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THE PERIPERSONAL SPACE: A SPACE TO INTER-ACT

Action- and Social-related Modulations of the Space around Us

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The Peripersonal Space:
A space to inter-act

Action- and social-related modulations of the space around us

Contents

Abstract

The zone that surrounds our body is of vital importance: we carefully monitor the objects (both animate and inanimate) that enter the boundaries of the immediate space around the body to interact with them. In the neurocognitive field such a space is captured by the concept of peripersonal space (PPS), a highly plastic representation that integrates tactile and visual stimuli presented on, and close to, the body. This system seems to contribute to the efficient guidance of actions, yet, a clear demonstration of a prominent role of PPS in control of actions is critically lacking. Strong support for this would derive from evidence that PPS plastic changes occur before rather than after movement onset. The results from the first study (Chapter II) reveal that visual and tactile information strongly interact already during the planning phase of action and this visuo-tactile interaction is further enhanced during subsequent movement phases. Such a visuo-tactile remapping of PPS that temporally precedes and subsequently accompanies overt motor execution is ideally suited to planning and guiding actions.

Recently, it has been suggested a possible involvement of PPS in the guidance of motor interactions between individuals. In social psychology, the space around the body is termed interpersonal space (IPS), defined as the area individuals maintain around themselves into which others cannot intrude without arousing discomfort. Because of some similarities between the PPS and IPS constructs, some authors have raised the question of whether they share some functional features. The second aim of my thesis is to test this hypothesis by taking advantage of another PPS remapping, namely that one induces by tool-use. The results of the second study (Chapter IV) show that “standard” tool-use ‘extends’ PPS, as measured by reaching distance toward a peer, but does not affect IPS, as measured by the comfort distance toward the same peer. In the third investigation (Chapter V), we introduced a novel form of “social” tool-use setting to test for both sensorimotor and social plasticity of the two spaces. The findings that social tool–use ‘extends’ PPS and ‘reduces’ IPS, inducing opposite changes on each representation, clearly disconfirms the hypothesis that there might be functional overlap between these sectors of space. Such examples of functional dissociation may therefore be sufficient to warn scholars to refrain from risky conflations between the two concepts.

If the assumption of functional identity with IPS does not appear to be legitimate, it is true that PPS is sensitive to social features. The last study (Chapter VII) is thus aimed at probing this sensitivity of PPS to a so far unexplored but fundamental social dimension: ownership. The results from the forth study indicate that, whether considered to be as individual or shared property, ownership of an object is critical for the PPS dynamic properties to emerge. Visual stimuli affected

touch perception more strongly at the movement onset than before, but only when the object belonged to the acting participant. Interestingly, a similar remapping was found when simply observing the peer acting on her own belonging. In a follow-up experiment we investigated PPS plastic changes when property of the target object was shared between the two agents. In this case, PPS remapping emerged not only when acting in first person, but also when observing the peer acting upon the shared object.

Taken together, these findings critically inform current theoretical models about space around our body and about its function in our sensorimotor and social inter-actions.

Riassunto

La zona che circonda il nostro corpo è di vitale importanza: monitoriamo attentamente gli oggetti (sia animati che inanimati) che valicano tale confine allo scopo di interagire con essi. Nel campo delle neuroscienze cognitive tale spazio è catturato dal concetto di spazio peripersonale (PPS), una rappresentazione altamente plastica che integra stimoli tattili e visivi presentati, rispettivamante, sul e vicino al nostro corpo. Questo sistema sembra contribuire efficacemente alla guida delle azioni, tuttavia una chiara dimostrazione del coinvolgimento del PPS nel controllo delle azioni é ancora assente in letteratura. Sostegno a questa ipotesi deriverebbe dall’evidenza che la plasticità del PPS possa esser innescata prima, piuttosto che dopo, l'insorgenza del movimento. I risultati del primo studio (Capitolo II) mostrano che le informazioni visive e tattili interagiscono significativamente già durante la fase di pianificazione dell'azione e che questa interazione visuo-tattile aumenta ulteriomente durante le fasi successive del movimento. Un tale processo di ‘remapping’ visuo-tattile del PPS, poiché precede temporalmente e accompagna successivamente l'esecuzione dell’atto motorio, sembrerebbe ideale per pianificare e guidare le nostre azioni.

Recentemente è stato suggerito un possibile coinvolgimento del PPS nella guida delle interazioni motorie tra individui. In psicologia sociale, lo spazio intorno al corpo è definito spazio interpersonale (IPS): la distanza che gli individui mantengono attorno a sé. Tale distanza, quando é valicata dagli altri, desta un sentimento di disagio. Alla luce di alcune analogie tra PPS e IPS, alcuni autori si sono domandati se i due construtti possano condividere delle caratteristiche funzionali. Il secondo scopo di questa tesi è testare questa ipotesi sfruttando un altro processo di ‘remapping’ plastico del PPS, ovvero quello indotto all'uso di uno strumento (tool). Il secondo studio (Capitolo IV) mostra che l'uso di uno strumento ‘estende’ il PPS, misurato come distanza di raggiungimento verso un’altra persona, ma non influenza l'IPS, misurato come distanza di comfort verso la stessa persona. Nel terzo studio (Capitolo V), abbiamo introdotto una nuova variante più sociale dell’utilizzo di uno strumento per esaminare la plasticità sia sensorimotoria sia sociale dei due spazi. I risultati ottenuti rivelano che l'uso sociale di uno strumento ‘estende’ il PPS e al contempo ‘riduce’ l'IPS. La dimostrazione che si possano indurre cambiamenti direzionalmente opposti tra le due rappresentazioni, falsifica l'ipotesi secondo la quale possa esserci una sovrapposizione funzionale tra PPS e IPS. Questi esempi di dissociazione funzionale possono quindi essere sufficienti per mettere in guardia gli studiosi al fine di evitare rischiose sovrapposizioni tra i due concetti.

Se l'assunzione di identità funzionale con IPS non sembra essere legittima, è comunque vero che il PPS è sensibile a variabili sociali. L'ultimo studio (Capitolo VII) è perciò finalizzato a sondare tale sensibilità del PPS verso una dimensione sociale fondamentale, ma finora inesplorata: l'appartenenza. I risultati del quarto studio indicano che, sia che si consideri una proprietà individuale o condivisa, l'appartenenza di un oggetto è una variabile critica per far emergere le proprietà dinamiche del PPS. Gli stimoli visivi, difatti, influenzano la percezione tattile in maniera più marcata all'inizio del movimento, ma solo quando l'oggetto dell'azione é il proprio. Da notare che un effetto simile emerge anche quando si osserva l'altra persona agire sul suo oggetto. In un esperimento successivo abbiamo studiato le modifiche plastiche del PPS quando la proprietà dell'oggetto è condivisa. Qui il 'remapping' del PPS emerge non solo quando si agisce in prima persona, ma anche quando si osserva l'altra persona agire sull'oggetto condiviso.

Questi risultati complessivamente forniscono evidenze critiche rispetto agli attuali modelli teorici sulla funzione dello spazio attorno al nostro corpo nelle interazioni sensori-motorie e sociali.

Résumé

L’espace entourant notre corps est d'une importance vitale: nous surveillons attentivement les objets (animés et inanimés) qui entrent dans les limites de l'espace à immédiate proximité du corps pour interagir avec eux. Dans le domaine des neurosciences cognitives, cet espace est exemplifié par le concept d'espace péripersonnel (PPS), une représentation hautement plastique qui intègre des stimuli tactiles et visuels présentés sur et près du corps. Cette représentation semble contribuer au guidage efficace des actions, cependant dans la littérature on ne retrouve aucune preuve substantielle de l'implication du PPS dans le contrôle des actions. Un argument en faveurs de cette hypothèse dériverait de la preuve que la plasticité du PPS peut effectivement survenir avant le début du mouvement, plutôt que pendant le mouvement. Les résultats de la première étude (chapitre II) révèlent que les informations visuelles et tactiles interagissent de manière significative déjà au cours de la phase de planification de l'action et que cette interaction visuo-tactile augmente ultérieurement au cours des étapes successives du mouvement. Un tel processus de « remappage » visuo-tactile du PPS, qui précède temporellement et accompagne par la suite l'exécution de l’action motrice, semble donc idéalement adapté à pour aider au guidage de nos actions.

Récemment, il a été suggéré que le PPS pourrait jouer un rôle dans le guidage des interactions motrices entre individus. En psychologie sociale, l'espace autour du corps est appelé espace interpersonnel (IPS), défini comme l'espace que les individus maintiennent autour d'eux et dans lequel les autres ne peuvent pas pénétrer sans susciter d'inconfort. En raison de certaines similitudes entre les représentions du PPS et du IPS, certains auteurs ont soulevé la question d’un éventuel partage de certaines caractéristiques fonctionnelles entre ces deux représentations. Le deuxième objectif de ma thèse etait de tester cette hypothèse en exploitant un autre processus de «remappage» plastique du PPS, c'est-à-dire celui induit par l'utilisation d'un outil. Les résultats de la deuxième étude (chapitre IV) montrent que l'utilisation «standard» d’un outil «allonge» le PPS, mesuré par la distance d’atteignabilité d’une autre personne, mais n'influence pas l'IPS, mesuré par la distance de confort envers la même personne. Dans la troisième étude (chapitre V), nous avons introduit une nouvelle variante plus sociale de l'utilisation d'un outil pour examiner la plasticité sensorimotrice et sociale des deux espaces. Les résultats obtenus révèlent que l'utilisation sociale d'un outil «allonge» le PPS et en même temps «réduit» l'IPS. La démonstration que l'on peut induire des changements directionnellement opposés entre les deux représentations, falsifie l'hypothèse selon laquelle il peut y avoir un chevauchement fonctionnel entre PPS et IPS. Ces exemples de

dissociation fonctionnelle peuvent donc servir à éviter une association inappropriée entre les deux concepts.

Si l'hypothèse de l'identité fonctionnelle avec l’IPS ne semble pas légitime, il n'en demeure pas moins que le PPS est également sensible aux variables sociales. La dernière étude (Chapitre VII) vise donc à explorer cette sensibilité du PPS vers une dimension sociale fondamentale, encore inexplorée: la propriété privée. Les résultats de la quatrième étude indiquent que la propriété d'un objet, qu’elle soit considérée comme individuelle ou partagée, est essentielle pour l'émergence des propriétés dynamiques du PPS. Les stimuli visuels influencent effectivement la perception tactile d'une manière plus marquée au début du mouvement, mais seulement lorsque l'objet appartient au participant. Il convient de noter qu'un effet similaire apparaît également lorsque l'on observe une autre personne agir sur l’objet qui lui appartient. Dans une expérience ultérieure, nous avons étudié les modifications plastiques du PPS lorsque la propriété de l'objet était partagée entre les deux participants. Dans ce cas, le «remappage» du PPS émerge non seulement lorsque le participant agit, mais aussi lorsqu'il observe l'autre personne agissant sur l'objet partagé.

Dans l'ensemble, ces résultats apportent une preuve critique par rapport aux modèles théoriques actuels de la fonction de l'espace autour de notre corps dans les interactions sensori-motrices et sociales.

Chapter I: The space around the body: Peripersonal space

“Il n'y a de réalité que dans l'action’’

Jean-Paul Sartre

1.1 Multiple spaces

Our surrounding environment is often perceived as a unitary and seamless. Although it does not seem to be reflected in the way in which we subjectively experience the outer world, an ever-growing body of scientific evidence reveals that the brain constructs various functionally distinct representations of space. Over the years, many authors tried to establish valid segmentations of space. Notwithstanding all had different reasons to hit the mark and different visions about how the space is divided, all agreed to maintain, to various degrees, a sort of boundary between who/what is close to our bodies from who/what is further away (Previc, 1990, 1998; Grusser, 1983; Cutting and Vishton, 1995; see also Hediger 1955; Hall, 1969).

In cognitive neuroscience a key division is between peripersonal space (hereafter PPS), that is the region of near space immediately surrounding our bodies in which objects can be grasped and manipulated, and extrapersonal space representations, that is the farther space where exploratory eye movements occur and objects cannot be reached without moving toward them (Holmes and Spence, 2004; Ladavas and di Pellegrino, 2015). This division was initially suggested by Brain (1941), who distinguished a grasping distance within arm’s reach from a walking distance to account for the selective impairment in one or the other sector of space following right-brain lesions. From a computational point of view, it makes indeed sense that the brain may represent objects situated in PPS differently from those in extrapersonal space. The best use of the brain limited resources might well be to plan only grasping movements to those targets of interest within reach, and to plan only locomotive movements to those targets situated at a distance. Obviously, the two action modules can be combined when somebody walks towards a desk to grasp a glass of water from its surface.

Hence, the hypothesis that space may be represented by multiple sub-spatial maps partly delimited by the body was further supported by seminal neurophysiological studies in the non-human primate brain (Hyvärinen and Poranen, 1974; Mountcastle, 1976; Leinonen and Nyman, 1979a, 1979b; Rizzolatti et al., 1981a, 1981b). For example, lesion studies in macaque monkey (Rizzolatti et al., 1983) revealed that the unilateral surgical ablations of the postarcuate cortex resulted in a severe neglect limited to the PPS associated with a deficit in the use of the contralateral hand. Namely, the animal exhibited a failure to grasp food with the mouth when presented contralesionally and a reluctance to use the contralateral hand. By contrast, unilateral ablation of the pre-arcuate cortex (area 8), corresponding to the frontal eye-field or FEF, resulted in a decrease of eye movements contralateral to the lesion and a neglect of the contralateral hemispace, more prominent for ‘far’ space than for that near the animal (Rizzolatti et al., 1983; Schieber, 2000). Since these early works from 70-80’s, a plethora of studies in monkeys and humans (in both healthy and pathological states) have explored the functional features of the specific area close to the body, viz. PPS.

