is exemplified by the range of topics covered in this special issue. Such a variety of topics and widening of interest from different domains in the research on peripersonal space may come at some costs, though, and we wish to highlight some recommendations for future research. First, we agree with de Vignemont and Iannetti (2015) in identifying a definitional issue, and we emphasise that the use of the term 'peripersonal space' is at risk of conflation. Even in this special issue, peripersonal space sometimes is employed to refer to different sectors of space, such as the personal space, the reaching space, the working space and even the interpersonal space. Adopting a stricter terminology will facilitate the understanding of the possibly different functions subserved by these spatial representations and their neuronal underpinnings. We

therefore encourage constraining the label 'peripersonal space' to its physiologically inspired definition, i.e., the multisensory, body-part-centred representation of the space immediately surrounding the body (Rizzolatti et al., 1981).

Adopting a more precise taxonomy will additionally help to identify the most appropriate measures for peripersonal space and other spatial representations. We believe that trying to identify convergent and more specific measures (i.e., dependent variables) of the sensorimotor and social aspects of the peripersonal space will represent an invaluable and critical step toward a full understanding of how the brain codes for peripersonal space (see Holmes, 2012), and would likely contribute to identifying the benefits which came with the evolutionary selection of such a brain function.

A third aspect we think deserves the attention of future studies is the relationship between multisensory coding of peripersonal space and attention, as the risk of conflation exists also in this respect. So far, very few attempts have been made to operationally define how to disentangle the study of cross-modal attention from that of multisensory processing (see van der Stoep et al., 2015 footnote 3 in this special issue). Rare but notable exceptions suggest that peripersonal space coding can be relatively immune to overt and covert orienting of attention (Makin et al., 2009), which may however decrease multisensory integration (van der Stoep et al., 2015). Again, we foresee that substantial progress in the understanding of peripersonal space will be achieved if the crossmodal attentional and multisensory coding processes are addressed specifically and their potential interactions unveiled.

Last but not least, it seems of paramount importance that future studies try to qualify the functional significance of plastic changes in peripersonal space. Several previous reports, as well as in this SI, have focused on the 'expansion' of peripersonal space following tool-use, or exposure to looming stimuli or painful stimuli (Romano et al., 2015). Indeed, as is the case for plasticity in other domains, the same phenomenon variously referred to as a 'widening' of the peripersonal space has been placed in relation to different behavioural features: changes in implicit reaching capabilities (Cardinali et al., 2009; Canzoneri et al., 2013; Bassolino et al., 2015; Finisguerra et al., 2015) and explicit perceptual reaching judgments (Bourgeois et al., 2014), as well as both positive valuation of a fair confederate (Teneggi et al., 2013) and negative valuation of sound-mediated emotions (Ferri et al., 2015). One possible mechanism that may account for these apparent discrepant findings may be that expansion of visuotactile coding depends on the behavioural relevance of the visual stimulus. However, further studies are clearly needed to understand how peripersonal space is modified and to help building more complete and satisfactory models of peripersonal space functioning.

The study of peripersonal space is in rapid expansion and the papers gathered in this Special Issue provide a useful overview of the current state of knowledge. We hope they will serve as a solid base for further hypotheses and investigations in this field of research.

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