In this introductory session I will describe the single cells, areas, cortical functional networks in monkey’s brain proposed to underlie the PPS representation, as the definition of PPS itself originates from single-unit electrophysiological studies in non-human primates. Despite their heterogeneous nature, the majority of these papers will be framed within an action-based perspective of space pointing to dynamic and bidirectional links between PPS representation(s) and actions.

1.2 Peripersonal space in the monkey brain

Objects at a distance can typically be perceived through a limited number of senses such as vision, audition, and olfaction. Conversely, objects nearer to, or in contact with, the body surface can virtually impact upon all our sensory systems. The brain's processing of stimuli in PPS is therefore quite complex ad involves more modalities of sensory information. Besides, it is not the case that any one single brain area is responsible for maintaining a representation of space, as once thought, but PPS is rather an emergent property of a network of interacting and well-connected cortical and subcortical areas (Rizzolatti et al., 1997; Graziano and Gross, 1998; Spence and Holmes, 2004; Clery et al., 2015a).

1.2.1 A multisensory space

Pivotal single-cell recording studies on the macaque monkey brain releveled a special set of neurons within the ventral premotor cortex strongly responding to tactile stimulation. Neurons in the histochemical area F4 (the caudal portion of the inferior part of the premotor cortex, see Figure1.1) containing representations of arm movements, also features relatively large tactile receptive fields. Such respective fields are mainly located on the animal's hands, arm, face, and neck (Gentilucci et al., 1983, 1988; Rizzolatti et al. 1981a, 1981b), as if to form a broad map of the body. A large proportion (85%) of these tactile neurons also discharges in response to visual stimulation. Specifically, such cells in area F4 respond weakly to visual stimuli presented far from the body, whereas the most effective response, in terms of spike discharge rate, is evoked primarily by three-dimensional objects moving close to the tactile receptive field. According to the depth of the visual receptive fields protruding out of the skin surface, these bimodal visuo-tactile neurons were originally subdivided into pericutaneous (54%) and distant peripersonal neurons (46%). The former class of neurons responds best to visual stimuli presented in the very close vicinity (up to 10 cm away from the body), while the latter class responds also to visual stimuli presented at a further distance from the skin, but always within monkey's reaching distance (Rizzolatti et al., 1981a,1981b). For the sake of simplicity, I will refer to both as "peripersonal" neurons, as one of distinctive features of either subpopulation is that their visual receptive fields are limited in depth from the somatosensory receptive fields of a specific body part and remain "anchored" to that body part. Indeed, the size of the visual receptive field not only matches and spatially overlaps the size of the tactile one, but also extends from the body for varying distances (typically from ~5 to ~50 cm).

That is to say, the visual and tactile receptive fields of these bimodal cells create a single responsive region mapping the skin and the space closely surrounding it. Since the visual responses are generally independent of gaze direction, the visual information in F4 region is spatially related to the body parts on which the tactile receptive fields are located (Fogassi et al., 1992; Gentilucci et al. 1983; see Figure 1.2). Here is to note that the visual receptive field seems to be "anchored" to the somatosensory receptive field on a body part because it moves congruently with it, keeping thus a rough spatial match between the locations of the visual RF and the body part with every displacement (Graziano et al., 1994). This is demonstrated by the fact that passive displacement of the arm causes a congruent shift of the location of the visual receptive field of neurons presenting somatosensory receptive field on the limb. In a similar vein, when the head is turned, but not when visual fixation changes, the visual response of neurons with tactile receptive fields on the face is updated following the spatial position of the face (Graziano et al., 1997a, 1997b). This result provides strong evidence for a body part-centred reference frame, since the neuronal responses were tested both when the monkey was fixating a particular position, and when fixation was not controlled. Regardless of the direction of gaze, neurons with somatosensory receptive fields on a given body part are specifically activated by visual stimuli presented near that given body. For some neurons the spontaneous or evoked firing rate is modulated by eye position, but the portion of space eliciting the maximal visual response does not change when the eyes moved.

Such a peculiar interaction between different receptive fields is not limited to visuo-tactile cells, since neural activity in F4 can be trigged by visual, as well as auditory signals. Indeed, some neurons responding to a somatosensory stimulus located on the back and the side of the head also discharge when a visual and/or auditory stimulus is administered next the body part being stimulated tactilely (Graziano et al., 1999). To anchor their multisensory receptive fields to a given body part and to maintain their spatial alignment, these neurons integrate proprioceptive information too (see also Figure 1.3). When exposed to conflicting visuo-proprioceptive conditions, the firing rates of the F4 neurons elicited by approaching stimuli is modulated by the position of the monkey's real arm as well as by the position of a fake arm placed in a realistic posture (Graziano et al., 1999).

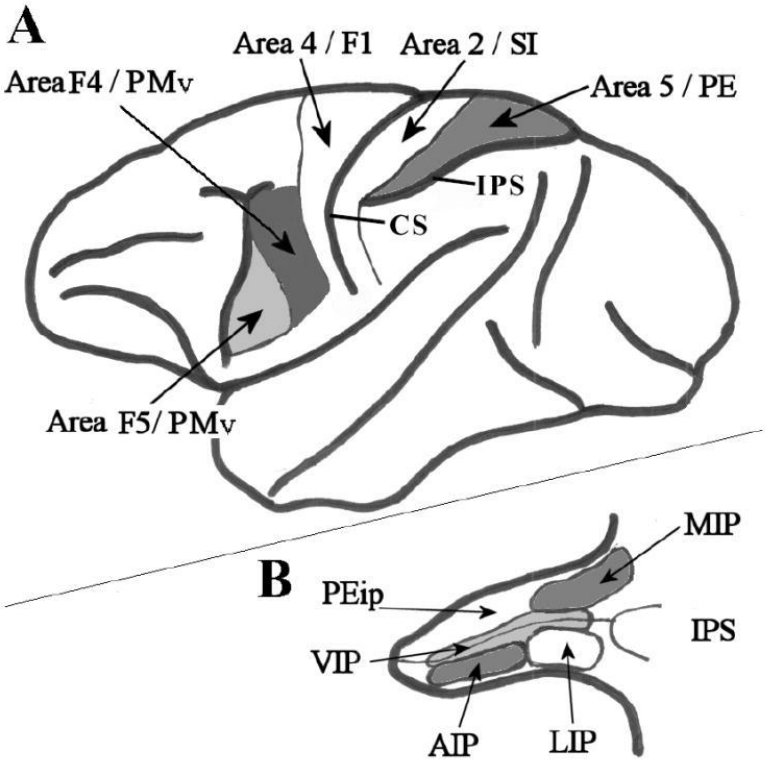


Figure 1.1 Selected cortical areas of the macaque monkey brain. A. Lateral view of the whole brain. Thick black lines represent major cortical boundaries and sulci. Thin black lines represent cortical area boundaries. Area 4/F1 - primary motor cortex; Area 2/SI – primary somatosensory cortex; Area 5/PE – posterior parietal association cortex/superior parietal lobule; Area F5/PMv and Area F4/PMv – ventral premotor cortex; IPS – intraparietal sulcus; CS – central sulcus. B. The intraparietal sulcus has been opened up to reveal multiple and heterogeneous visual and somatosensory posterior parietal areas. Thick lines represent the superficial border of the sulcus; thin black lines mark the fundus of the sulcus. Other lines indicate the boundaries of cortical areas as follows: MIP – medial intraparietal sulcus; LIP – lateral intraparietal sulcus; AIP – anterior intraparietal sulcus; VIP –ventral intraparietal sulcus; PEip – intraparietal portion of area PE (from Holmes and Spence 2014; redrawn from Rizzolatti et al., 1998).

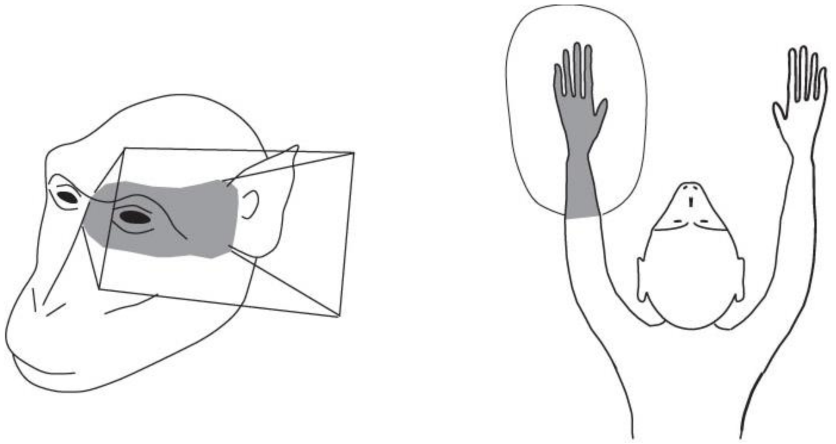


Figure 1.2 Multimodal neurons in the monkey brain that encode the space near the body. Each neuron responds to touching a specific part of the body called the neuron's tactile receptive field. The same neuron responds to visual stimuli in the space near the tactile receptive field. Two examples are depicted. From Graziano and Gross (1998).

Another premotor area, i.e. the rostral subregion F5 of area 6, harbours similar visuo-tactile neurons (see Figure 1.1). However, as compared to those present in F4 region, bimodal neurons in F5 are less numerous and show smaller tactile receptive fields, which are frequently located on the face, the hand, or both. It is important to acknowledge another significant difference: albeit visual stimuli presented near the body result in stronger firing rate, what seems to be crucial in triggering the response of these neurons is instead the size of the stimuli (Rizzolatti et al., 1988; see also session 1.2.4).

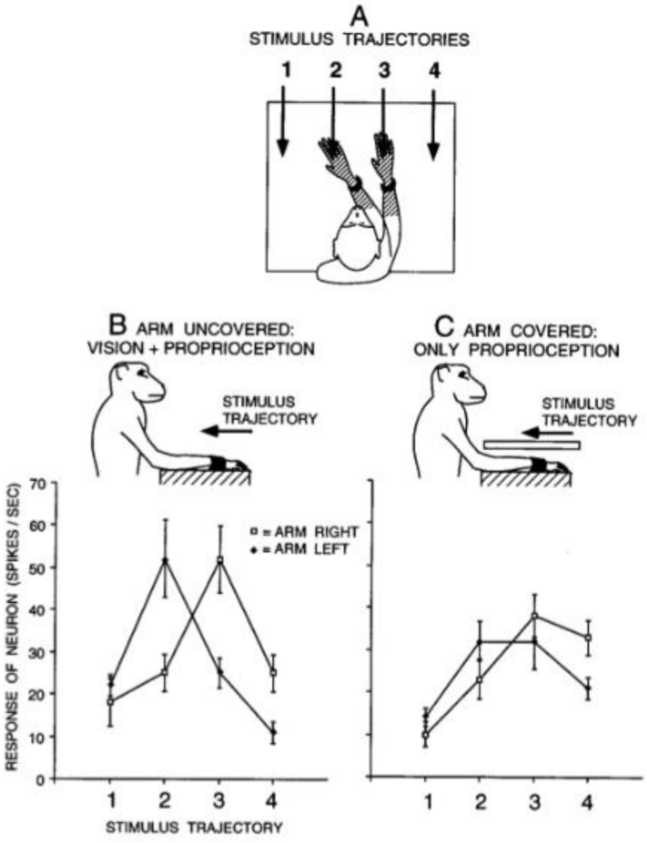


Figure 1.3 Visual responses of a typical premotor neuron with a tactile RF (hatched) on the forearm and hand, and a visual RF within 10 cm of the tactile RF. (A) On each trial, the arm contralateral to the neuron was fixed in one of two positions and the visual stimulus was advanced along one of four trajectories. For this neuron, the two arm positions were chosen to align the visual RF near the hand and forearm with trajectories 2 and 3. For other neurons, the arm was moved to different extents depending on the location of the visual RF, to better capture the movement of the visual RF with the arm. (B) Responses of the neuron to the four stimulus trajectories when the arm was visible to the monkey. When the arm was fixed on the right, the response was maximum at position 3. When the arm was fixed on the left, the maximum response moved to the left, to position 2. (C) Responses of the neuron when the arm was covered. The movement of the visual RF with the arm was reduced but not eliminated, indicating that the neuron combined both proprioceptive and visual information about the position of the arm. Each point is a mean of 10 trials. Error bars are standard error. Adapted from Graziano et al., 1997.

Visuo-tactile neurons with similar properties have been also discovered in two regions of the posterior parietal cortex heavily connected with F4 (Matelli et al., 1984a, 1984b), namely area 7b and the ventral intraparietal (VIP) area. Electrophysiological studies in awake monkeys demonstrated that, similarly to neural cells in the ventral premotor cortex, visuo-tactile integration in these areas arises at the single unit level (Hyvärinen and Poranen 1974; Mountcastle et al. 1975; Hyvärinen 1981; Leinonen et al. 1979; Leinonen and Nyman 1979; Robinson et al. 1978; Robinson and Burton 1980a, 1980b; Hyvärinen 1981). In particular, area 7b presents a coarse somatotopic organization with a face representation on the upper inferior parietal convexity, followed by arm, hand, and foot representations located laterally, along the inferior parietal convexity (Hyvärinen and Shelepin 1979; Hyvärinen 1981, Robinson and Burton 1980a, 1980b). Although this region is prevalently a somatic area with most of its neurons being somato-motor or somatosensory, a part of the neurons studied in this area is, in fact, visuo-tactile (Gross and Graziano, 1995; Hyvärinen, 1981). In the regions representing the face and arm about one third of the cells are described as bimodal, with visual receptive fields being spatially aligned with the tactile receptive fields (Hyvärinen and Porane, 1974, Hyvärinen and Shelepin 1979; Lionene and Nyman 1979), whereas another portion of bimodal neurons has bilateral receptive fields located on the limbs, sometimes covering the whole body (Leinonen et al., 1979). Most of the cells in 7b respond preferentially to visual stimuli moving toward the skin, within about 10 cm of the tactile receptive fields, although stimuli presented further away, but still within a reachable distance, are also effective. Notably, the neural response in 7b can be both independent (Graziano and Gross 1995) and dependent of the position of the arm (Leinonen et al., 1979).

The ventral intraparietal area (area VIP), located in the fundus of the intraparietal sulcus and receiving projections from the middle temporal visual areas, as well somatosensory, auditory, and vestibular regions (Graziano and Cooke, 2006, see Figure 1.1), contains visual as well as visuo-tactile neurons (Colby and Duhamel 1991; Colby et al., 1993; Duhamel et al., 1998, Avillac et al., 2005). VIP bimodal neurons mainly respond to visual stimulation presented within a few centimetres of the tactile receptive field and show a strong sensitivity to speed and direction of motion of both visual and tactile stimuli (Duhamel et al., 1998). Unlike area 7b neurons, somatosensoty receptive fields in VIP are primarily located on the face and head and their visual receptive fields are anchored to the region of space around the face (Colby et al., 1993). Moreover, some VIP neurons are trimodal, responding to visual, auditory and tactile stimuli, with the three different receptive fields usually aligned (Schlack et al., 2003).

Some studies have revealed a similar pool of multisensory neurons devoted to represent the space near the body in the putamen (Graziano and Gross 1993, 1995), a subcortical structure of the primate brain that receives projections from inferior area 6 and area 7b (Cavada and Goldman-Rakic 1991; Matelli et al., 1986). The putamen has a complete somatotopic map of the body and, like the bimodal neurons described above, visual and tactile receptive fields of bimodal cells in this structure display a rough spatial correspondence, with the visual receptive field anchored to the tactile one. A large proportion of bimodal neurons has cutaneous receptive fields cantered on the face (Graziano and Gross, 1993) and responds best to visual stimulation administered within 10-20 cm from the face skin. Visuo-tactile neurons centred on the arm respond visually when the arm under the monkey’s view, but not when the arm is moved out view (Graziano and Gross 1995).

1.2.2 A dynamic multisensory-motor space

Peripersonal space has been so far depicted as a static functional representation, determined by fixed body constraints such as the within reach space around the body or around the head. Yet, there is abundant evidence that PPS should rather be considered as extremely dynamic and rapidly adjusting to both endogenous and exogenous factors, being readily modifiable and shaped by sensorimotor experience.

Again, such a dynamic signature of PPS was first captured by single-cell recording studies in monkeys. For example, it has been demonstrated that the depth of visual receptive fields of F4 neurons is not fixed, but can increase with increases in the velocity (20–80 cm/s) of a visual stimulus approaching the tactile receptive fields, such that fast-moving stimuli are signalled earlier than slow-moving ones (Fogassi et al., 1996). Visual receptive fields of bimodal neurons in the medial anterior intraparietal sulcus and in the post-central gyrus seem to have a somewhat similar plasticity. Iriki and colleagues (1996) trained monkeys to use a rake as a tool to reach for food pellets placed out of their reaching distance. After this training with the tool, the visual receptive field of some bimodal neurons were elongated along the axis of the rake. The elongated visual receptive fields seemed to have expanded toward the tool tip, such that the rake appeared to be included within the visual receptive fields. This was the case for both “distal” cells, whose tactile receptive field was on the surface of the hand, and “proximal” cells, whose tactile receptive field was on the skin of the shoulder. Remarkably, a few minutes after withholding the active use of the rake, the visual receptive fields apparently shrank back to their original size. Such a change to occur requires active tool-use: no modification was observed if the rake was just passively held by the animal, therefore suggesting the tool has to be actively employed to perform an action (see Figure

1.4). Moreover, a positron emission tomography (PET) study from the same group further extended this finding, describing the cortical activation of the presupplementary motor area and the premotor cortex at locations matching F4 and F5 areas (Obayashi et al., 2001). Parietal regions are also crucial, since the tool-dependent changes increased cortico-cortical afferents to the intraparietal sulcus (Hihara et al., 2006) and the expression of neuronal plasticity markers in this cortical region (Ishibashi et al., 2002a, 2002b) .

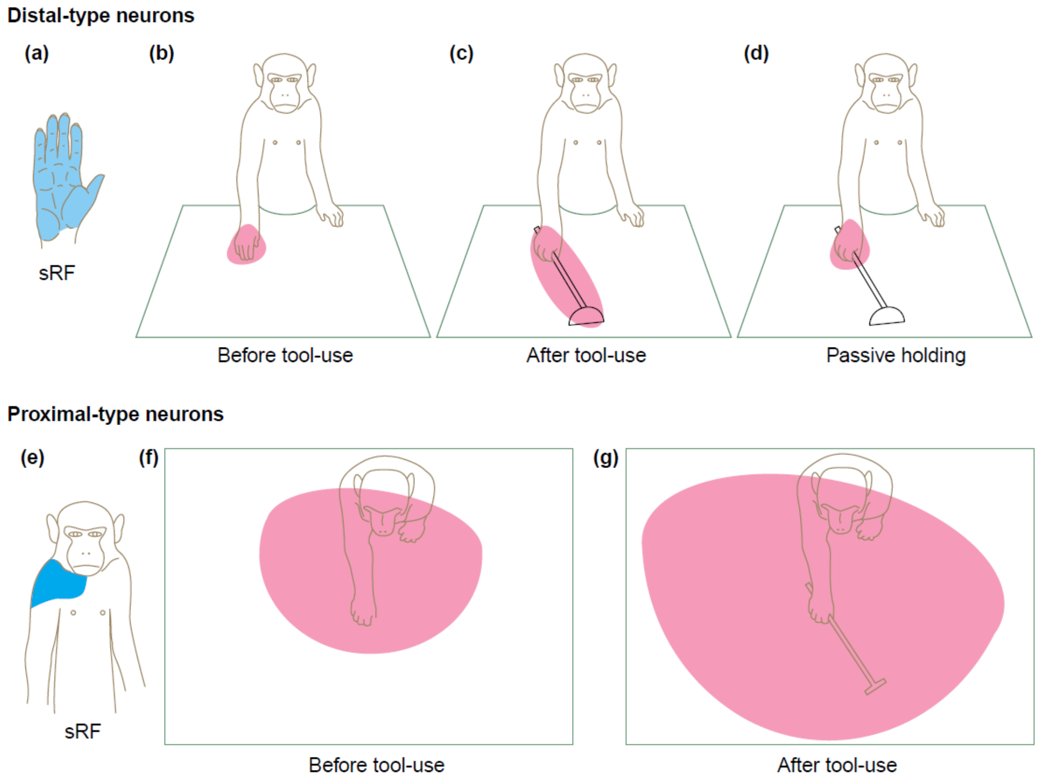


Figure 1.4. Changes in bimodal receptive field properties following tool-use. The somatosensory receptive fields of cells in this region were identified by light touches, passive manipulation of joints or active hand-use. The visual receptive field was defined as the area in which cellular responses were evoked by visual probes (the most effective ones being those moving towards the somatosensory receptive field). (a) somatosensory receptive field (blue area) of the ‘distal type’ bimodal neurons and their visual receptive field (pink areas) (b) before tool-use, (c) immediately after tool-use and (d) when just passively grabbing the rake. (e) somatosensory receptive field (blue area) of ‘proximal type’ bimodal neurons, and their visual receptive field (pink areas) (f) before and (g) immediately after tool-use. From Maravita and Iriki 2004.

The dynamic changes of visual receptive fields observed in case of objects approaching the body (Fogassi et al. 1996) or after active tool-use (Iriki et al. 1996) point to another critical aspect: the link of PPS coding with motor responses. The neural response of visuo-tactile cells in inferior premotor area 6 (Gentilucci et al. 1988; Rizzolatti et al. 1981c, 1987, 1988, 1997), parietal area 7b

(Hyvärinen 1981; Hyvärinen and Poranen 1974; Hyvärinen and Shelepin 1979; Leinonen 1980; Leinonen et al. 1979; Leinonen and Nyman 1979; Robinson et al. 1978), and the putamen (Crutcher and DeLong 1984) is elicited by passive visual and tactile stimulation as well as during motor activity.

In the premotor cortex the visual responses of some neurons are enhanced when performing reaching and grasping movements toward an object (Godschalk et al., 1981, 1985; Kurata and Tanji 1986; Rizzolatti et al., 1981c; 1990). Interestingly, the active movements and the sensory receptive fields appear to share related functional roles. Neurons with visuo-tactile receptive fields around and on the face also responded during reaching movements of the arm toward the upper part of space that corresponds to their visual receptive fields. In other words, not only visual and tactile receptive fields, but also motor response fields are in spatial register: the motor activity of these neurons is maximal when the movement is directed to reach into the region of space coded by the bimodal neurons. As a result, the sensory and motor responses appear to be expressed in a common coordinate system (Caminiti et al., 1990). In addition, the posterior parietal cortex is accordingly related to approaching movements of a body-part toward external objects and show motor properties, similarly to the premotor region (Rizzolatti et al., 1997, Debowy et al., 2001; Fogassi and Luppino 2005; Ferraina et al., 2009a, 2009b). Note that the activation during grasping actions in monkey's posterior parietal areas starts before the beginning of the movement and persists during the whole action. The predominant activation moves then to SI only when the hand enters in contact with the target object (Gardner et al., 2002). Remarkably, this posterior parietal activation before and during the overt motor activity involves areas of the monkey's brain where bimodal neurons have been found, such as area 7b. Lastly, ablation and reversible inactivation of premotor and parietal region seem to produce very similar patterns of deficits, most of which impairs the execution of visually guided reaching actions (Moll and Kuypers 1977; Battaglini et al. 2002; Deuel and Regan 1985; Ettlinger and Kalsbeck 1962; Faugier-Grimaud et al., 1978; Gallese et al., 1994; Halsban and Passingham 1982). As mentioned earlier, removal of post-arcuate lesions to area 6, including areas F4 and F5, results in a severe impairment in grasping with mouth (Rizzolatti et al., 1983). The hand shaping that relies on the visual properties of the object to be grasped is disrupted following the inactivation of F5, and a similar impairment is observed following AIP inactivation (Fogassi et al., 2001; Gallese et al., 1994). To conclude this paragraph, these results therefore contribute collectively to raise the compelling possibility that the multisensory representation of PPS might serve some motor function.

1.2.3 Mirroring the (peripersonal) space

In accordance with the motor properties of PPS, the regions devoted to near space coding are immediately adjacent to, or coextensive with, brain areas containing another particular set of visuomotor neurons. In the ventral premotor cortex, visuomotor cells of area F5 are classically subdivided into two categories: "canonical" and "mirror" neurons. "Canonical" neurons discharge to visual presentation of objects and to actions towards such objects, both in the dark and in the light. Because of this, such class of neural cells is proposed to underlie visuomotor transformation for grasping (Murata et al., 1997; 2002; Raos et al., 2006). On the other hand, “mirror” neurons selectively respond during action execution as well as during observation of someone else performing the same action. Such class of neural cells is instead thought to be involved in action understanding (di Pellegrino et al.; 1992, Gallese et al., 1996; Rizzolatti et al., 1996; Rizzolatti and Matelli, 2003). In the rhesus monkey’s premotor cortex, mirror neurons not only are activated by both the execution and the observation of motor acts, but they are also modulated differentially by the location in space of the observed motor acts relative to the monkey. A subset of mirror neurons show selectivity from actions performed within the observer’s PPS rather than in its extrapersonal space, while another subset show the opposite selectivity for actions performed in extrapersonal space. Even more interestingly, a portion of these spatially selective mirror neurons encodes space according to a metric representation, whereas other neurons encode space in operational terms, changing their properties according to the possibility that the monkey will interact with the object (Caggiano et al., 2009). When accessibility to PPS is limited, for instance by placing a transparent barrier in front of the monkey, the firing rate of several PPS mirror neurons are reduced during observation of actions performed in portion of the space now inaccessible. In other terms, when the border changed the previously reachable space of the monkey into non-reachable space, the PPS mirror neurons did not respond anymore. Accordingly, extrapersonal mirror neurons start to respond to observation of actions performed in the inaccessible PPS, as indicating that when PPS is inaccessible for action, it is represented as farther extrapersonal space. Such results therefore suggest that it was the currently reachable space that was important in evoking a response in these “extrapersonal” and “peripersonal” mirror neurons.

Along with this, a subpopulation of F5 neurons actually shares both canonical and mirror properties, termed therefore “canonical-mirror” neurons. The responses of canonical and “canonical-mirror” neurons to the presentation of graspable objects typically require the stimulus to be in PPS. In contrast, the responses of mirror and canonical-mirror neurons evoked by action observation are present irrespectively of whether the action being observed by the monkey is performed in peripersonal or in extrapersonal space. Also in these hybrid visuo-motor cells, space-constrained coding of objects mostly relies on an operational (action possibility) rather than metric (absolute distance) reference frame. Moreover, such canonical-mirror neurons appear to code object as target for both one's own and other's action, suggesting that they could play a role in predictive representation of others' impending actions (Bonini et al., 2014). In addition, mirror neurons can also be found in parietal area 7b (Fogassi et al., 2005; Fogassi and Luppino, 2005). Like the “canonical” 7b neurons, these cells discharge differentially to simple movements and to complex goal-directed sequences of actions, and are proposed to play an important role in the organization of natural ecological actions (Bonini et al., 2010).

All together, these experiments reveal that a set of neurons encodes the observed motor acts not only for action understanding (Gallese et al., 1996; Rizzolatti et al., 1996; Rizzolatti and Fogassi, 2014) but also to analyse such acts in terms of features that are relevant to generating appropriate behaviours within and beyond the action space (Caggiano et al., 2009). If, on one hand, the space where the executed or observed action constrains the neural responses of the visuo-motor cells, on the other hand, coding of space could potentially benefit of similar mirroring processes.

As proof of the existence of a mirror neuron-like mechanism encoding the PPS of other individuals, Ishida et al., (2010) described in area VIP “body-matching neurons” that respond to visual stimuli presented near a specific body part of the monkey being recorded from, as well as to visual stimuli presented near the corresponding body part of the human experimenter. Like the typical PPS neurons, the majority of the recorded neurons exhibit visual receptive fields around the tactile receptive fields anchored on a single body part (e.g., cheek, forearm, and trunk), selectively discharging when visual stimuli were delivered within monkey’s PPS (approximately 30 cm from the skin). However, the novel finding to emerge from this study was the some bimodal neurons exhibit both visuo-tactile receptive fields on the monkey’s body and visual receptive fields close to the experimenter’s body. Such neurons respond selectively to a visual stimulus delivered at a distance of 120 cm from the monkey’s body parts (i.e., beyond the monkey’s PPS) but close to the corresponding experimenter’s body parts (i.e., within the experimenter’s PPS). As an example, a neuron with a tactile receptive field on the arm responds to visual stimuli both presents around the monkey's own arm and delivered around another individual's arm, the experimenter in this case (see Figure 1.5). Importantly, the neuron failed to respond when the same stimulus was presented close to other body parts of the experimenter or in the absence of the experimenter, ruling out visual attention as an alternative interpretation of the findings.

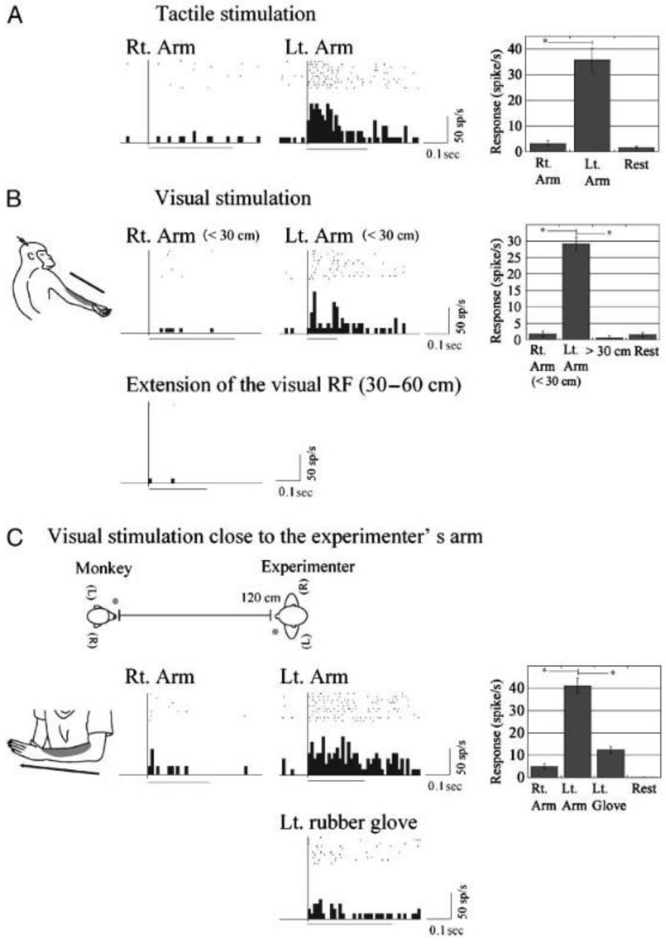


Figure 1.5. An example of body-matching neuron. Location of tactile receptive field of this neuron is on the monkey's left forearm, with visual receptive field anchored close to the same part of the tactile RF (A and B). A tactile stimulus (hand touch by the experimenter) moved from proximal to distal across the tactile receptive field of the neuron. The neuron preferred nearby stimuli within 30 cm of the monkey's left forearm when the experimenter was absent (<30 cm). The neuron was most active for visual motion of the experimenters' hand in the same direction. (B, below) Responses to visual stimuli more than 30 cm from the monkey's left forearm. In both modalities, responses to stimuli on/near the left arm were significantly stronger than those in other conditions. (C) Visual responses to experimenter's forearms. This neuron was active when the monkey observed the experimenter stroking his own left forearm from proximal to distal. (C, below) Response to a left-hand rubber glove similar to the arm of the experimenter. Visual responses to the left forearm of the experimenter were significantly stronger than those under other conditions. From Ishida et al., 2010.

1.2.4 Multisensory network of PPS coding

The neurophysiological contributions outlined above revealed a pool of at least four characteristic regions in the macaque brain, namely premotor inferior area 6, parietal areas 7b and VIP, and the putamen, featuring similar visuo-tactile proprieties. These areas are heavily interconnected, forming a tight network (Matelli and Luppino 2001; Rizzolatti et al. 1997, 1998, 2002; Graziano and Gross, 1998; Rizzolatti and Sinigaglia, 2010). The inferior parietal area 7b and superior parietal area 5 send projections respectively to inferior and superior part of premotor area 6 (Pandya and Vignolo 1971; Strick and Kim 1978; Godschalk et al. 1984; Matelli et al. 1984a, 1984b). Reciprocal connections are also sent back from premotor area 6 to the respective parietal areas (Rizzolatti et al. 1997). Likewise, this parieto-frontal network projects also to the putamen (Kunzle 1978; Weber and Yin 1984; Cavada and Goldman-Rakic 1991).

As a whole, neurons in this network mainly share some common features:

- visual and tactile receptive fields are in spatial register, visual receptive fields matching the location of tactile receptive fields on body surface;
- visual receptive fields are limitedly extended in depth, being restricted to the space immediately surrounding the body part;
- visual stimuli moving close the primate’s skin modulate the neurons’ responses stronger than farther stimuli, the discharge decreasing as the distance between visual stimulus and somatosensory receptive fields increases;
- visual receptive fields operate in coordinate systems centred on body parts, remaining anchored to the tactile receptive fields of a given body part when this is moved;
- visual receptive fields feature dynamic properties in such a way that they can be modified as a function of the interaction with the environment;
- bimodal neurons are functionally and dynamically related to motor actions, so that the dynamic aspects of the visual receptive fields may depend on the execution of specific motor actions.

Notwithstanding such similarities, some key functional differences need to be highlighted. For illustrative purposes only, within the parieto-frontal network implicated in near space coding I will distinguish two functional, partially distinct, sub-circuits subserving PPS representation (see also de Vignemont and Iannetti 2015 for a review about the functional distinction of PPS in humans). The first PPS sub-circuit is formed by VIP and F4 (Rizzolatti and Luppino 2001, Rizzolatti and Sinigaglia, 2010; Clery at al., 2015a). In premotor area F4 visual information is primarily anchored to the arm/hand, while in parietal area VIP is primarily anchored to the head/face. Besides having strong anatomical connections, the two regions show some functional homologies. Specifically, the electrical microstimulation of VIP region produces eye blinking and defensive-like movements, including flinching as if avoiding or protecting the head from attack or collision (Cooke and Graziano 2003; Graziano and Cooke 2006). In F4 a similar motor repertoire is elicited by electrical microstimulations of visuo-tactile neurons on the head. At sites with visual and tactile receptive fields anchored to the arm or hand, fast withdrawal of the hand to a protective posture behind the back is evoked (Cooke and Graziano, 2004; Graziano et al., 2002; Graziano and Cooke, 2006). Although distinct contributions of area VIP and area F4 to such a motor repertoire seem to co-exist, as highlighted by the comparative electrical microstimulation study performed by Graziano and colleagues, these observations document the involvement of this VIP-F4 circuit in defence and obstacle avoidance behaviour. Hence, one could speculate that this network could subserve the function of protecting the animal by maintaining a margin of safety around the body, with a specific emphasis on two vulnerable body parts, viz. the head and the arm/hand (Graziano and Cooke, 2006; Clery et al., 2015a).

The second circuit within the parieto-premotor network is formed by AIP and 7b in the parietal pole and area F5 in the frontal pole (Rizzolatti and Sinigalgia, 2010; Matelli and Luppino, 2001; Rizzolatti and Matelli, 2001). Notably, AIP is not described to contain bimodal visuo-tactile neurons, but it rather represents 3D object structure, possibly contributing to the definition of the motor affordances of objects. AIP is in fact functionally specialized in the visuomotor transformation involved in grasping actions and in the online adjustment of the hand and finger configuration for a secured interaction with the objects (Murata et al., 2000). Although AIP region does not appear to contribute to PPS coding per se, given the strong anatomical connections and functional homologies with F5 and 7b, it may provide the sensorimotor transformations aimed at guiding movements in PPS. The 7b-F5 circuit has visual and tactile as well as motor proprieties that might play a central role in unfolding grasping actions. As described earlier, some cells in 7b area also discharge during motor activity (Hyvärinen 1981, Hyvärinen and Shelepin, 1979; Leinonen, 1980; Leinonen et al., 1979; Leinonen and Nyman, 1979; Robinson et al., 1978). Their activity is evoked by the execution of different actions, from simple movements such as grasping a specific object, to more complex sequences of movements such as grasping to bring to the mouth (Fogassi et al., 2005; Fogassi and Luppino, 2005). Further, a small portion of area F5 neurons discharge when visually presenting 3D objects, similarly to AIP neurons, exhibiting selective responses for specific shape, size, and object orientation. Such a visual response is independent of whether an action toward the target is performed or not (Murata et al., 1997). In light of this multisensory hand-related features that are tightly associated with goad-direct action, one could think that this parieto-frontal circuit is more dedicated to planning and execution of actions to interact with objected located with the nearby environment.

It is worth mentioning here another network involving area 5 that, although it is not mainly devoted to the representation of PPS, is specialized for sensorimotor transformations necessary for reaching (Buneo et al., 2002). Some studies indicate that medial regions of area 5 combine tactile, proprioceptive, and visual signals with motor commands to generate a plan of action toward targets in space, and subsequently monitor its execution (Kalaska et al., 1983; Andersen et al. 1997; Batista and Andersen 2001; Buneo and Andersen 2006; Fattori et al. 2004; Ferraina et al. 2001; Galletti et al., 1993, 2003). For example, in the macaque, neurons located in the caudal part of the medial intraparietal area (MIP, see Figure 1.1) are involved in the coordination of hand movements and visual targets. MIP projects to dorsal premotor cortex area F2 and responds to visual or visual/somatosensory stimuli, accordingly with the direction of hand movements toward a visual target.

The monkey V6 complex is another area of particular importance for the visuo-motor transformations needed to plan and execute reaching movements. The V6 complex consists of a purely visual V6 area that receives input from early visual areas and sends output to the V6A visuo-motor area and MIP. In particular, area V6A is located on the anterior bank of the parietooccipital sulcus and on the medial surface of the parietal lobe and projects predominantly to area F2 in the dorsal premotor cortex (Matelli et al., 1998). This region codes the direction of arm movement and the hand ⁄ arm position in space (Fattori et al., 2005). MIP and part of V6A are sometimes referred to as the parietal reach region (PRR, Andersen and Buneo 2002). However, reaching-related responses are present also outside PRR, in areas 7a, 7m, PEc (caudal part of superior parietal area PE), and 5 (Kalska et al, 1983; Sakata and Taira 1994; Ferraina et al., 2001; Breveglieri et al., 2006; Graziano 2001). In addition, PRR responds not only during arm movements but also during eye movements (Batista et al., 1999), suggesting a relative functional specialization of these areas (Andersen and Cui 2009). Therefore, it remains unclear how much these parieto-frontal circuits are functionally specific and segregated and how they interact each other to represent the body and its relation to external near space during reaching. Though these circuits are at least partially dissociable, together seem to play a major role in the guidance of goal-directed arm movements.

1.2.5 In a nutshell…

Summarizing what we have seen thus far, the special role of the space in terms of multisensory interactions involving the stimulation of the body has been inspired by the results of neurophysiological investigations documenting the existence of visuo-tactile neurons in macaque’s parieto-frontal areas. One of the peculiar characteristic common to all these cells is that they specifically respond to stimuli presented on and close to the body, but not to those stimuli that happen to be presented further from the body (e.g., Rizzolatti et al., 1981a; Graziano and Gross 1994; Graziano et al., 1999). As for the functions of such particular multisensory interactions in this region of space, the integration of visual/auditory, proprioceptive, and somatosensory stimuli seems to contribute to the efficient guidance of actions and defensive behaviours in response to those events that are observed to happen in PPS (Rizzolatti et al., 1997; Graziano and Cooke 2006; Holmes and Spence 2004, Brozzoli et al., 2014; Clery et al., 2015a). Such a representation operates in body part-centred reference frames and demonstrated significant plasticity, appearing thus a functional system to assist the acting body in daily interactions with objects.

In humans, a functionally homologous coding of PPS is largely supported by behavioural experiments in brain-damaged [paragraph 1.3.1] and healthy individuals [paragraph 1.3.2] as well as by recent functional neuroimaging studies identifying multisensory integrative structures coding the space in the human brain [paragraph .1.3.3]. In the session that follows, I will describe evidence in humans corroborating the existence of an integrated representation of space.

1.3 Peripersonal space in the human brain

By close analogy with monkey data, a wealth of experiments demonstrates stronger multisensory interaction in near rather than far space in humans. The strong dependence of the multisensory interactions on the distance of visual (or acoustic) information from the body has been taken as proof of the existence of a PPS coding in the human brain similar to what I previously described in monkeys brain. Numerous reports on behavioural effects of brain lesions have played a critical role in understanding of such a system, often employing direct adaptations of animal paradigms in order to seek as well as to exploit homologies. In this respect, seminal scientific assessments of neurological condition such as extinction and neglect has provided considerable insight into the behavioural characteristics of multisensory spatial representations (di Pellegrino et al., 1997; Ladavas and Farnè 2004; Halligan and Marshall, 1991; Berti and Frassinetti, 2000). Convincing evidence for visuo-tactile interactions is also available in healthy people, in the form of distance-dependent crossmodal and multisensory behavioural effects that are seen under appropriate experimental conditions (Spence et al., 2004a, 2004b; Blanke et al., 2015). Furthermore, several functional neuroimaging studies in the human brain provide neural support the existence of multisensory integrative structures involved in PPS (Makin et al., 2007; Sereno and Huang 2006; Brozzoli et al., 2011; Ferri et al., 2015a).

1.3.1 Peripersonal space in the damaged human brain

Extinction is a clinical sign following brain damage, typically the right frontal and parietal cortex. Patients are able to detect a single stimulus presented ipsi- or contra-lesionally, but fail to report the contralesional stimulus when a concurrent stimulus is presented on the ipsilesional side. In other terms, they cannot detect contralesional stimuli under conditions of double simultaneous stimulation, thus revealing the competitive nature of this phenomenon (di Pellegrino and De Renzi 1995; de Hann et al., 2012). Several works have shown that extinction can emerge even when concurrent stimuli are presented in different sensory modalities. For instance, a visual stimulus presented near to the ipsilesional hand can extinguish a touch delivered on the contralesional hand (di Pellegrino et al., 1997). Critically, such a crossmodal visuo-tactile extinction appears to be stronger when visual stimuli are presented in near as compared to far space: less modulatory effects of vision on touch perception were indeed observed when visual stimulation was presented far from the space immediately around the patient’s hand. This phenomenon has been interpreted as a result of multisensory processes coding a PPS presentation centred on the hand (di Pellegrino et al., 1997).

Specifically, in cross-modal visual–tactile extinction paradigms, a visual stimulus administered near a given ipsilesional body part, say the hand, strongly activates the corresponding somatosensory representation of this effector. The simultaneous activation of a somatosensory representation of the left hand by a tactile stimulus *and* of the right hand by a visual stimulus in PPS produces an extinction of those stimuli delivered on the left hand. This is due to the fact that extinction becomes manifest when there is a competition between more than one spatial representation, resulting in a failure to report the weaker representation, i.e., that of the left hand in previous example (Lavadas, 2002). In keeping with the monkey neurophysiological findings, visual responses to stimuli presented near the patient's hand remain anchored to the hand when it is moved to the opposite hemispace (di Pellegrino et al., 1997). This convincingly corroborates the hypothesis that visual information is processed by a mechanism that takes a specific body part as reference and congruently follows it, staying anchored to this reference when the body part changes location. That is, multisensory interactions disclosed by extinction patients' performance arise in a body part–centred fashion (Ladavas 2002).

A converging line of studies suggests that another body part that might be implicated in the same mechanism is the face (Lavadas et al., 1998). As for the hand, in patients with tactile extinction, visual stimulation in the space close to the ipsilesional side of the face extinguished tactile stimulation on the contralesional side to the same extent as did an ipsilesional tactile stimulus. Instead, when visual information was presented far from the face, cross-modal extinction effects resulted to be dramatically reduced (Farnè et al. 2005a). Notably, the extinction was stronger when the homologous body part has being stimulated (i.e., left + right cheeks, and left hand + right cheek) rather than non-homologous body parts (i.e., right hand + left face and right face + left hand). In spite of being near the body, visual stimuli presented close to non-homologous body parts were treated as if they were far from the body, most likely because they are far from the relevant homologous body part. This demonstrates that different spatial regions, adjacent to different body parts, are represented separately, thus revealing that PPS is organized in a modular fashion (Farnè et al. 2005a).

Paralleling the monkey neurophysiological data showing that neurons in F4 integrate touch, vision, and audition (Graziano et al., 1997a, 1997b), crossmodal interactions between touch and audition in human PPS were first reported in right brain-damaged patients (Ladavas et al., 2001). In particular, contralesional tactile extinction on the neck was stronger when acoustic stimuli were delivered close to, as compared to far from, the ipsilesional side of the head. Moreover, crossmodal audio-tactile extinction was more severe in the patients' rear space than in the front space (Farnè et al., 2002). This could perhaps indicate the former space might indeed represent the ideal space to auditory–tactile interactions because an object approaching the head from the rear space (where vision is not available) can be perceived only through the sound or noise it produces. In contrast, an object approaching the head from the front space would mainly benefit of visual information. This different sensitivity demonstrated that different degrees of multisensory integration may occur depending upon the functional relevance of a given modality.

Solid and convincing evidence in favour of the existence of a selective representation for the space near the body in humans derives from another pathological condition following right brain hemisphere, i.e., neglect (Schenk and Karnath 2012 for a recent review). Despite the absence of any gross primary sensory impairment, patients with neglect present a peculiar reduction of response and attention to sensory events occurring in the left (contralesional) hemispace. Several studies have confirmed that the neglect syndrome can affect selectively the space near the body or far from the body, since cases of neglect restricted to PPS have been described (Berti and Frassinetti, 2000; Beschin and Robertson, 1997; Bisiach et al., 1986; Guariglia and Antonucci, 1992; Halligan et al., 2003; Halligan and Marshall, 1991; Ortigue et al., 2006), as well as cases of neglect restricted to extrapersonal space (Coslett et al., 1993; Cowey et al., 1994, 1999; Vuilleumier et al., 1998; Ortigue et al., 2006). Incidentally, this double dissociation, analogous to that one reported in lesion studies in monkey, constitutes further support to the notion that the human brain selectively represents the two regions of space.

Continuing the human-monkey analogy, the human representation of PPS exhibits a degree of functional plasticity too. Even though typically a far visual stimulus, being outside PPS, weakly influences tactile processing, the use of tools can change the way the brain processes visual stimuli in far space. The mostly accepted idea is that the use of a tool that elongates the arm, and therefore the reaching capabilities of the body, can induce an elongation of PPS (Berti and Frassinetti, 2000; Farnè and Làdavas 2000; Maravita et al., 2001; Maravita and Iriki 2004, however see also Holmes 2012). Objects located in far space, when repeatedly reached with the tip of a tool, may be coded as if they were near to the body and, thus, the visual information coming from those distant objects undergoes to increased interaction with tactile processing. Through tool-use it is therefore possible to functionally remap space, so that “far becomes near” (Berti and Frassinetti, 2000). In a single case report, Berti and Frassinetti (2000) reported what it can be considered the first functional “remapping” of humans PPS. They described a patient showing a severe neglect selectively affecting the space near the body, as indexed by a line bisection task (a standard procedure for the neglect assessment of pathological rightward bias) whereby the bias was apparent in the near, but not far space. Performance was indeed comparable to controls, when the patient was requested to bisect lines in the far space by means of a laser pointer. Crucially, the rightward bias reappeared when the same task was performed with a stick, used by the patient to bisect the line in a far position: in this case, her neglect was as severe as that observed in near space. This would appear to indicate that the stick, acting as an artificial extension of the patient's body, caused the remapping of the far space into near space.

Similar results have been described in extinction patients who, compatibly with a tool-use-dependent remapping, showed changes in cross-modal extinction assessment following tool-use: visual stimuli presented in far space induced stronger cross-modal extinction after the use of a 38-cm rake to retrieve distant objects (Farnè and Ladavas 2000; see also Bonifazi et al. 2007; Farnè et al. 2005b, 2007, see Figure 1.6). Specifically, when patients were tested for visuo-tactile extinction before tool use, immediately after a 5-min period of tool use, and after a further 5- to 10-min resting period, far visual stimulation was found to induce more severe contralesional extinction only immediately after tool use. However, such effects were ephemeral, disappearing after a few minutes of tool inactivity. In addition, while passively holding the tool is not sufficient to trigger changes in PPS, it appears that it is the functional instead of the mere physical length of a tool that can modulate the extent of PPS elongation (Farnè et al., 2005b, 2005c, Farnè and Ladavas, 2000). As a whole, these results correspond well with neurophysiological findings revealing that that definition of peri- and extrapersonal space is not demarcated a priori, but it may be derived functionally, depending on movements that allow the body to interact with objects in space.

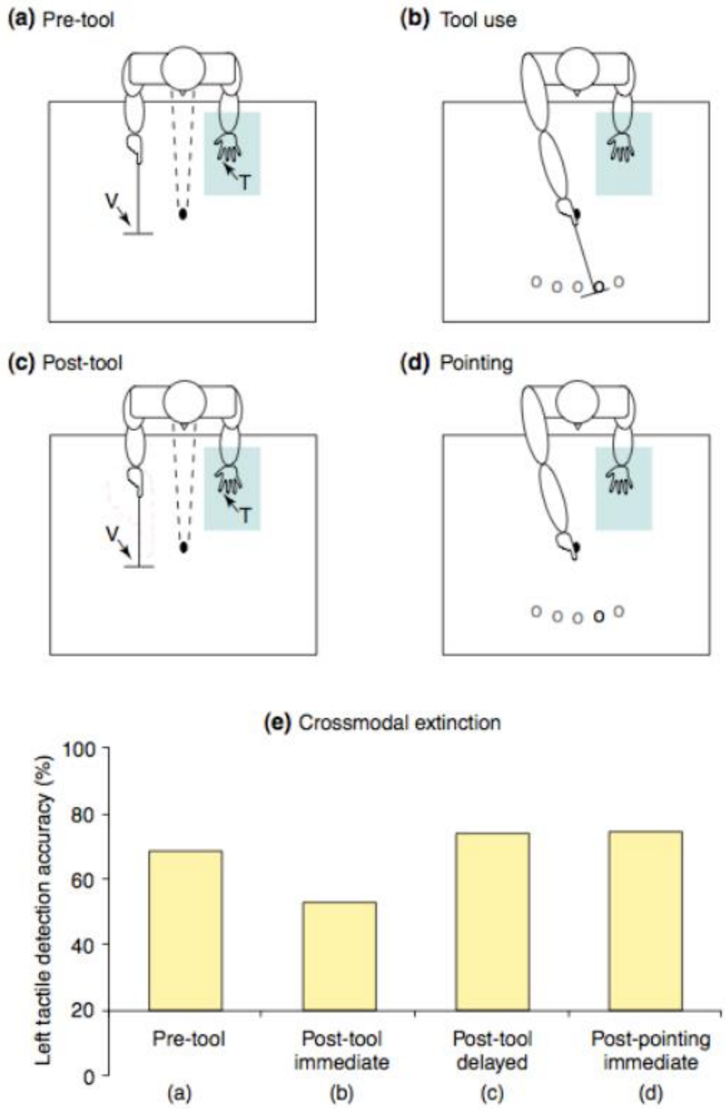


Figure 1.6. Schematic drawings of the experimental set-up in a study to assess the s cross-modal visual–tactile. (a). The location of visual (V) and tactile (T) stimulation is indicated by arrows. Crossmodal extinction was assessed before (a) and after (c) the patient used a rake to retrieve distant fishes (b, open circles) or pointed towards them (d). The patient's left hand was always occluded from view by a cardboard shield (shaded area). The large dotted red hand symbolically represents the extension of the reaching space of the patient's hand. (e) Mean percentage correct detection of the left tactile stimulus in each experimental condition. (Modified from Farnè and Ladavas, 2000; adapted from Ladavas, 2002).

1.3.2 Peripersonal space in healthy individuals

Highly converging evidence in favour of distinct multisensory representations of space comes from studies about the interference that visual or auditory information can exert over touch perception in neurologically unimpaired people.

One of the best-known paradigms used to investigate this issue is the cross-modal congruency task (Spence et al., 1998, Spence et al., 2004a; Spence and Driver 2004; Shore et al., 2006; Macaluso and Maravita, 2010; Costantini et al., 2017). In a typical crossmodal congruency study, participants receive a vibrotactile stimulus either at the thumb or the index finger of the hands while holding two foam cubes, one in each hand (see Figure 1.7 for a schematic illustration). The target tactile stimulation is presented together with a visual stimulus (distractor), independently on an unpredictable trial-by-trial basis, from one of the four possible stimulus locations. Thus, for each trial the visual distractor could be either close to the tactilely stimulated hand or to the other hand. The visual distractor could be "congruent" (same) or "incongruent" (different) in elevation with the tactile target stimuli. Participants are required to make a series of speeded elevation discrimination (e.g., up/down) responses by pressing a foot pedal, reporting whether tactile target stimuli are presented at the index finger (up) or thumb (down) of either hand. Simultaneously, participants have to try ignoring the visual distractors presented at approximately the same time.

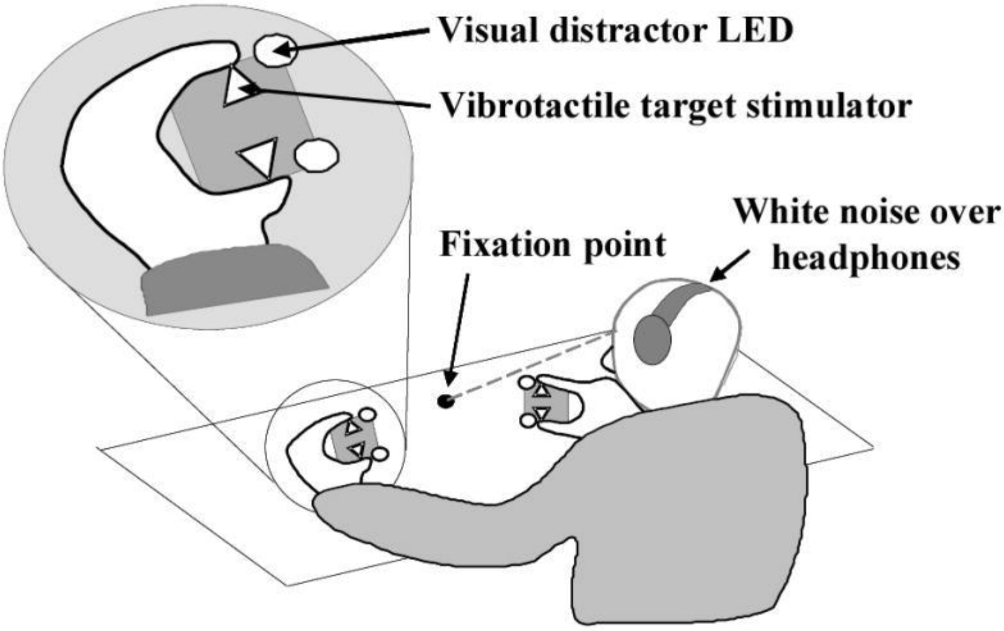


Figure 1.7 The visuo-tactile crossmodal congruency task. Participants hold a 'stimulus cube' containing vibrotactile stimulators (open triangles) and visual distractor LEDs (open circles). Participants look at a central fixation point (filled circle) situated midway between the two hands. White noise presented over headphones masks the sound of the vibrotactile stimulators. The inset shows a magnified view of the participant's left hand holding one of the stimulus cubes. Adapted from Holmes and Spence (2004).

The overall effect is that participants are normally significantly worse (both slower and less accurate) at discriminating touches when visual distractors are presented at incongruent elevations (when distractors is presented at a different elevation as compared to the vibrotactile stimuli), rather than at a congruent elevation (when distractors and vibrotactile stimuli are presented at the same elevation), regardless of whether they were presented on the same or on the other hand. The difference in performance between incongruent and congruent trials, known as Cross-modal Congruency Effect (CCE), is thus a measure of the amount of the cross-modal visuo-tactile interaction (Spence et al., 1998, Spence et al. 2004a). This effect is more pronounced when the vibrotactile target and the visual distractor stimuli are presented from approximately the same location (e.g., from the same foam block) than when they come from different locations (i.e., from two different foam blocks, one held by one hand and the other by the other hand). The modulation of visual distractors over touches in this paradigm is resistant to practice and does not seem to reflect a response competition. Rather, the CCE would appear to be a phenomenon reflecting the integration of visual and tactile information. More relevant here is the different influence exerted by the visual information whether the visual distractor was presented near to as compared to far from the tactile targets. In analogy with the cross-modal extinction studies and the neurophysiological properties of visuotactile neurons, Spence and colleagues (2004b) showed that the CCE was especially stronger when the visual information occurred close to the tactually stimulated body part rather than in far space. To specifically demonstrate this, the authors investigated the cross-modal congruency effect displacing one hand in a far position with respect to visual distractors, thus systematically varying the spatial proximity between target and visual distractor. As a result, they revealed that interference exerted by the visual distractors over the tactile modality was dependent upon the spatial distance between them (Spence et al., 2004b). Additionally, when the posture of participants was manipulated, this cross modal effect changed accordingly. For instance, in a crossed hand condition, if the right hand is placed in the left hemispace, a visual distractor in the left space affected tactile discrimination at the right hand. Such a modulation would confirm that the CCE arises in a reference system that is anchored to the stimulated body-part, (e.g. Macaluso et al., 2005; Spence et al. 2004b; Spence et al., 2001). Critically, similar results were obtained when the visual stimulus was presented close to a fake, realistic hand placed on the table in front of the participants, but only when the hand was placed in an anatomically plausible posture (Pavani et al., 2000, see also Farnè et al., 2000 for a similar result on extinction patients).

Using the same approach, the effect of tool use in near and far space has been investigated thoroughly in healthy individuals through the crossmodal congruency task (Maravita et al., 2002; Holmes et al., 2004, 2007, however see also Holmes 2012). Without going into too much detail, such studies have shown that active tool-use increases the salience or effectiveness of visual stimuli presented at the tip of the hand-held tool.

Tool-use-dependent changes in the representation of space around the tool have also been documented by using the auditory modality (Canzoneri et al., 2013a). Serino and co-workers (Serino et al., 2007) provided behavioural support that audio–tactile integrative mechanisms are also dynamically modulated in PPS and that, more importantly, such plastic changes are associated with expertise for specific tools. They first showed that in healthy subjects the auditory PPS is normally limited to the area surrounding the hand. Then, after using a blind cane for a few minutes to explore the environment, auditory PPS extended towards far space. As expected, when the same participants were tested the following day, the previously extended PPS shrank back to its original dimension. While in healthy participants active training was required to induce such extension, in sharp contrast, in blind people who would use the cane in everyday life auditory PPS was already extended towards the cane tip while holding it. However, when they were passively holding a weight-matched cane handle (i.e., not providing any gain in reachability), their PPS was limited to the area around their hand, just as in the healthy subjects before the cane-use. Such a functional specificity of tool-induced plasticity has been corroborated by analogous findings reported for use of the computer mouse (Bassolino et al., 2010). Merely holding a mouse in the hand habitually used to control the mouse (the right one) extended auditory-interactions to the space near the screen. Such effects were found only when the mouse was actively used, and not just passively held, in the hand not habitually used to control the mouse (the left one). Suggesting again that tool-induced plasticity exhibits a relatively high level of specificity, it has been demonstrated that a tool have to give a functional benefit to the arm in order to shape PPS. In a recent work Bourgeois and colleagues (2014) assessed the effect of two functionally different tools on the perception of reachability (i.e., whether an object is within reach), as an index of PPS extent. They required participants to perform a reachability judgement task, before and after using either a long tool increasing the arm length by either 60 cm (70-cm-long tool + 10-cm handle) or a short tool, leaving the arm length unchanged (10 cm long, 10-cm handle). As expected, reachability judgments were selectively modified by long tool-use, as subjects considered farther locations to be reachable only after using the long tool. Conversely, after using the short tool, which did not substantially alter the reaching space, the described effect failed to appear, thus highlighting the importance of the gain in reachability provided by a tool as an essential component to lead to a PPS modulation. Furthermore, mere tool-use observation, while passively holding the same tool, would actually appear to be sufficient in remapping PPS (Costantini et al., 2011). Collectively, these recent works seem to challenge the initial idea that plastic modifications of PPS require the tool to be actively utilized, as originally advocated by electrophysiological and neuropsychological evidence. These apparently contrasting results can be reconciled if interpreted in the light of the hypothesis that the functional experience with the tool, rather than its active or passive use, seems ultimately to play a prominent role (Martel et al., 2016; Farnè et al., 2005b, 2005c, see also Serino et al., 2015a for a computational model).

1.3.3 Neuroimaging PPS in the human brain

More recently, brain imaging techniques have been employed to unravel the anatomical underpinnings and functional mechanisms of human PPS as well as to emphasize the homologies with the electrophysiological findings in the monkey brain. Before introducing this issue, I wish highlighting that caution should be exerted when comparing studies in nonhuman and human primates, especially with respect to possible homology relations between areas in the association cortices.

Although brain activations have most often been reported in premotor and posterior parietal cortex (see Grivaz et al., 2017 for a meta-analysis, see also Figure 1.8), they also encompassed a larger network containing areas such as to the lateral occipital cortex (e.g. Makin et al., 2007), the parietal operculum (e.g. Tyll et al., 2013), the insula (e.g. Schaefer et al., 2012), the cerebellar cortex (e.g. Brozzoli et al., 2011), and the putamen (e.g. Gentile et al., 2011). Furthermore, while only few investigations examined neural correlates of the space surrounding the face, many of these studies have focused on the processing of hand-centred multisensory space.

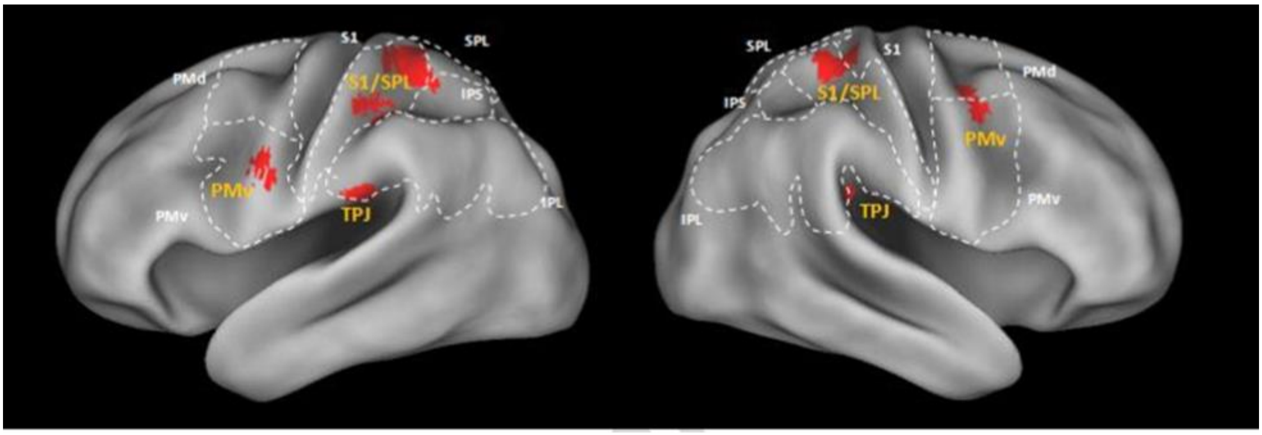


Figure 1.8 Cortical regions involved in human PPS. Visualization of the results from one of the meta-analysis performed by Grivaz et al., (2017, see the paper for methodological details) with approximate location of cytoachitectonically and functionally defined regions (surrounded by white dashed lines). SPL superior parietal lobule, S1primary somatosensory cortex, IPL inferior parietal lobule, IPS intraparietal sulcus, PMv/d ventral/dorsal premotor cortex.

An early study disclosed an overlap between brain activity related to tactile stimuli delivered on the face and that one related to visual and tactile stimuli approaching the face. This overlapping activity was observed in intraparietal sulcus (IPS), ventral premotor cortex (PMv) and the lateral and inferior parts of postcentral gyrus (Bremmer et al., 2001). In agreement with these results, Sereno and Huang (2006) found that in IPS topographic maps of tactile and proximal visual stimuli are aligned and that IPS activity codes stimuli in a face-centred reference frame. With all the possible cautions, IPS was proposed, basing on this result, as the human homolog of area VIP. Quinlan and Culham (2007) reported instead a representation of face PPS in another region: the dorsal parieto-occipital sulcus (dPOS). In this study, subjects viewed looming and receding moving visual stimuli presented close to (from 13 to 17 cm), at an intermediate distance (from 33 to 43 cm) or far away from their face (from 73 to 95). In dPOS, blood oxygen level–dependent (BOLD) contrast increased for closer stimuli. Interestingly, this was not the case in the putative human VIP, which was activated by moving stimuli irrespectively of their distance from the face.

Similar cortical activations were displayed for the multisensory representation of the hand space. Makin and co-workers (2007) identified regions within IPS, lateral occipital complex (LOC), and PMv (ventral premotor cortex) showing significantly stronger activation in response to a ball approaching the subject's hand (near condition), compared to when the same stimulus moving away from the subject's hand (far condition, up to 70 cm from the hand). This differential near-far activation (i.e., within or outside the hand PPS) was further modulated by proprioceptive hand position signals as well as body-related visual information, compatible with coding in a hand-centred reference frame. When the hand was retracted, the preferential activation for the near vs. far condition disappeared, thereby indicating that these brain regions do not simply respond to low-level visual differences in the near and far ball conditions. Moreover, the selective activation for the near ball condition in IPS was also present when viewing a fake hand at the near location (even if the participant’s real hand was retracted), but was absent in LOC and PMv, if participants positioned their hand far from the location of the near stimulus.

Gentile and colleagues (2011) examined how these regions of the brain integrate visual and tactile stimuli delivered in the near hand space. While participants were in the scanner gazing at their hand, unisensory and multisensory stimuli were presented in the space immediately surrounding the hand. Superadditive, nonlinear BOLD responses during multisensory visual–tactile stimulation were observed in the cortex lining IPS, the insula, the dorsal premotor cortex, and the putamen, similarly to multisensory integration regions in animals (Avillac et al., 2005; Stein and Stanford, 2008). Such effects further depended on the spatial and temporal coherence between visuo-tactile inputs. In a second investigation the same authors (Gentile et al., 2013) joined tactile stimulation of the participant's real hand with the visual presentation of a virtual hand while manipulating spatial congruency (i.e., manipulating the direction of visual and tactile stimulation) and temporal synchrony of stimulation (i.e., with synchronous or asynchronous visuo-tactile stimulation). Activations in IPS, in ventral and dorsal PM, in LOC, and in the cerebellum varied as a function of the spatial and temporal congruency of visuo-tactile hand stimulation and were modulated by proprioceptive and visual signals related to the hand (similarly to Makin at al., 2007, see Figure 1.9).

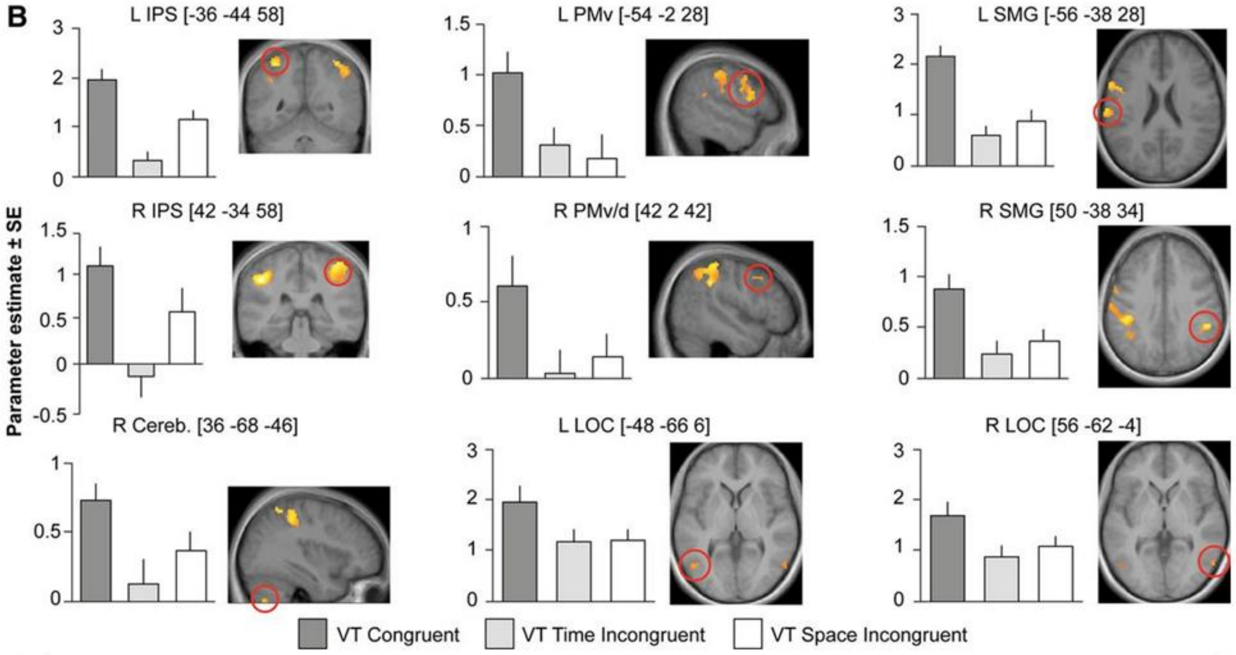


Figure 1.9 Bar charts displaying the parameter estimates for all significant peaks of activation as a function of visuo-tactile temporal and spatial congruency. The coordinates are given in MNI space. For display purposes only, the anatomical location of the peak is indicated by a red circle on an activation map displayed on a coronal, sagittal, or axial section from the average structural image. L/R, left/right; PMv/d, ventral/dorsal premotor cortex; SMG, supramarginal gyrus. Adapted from Gentile et al., 2013.

In a series of neuroimaging studies, Brozzoli and colleagues used a BOLD adaptation parading for revealing neuronal population with a visual selective response for events occurring within the space near the hand. Compared to the standard neuroimaging approach, fMRI adaptation has the capacity to reveal population of neurons selective to specific stimulus features within a single voxel and, therefore, is perhaps more closely related to electrophysiological recordings (Grill-Spector et al., 2006). In the first study Brozzoli and colleagues (2011) found that IPS, the inferior parietal lobe (supramarginal gyrus), the dorsal and ventral PM, the cerebellum, and the putamen showed reduced activation (adaptation) to consecutive visual stimulation near the hand, but not for consecutive far stimuli, compatible with their role in multisensory perception within PPS. Indeed, these areas displayed a reduction in the BOLD response specifically when the object was repeatedly moved in the near location with respect to the outstretched hand. By contrast, such significant reduction in the BOLD signal was not detected when the hand was retracted. Presenting the object in the far location did not produce a differential BOLD adaptation across the conditions, regardless of whether the hand was stretched out in view or retracted. A follow-up study of the same group (Brozzoli et al., 2012) exploited fMRI adaption to investigate whether regions in the intraparietal and premotor cortices remap the PPS of the hand as it is moved in space, that is to say whether the visual selectivity for the space near the hand is "anchored" to the hand. In line with the hypothesis, IPS and premotor areas showed adaptation effects when the stimulus was presented near the hand. Critically, the effect followed the hand when it was moved across two positions in space. These results further revealed that inducing illusory ownership for a fake hand through prolonged synchronous visuo-tactile stimulation remaps the space around the fake hand as PPS, thus paralleling earlier neurophysiological findings in the monkey brain (Graziano et al., 2000).

Lastly, in keeping with previous studies, Ferri and colleagues (2015) identified a region of the premotor cortex that responded to tactile stimulation on the hand depending on the sound (near vs far) location. Interestingly, the extent of individuals' PPS was not predicted by the level of neural activity (i.e., mean BOLD) elicited by near versus far stimulation. Rather, the inter-trial variability (i.e., the modulation of the standard deviation of the BOLD signal after stimulus onset) in the responses to far stimuli predicted the location of PPS extent at the individual level. Specifically, PPS was closer to the body in participants whose neural activity in the premotor cortex was more variable when the sound was presented in the far space. This result is especially interesting because it suggests that the processing of far stimuli is also critical in defining PPS and because it represents the first attempt to actually investigate the neural mechanisms explaining how PPS differs among individuals.

1.3.4 In a nutshell…

More recent research has corroborated, built on and extended the findings described through the electrophysiological approach. Neuropsychological observations support the claim that space is divided into separable regions. For example, deficits in the orienting of visuospatial attention in PPS have been reported after brain damage, while visuospatial orienting in extrapersonal space remains intact (or vice versa, e.g., Aimola et al., 2012; Halligan and Marshall, 1991, Cowey et al., 1994). The results of studies of cross-modal extinction also point to a similar conclusion. Differences in the magnitude of cross-modal extinction have been observed in right brain-damaged patients when visual stimuli are presented from either close to, or further away from, body parts (di Pellegrino et al., 1997). Moreover, PPS can be ‘extended’ by simply modulating the area that an individual can reach by means of, say, the use of a tool (Berti and Frassinetti, 2000; Farnè and Ladavas, 2000). A visual stimulus located in far space, when repeatedly reached with the tool, may be processed as if it is close(r) to the body and, thus, have an stronger influence over PPS multisensory interactions (Maravita and Iriki 2004; Di Pellegrino and Lavadas, 2015).

Similarly to what found in brain-damaged patients, a series of behavioural experiments in neurotypical humans has shown that the PPS representation in the healthy brain reflect the same principles of multisensory interaction. Typically these studies measure the strength of the effects induced by visual or auditory stimulation over the performance on tactile tasks to probe the layout of PPS (Spence el al., 2004b, Serino et al., 2007). A selective review of this literature reveals that the strength of multisensory interactions appears to decay as a function of the distance between visual (or auditory) and tactile information (Spence et al., 2004a), to follow a body part–centred frame of reference (Spence et al., 2004b), and to be remapped after the use of a tool that functionally extends action capabilities (Maravita et al., 2002; see also Holmes, 2012).

Functional brain imaging findings in healthy humans provide further support for the homologies between neurophysiological research and the neural bases of PPS in the human brain. A recent meta-analysis of functional neuroimaging studies identifies a bilateral PPS network, including superior parietal, temporo-parietal and ventral premotor regions, that nicely fits with the anatomical locations of the monkey visuo-tactile network (Grivaz et al., 2017). In particular, brain areas representing near-face and near-hand space in body-centred coordinates through visual and tactile maps have been reported in the anterior section of the intraparietal sulcus and in the ventral premotor cortex (Bremmer et al., 2001; Makin et al., 2007; Sereno and Huang 2006; Gentile et al., 2013). Furthermore, some studies have additionally identified the superior parietal occipital junction as a potential site for representing near-face and near-hand visual space (Gallivan et al. 2009; Quinlan and Culham 2007). This new line of research not only extends our current knowledge of the PPS neural network but may also guide further electrophysiological studies to come.

1.4 Peripersonal space in action

Evidence from neuroimaging allows demonstrating that several sensory and motor regions modulate their neural activity to visual or auditory stimuli based on their distance from the hand or the face. However this approach does not enable us to determine the direct involvement of such representations in motor processing. As already mentioned, a series of findings in monkeys clearly indicate the strong link existing between PPS and action. To date, despite the advocated role of PPS in motor functions, paradoxically in almost all the investigations participants has been static (siting passively or, on occasion, standing still) and PPS representation has assessed in completely static conditions. On the contrary, presentation of dynamic stimuli provides information on the updating of multisensory interactions when objects approach the static observer (e.g., Fogassi et al., 1996). Also, when humans are interacting with the environment (e.g., during grasping) or actively moving through (e.g., while walking), the position of the body in space will change constantly relative to the stimuli in the environment. Because of this, the representation(s) of PPS will obviously need to be updated in order to maintain effective interaction with the external stimuli (Holmes and Spence 2004; van der Stoep et al., 2016). A series of findings in humans support the view that the multisensory interactions in space vary depending not only as a consequence of object moving around the body but also depending on the movements of the body in the environment. Finally, recent research has tried to experimentally assess the link between multisensory processing and motor actions, filling thus the gap between the multisensory perceptual investigation of PPS and its involvement in the execution of action.

Because of the relevance of moving objects to the PPS system, Canzoneri and others (2012) developed a paradigm enabling to investigate the influence of dynamic auditory stimuli on tactile perception. In an audio-tactile task, the authors measured reaction times to a tactile stimulus applied to the right index finger while dynamic sounds, which gave the impression of either approaching or receding from the subject’s hand, were presented. Tactile stimulation was delivered at different temporal delays from the onset of the sound, such that it occurred when the sound source was perceived at varying distances from the body. Participants were simply asked to respond to touches as fast as possible, trying to ignore the sound. It was found that an auditory stimulus speeded up the processing of a tactile stimulus applied to the hand when the sound was administered within a limited distance from the hand. Also, such boosting progressively decreases as a function of the perceived approach of the acoustic stimulus. Thus, the authors were able to mark “a boundary”: the critical region within which approaching auditory stimuli facilitated the participants' detection of tactile stimuli. Moreover, results additionally suggested that approaching sounds had a stronger spatially-dependent effect on tactile processing compared to receding sounds. In line with the finding that selectivity of some VIP and F4 neurons appears as optimally tuned for the detection of dynamic looming visual stimuli (Colby et al., 1993; Bremmer et al., 2002a, 2002b; Rizzolatti et al., 1981; Graziano et al., 1997), such cross-modal processing of approaching stimuli is evident also for looming visual information (Kandula et al., 2014). Tactile sensitivity is enhanced at the predicted location and predicted time of impact of a looming visual stimulus to the face when compared to baseline tactile sensitivity or when looming stimulus not is temporally or spatially predictive. To note that tactile perception is also enhanced, as compared to baseline tactile sensitivity, when the looming stimulus brushes past the face without however predicting an impact to the face, that when the looming stimulus is within face PPS (Clery et al., 2015b).

Relevant for this review, in a series of investigations inspired by the macaque neurophysiological works, Makin and colleagues tested rapid motor responses to “real” three-dimensional objects approaching the hand (Makin et al., 2009; 2015). They asked participants to perform a simple button-press motor response with the right index finger, while a task-irrelevant three-dimensional ball suddenly fell just above the participants’ responding hand (near condition), or at a distance (far condition). To assess the effects of the rapidly approaching stimulus on the excitability of the motor system, single pulse transcranial magnetic stimulation (TMS) was applied to the contralateral primary motor cortex to elicit motor evoked potentials (MEPs) in the responding hand. The sudden appearance of this potentially threatening visual stimulus was associated with a reduction in corticospinal excitability at the very early and specific time window of 70-80 ms following its appearance. This inhibition is proposed to reflect the proactive suppression of an automatic avoidance-related response during the execution of the task-related response. Indeed, when the two motor behaviours (i.e., the avoidance- and the task-related responses) were uncoupled, the approaching ball had an opposite, facilitatory effect on corticospinal excitability. Critically, both the rapid inhibition and facilitation of corticospinal excitability were hand-centred. Regardless of the location of both overt gaze and covert spatial attention, this motor response was selective for approaching stimuli, depending mostly on the distance of the ball from the hand. These observations thus reveal a direct and fast connection between the visual processing of information in the space near the hand and the on-going motor behaviour, suggesting a role for PPS representation in motor responses, for example to avoid rapidly approaching (and potentially threatening) objects (see also Serino et al., 2009; Avenanti et al., 2012 for related results for auditory stimuli). For such a sensorimotor system to be really effective, not only general information about whether the hand is approached, but also the more specific information about which hand is approached, should be processed rapidly. Using the same approach, it was demonstrated that within a very short time-window of 70ms from the appearance of the ball, the motor system is already capable of coding which hand this object potentially threatens. These findings therefore provide support for the general claim that PPS coding may well serve to perform defensive actions. As stated above, such a possibility has already been tested in monkeys through direct cortical microstimulation by Graziano and colleagues (Graziano and Cooke 2006, Cooke and Graziano, 2003, 2004; Graziano et al., 2002), who studied macaque motor activity during defensive movements evoked by aversive cutaneous stimulation. They identified in VIP a startle-related muscular activity occurring as early as ~20 to 30 ms after stimulus onset and a later muscle response starting ~70 ms after stimulus onset. Similar motor responses were also evoked by electrical microstimulation of the premotor cortex. Although comparisons between data arising from monkeys and humans should be made with caution, the hand-centred modulations of motor excitability are similar to the response properties of macaque bimodal neurons. Indeed, independently of the retinal position of the visual stimulus, modulations in motor excitability varied with the distance of the object from the hand and were specific for three-dimensional objects approaching the hand. As suggested by Makin and colleagues (2009, 2012, 2015), these hand-centred mechanisms may play a specific and prominent role in the rapid selection and control of manual actions.

Last, related to this issue is the observation that 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. whether the stimulus is mapped within PPS or not (Sambo and Iannetti, 2013). Although the HBR is an entirely subcortical response, when the stimulated hand is placed closer to the eye the reflex magnitude is dramatically increased. The authors suggest 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 therefore indicates 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. In addition, the hand blink reflex is highly dependent upon cognitive expectations and inferences, given that, for instance, it is enhanced only when participants expect to receive stimuli on the hand (placed close to the face, Sambo et al., 2012b). Finally, the HBR enhancement by hand–face proximity is suppressed when a thin wooden screen is placed between the participants' face and their hand. This seems therefore to indicate that creating a virtual separation between the face and hand can reshape and reduce the extension of PPS.

These multisensory and motor interactions might be adaptive not only for defensive, but also for appetitive actions, such as grasping (e.g., Gardner et al., 2002; 2007; Marzocchi et al., 2008). In this respect, the properties of multisensory neurons underling PPS representations may allow the brain to represent a target object in a coordinate system centred on the body (e.g., the hand, the head, the trunk) that, in addition, could be continuously updated during bodily movements. Since sensory stimuli coming from an external object are initially processed in sensory-dependent reference frames (e.g., visual stimuli in eye-centred, auditory stimuli in head-centred, tactile stimuli in body-centred frames), their coordinates need to be aligned for integration for controlling a moving body. To this aim, the same stimuli are coded with respect to a common body-centred reference frame (Colby, 1998; Andersen et al., 1997; Cohen and Andersen, 2002; Sereno and Huang, 2014; Bhattacharyya et al., 2009). The computations necessary for coding stimuli from different modalities in body-centred reference frames differ depending on the concerned body parts to which external stimuli are referenced to (Andersen and Buneo, 2002; Cohen and Andersen, 2002; Pouget et al., 2002, Bhattacharyya et al., 2009, Pesaran et al., 2010). For instance, given that our hands can move independently from our eyes, the brain needs to integrate information arising in an eye-centred reference frame with information about the current position of the hand relative to the body and to nearby potential target objects. In order to do so, eye-centred representations would have to be transformed into effector-centred representations to command movements directed towards those targets (Makin et al., 2012). It is worth recalling here the motor properties of parietal and frontal visuo-tactile neurons: these multisensory cells have been documented to respond when the arm is voluntarily moved within the reaching space of the animal and proposed to code goal-directed actions (Gardner et al., 2007; Rizzolatti et al., 1981a, 1981b, 1997). Hence, one could theorize that the same defensive anticipatory function featured by the PPS network in the case of avoidance reactions, may also have evolved to guide voluntary object-oriented actions. The two hypotheses are not mutually exclusive, given that one could even think that a more sophisticated grasping function could have developed from more primordial defensive machinery, using the same body-part centred coding of visual space (Brozzoli et al., 2014).

Only recently, though, research started investigating the link between PPS and voluntary motor behaviour in humans. The rationale behind this line of studies is that if the PPS representation guides the execution of voluntary free-hand (i.e., without tool) actions, then the motor program should induce a rapid online remapping of visuo-tactile spatial interactions. To test this hypothesis, multisensory interactions have been assessed during the execution of a grasping action (Brozzoli et al., 2009). Specifically, Brozzoli and co-workers employed a visuo-tactile interaction (hereafter VTI) task, a modified version of the classic CCE task, to measure how (much) VTI varied in real time during the action as a proxy for changes in PPS. In this task, healthy participants had to discriminate the location (up or down) of a tactile stimulus delivered to either of two digits (index or thumb) of one of the two hands. At the same time, they were asked to ignore a task-irrelevant visual distractor that was concurrently presented on the to-be-grasped target object (see Figure 1.10). There was no cue-target delay between tactile targets and visual distractors, thus enhancing the likelihood of causing multisensory integration instead of crossmodal spatial attention (McDonald et al., 2001; Van der Stoep at al., 2015). When compared to a static condition prior to movement initiation, the start of the grasping action selectively increased the influence exerted by visual inputs originating from the (far) target object on tactile stimuli delivered to the grasping hand. In addition, a further increase in the magnitude of VTI was observed shortly after (200ms) the onset of the hand movement.

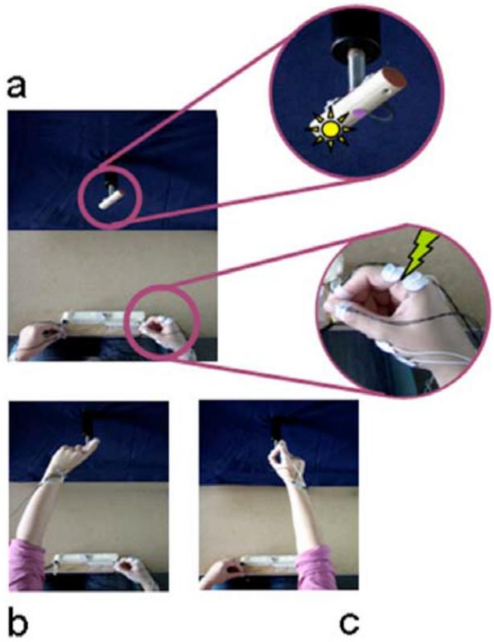


Fig 1.10 View of the visuo-tactile interaction task used by Brozzoli and others (2009) to assess the multisensory interaction during the execution of an action. (a) Bird’s eye view of the participant facing the to-be-grasped object. Electro-cutaneous targets (green zap) were delivered to the index finger (up) or thumb (down), while a visual distractor (yellow flash) could be presented from either the same (congruent, not shown) or different (incongruent) elevation. Visual distractors are embedded into the to-be grasped object. (b) and (c) are example of grasping actions. From Brozzoli et al., 2009.

Crucially, when the same action was performed with the non-stimulated hand, no multisensory modulation was observed, even though both hands displayed comparable kinematic profiles (Brozzoli et al. 2009). This result constitutes evidence in favour of the fact that the execution of a grasping movement triggers a motor-evoked remapping of the hand PPS and additionally reveals that PPS remapping can occur independent of tool-use (see also Serino et al., 2015a). Possibly as in the monkey brain, the human brain links sources of visual and tactile information that are spatially separated at the action onset, updating their interaction as a function of the phase of the action. It is interesting to note that the increase in the strength of the visuo-tactile interaction was present well before the hand comes into contact with the object, being triggering by action execution and further increasing during the early execution phase. This further online modulation of visuo-tactile performance suggests that the multisensory representation of the space around the hand might guide the action as it unfolds in time and space (Brozzoli et al., 2010). Such a dynamic, action-dependent modulation of PPS was replicated in a second study in which two types of actions were performed. Brozzoli and his colleagues assessed the effects of performing two different actions (i.e., grasping or pointing) towards the same object on the on-line modulations of PPS, as measured by VTI (Brozzoli et al., 2010). When compared to the static condition, the grasping and the pointing actions had similar effects of increasing VTI at the action onset. More interestingly, VTI further increased during the execution phase of the grasping, but not of the pointing action, when the kinematics of these movements started to diverge (see Figure 1.11). These findings therefore suggest that performing voluntary actions induce a continuous remapping of PPS as a function of the on-line contextual demands imposed by their kinematics. In other terms, as a further proof of the deep the relationship between PPS and the motor characteristics of the action, different multisensory interactions arise as a function of the required sensory–motor demands, being more important for actions that need relatively more complex sensory–motor transformations. If (at least part of) the remapping of PPS is already effective at the onset of the motor program, the visuo-tactile modulation will be kept unchanged. On the other hand, in the case of relatively complex object-oriented interactions such as grasping, the remapping of PPS will be dynamically updated with respect to the motor command.

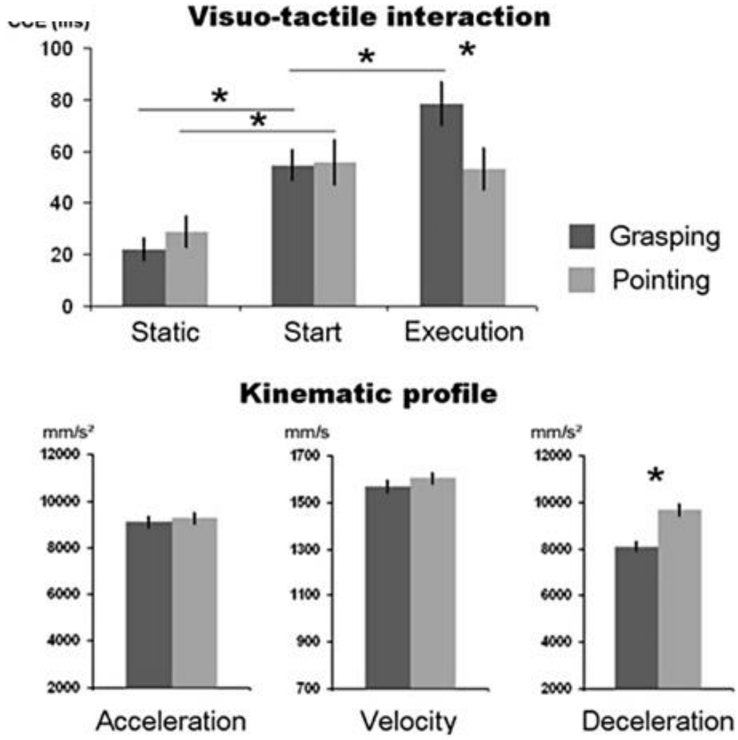


Figure 1.11 On-line modulations of PPS during actions. Upper panel. VTI changes during grasping and pointing movements as function of action phase. Lower panel. Kinematic changes of the transport component for both actions: peaks of acceleration (left part), velocity (central part) and deceleration (right part). Adapted from Brozzoli et al., 2010.

A similar remapping has been documented in the case of walking: PPS extends when participants walk as compared to when they were standing still (Noel et al., 2015). The boundary of the trunk PPS was assessed by measuring the spatial distance at which an approaching sound significantly speeded-up reactions to tactile stimuli on the participant’s body (see Canzoneri et al., 2012; Serino et al., 2015b). The experiment was conducted while the participants were either standing or walking on a treadmill, such that the relative distance between the participant’s body and the sound source was equivalent in the two conditions. However, while in the static condition sounds occurring closer than ~80-90cm from the participant decreased tactile RTs, in the walking condition the speeding-up of participants’ responses occurred for sounds farther than 2 m. The latter result therefore suggests that potential interactions between external stimuli and bodily stimuli are anticipated in the case of walking (Noel et al., 2015).

1.4.1 A space for body-object interactions? Interim summary

In the lights of such a wealth of demonstrations, an obvious yet critical question arises: why the brain should be endowed with a modular representation of space displaying multisensory and motor features?

A crucial point I tried to stress so far is that the encoding of near space has not only sensory, but also motor-related nature that qualifies PPS as multisensory-motor interface. Indeed, neurophysiological evidence in monkey demonstrated that neurons in premotor and parietal cortex and in the putamen have multisensory functions as well as motor functions (Rizzolatti et al., 1997). In humans, single-pulse TMS experiments have shown that visual (Makin et al., 2009) or auditory (Serino et al., 2009) information within PPS transiently modulate the excitability of the hand representation in the primary motor cortex. For this reason, PPS representations are probably best described as multisensory-motor interface(s), which serve to encode the location of nearby sensory stimuli to generate suitable motor acts. Arguably, the body part-centred PPS representations may provide an effective mechanism to guide actions both *towards* and *away* from nearby stimuli presented within reaching distance by using different effectors. Indeed, the encoding of the spatial position of external stimuli in a body-centred frame of reference has traditionally been suggested to facilitate the "possibility to act in space" in terms of approaching and defensive responses. Even for very simple actions, such as avoiding a stimulus coming towards the face or the hand (see Graziano and Cooke, 2006), or reaching to grasp an object, or getting food into the mouth (see Rizzolatti et al., 1997), the motor system needs to compute the position of the visual stimulus relative to the relevant body parts.

From a theoretical perspective, De Vignemont and Iannetti (2014) have accordingly proposed a dual model of PPS representations based on a functional distinction between bodily protection and goal-directed action. Protecting the body against physical threats is one of the vital functions the system should guarantee. By acting as an anticipatory multisensory-motor interface, PPS may serve for the early detection of potential threats approaching the body (Fogassi et al., 1996) in order to drive involuntary defensive movements (Cooke and Graziano 2003; Graziano and Cooke 2006). As already described, the most direct evidence in favour of this hypothesis comes from cortical electrical stimulation studies (although concerns have been raised in this respect; see Strick 2002). It is worth acknowledging that, by employing a similar paradigm it has been demonstrated that the stimulation of parietal visuo-tactile areas can induce not only movements that are compatible with defensive behaviour, but also movement's compatible with "appetitive" behaviours, such as reaching and grasping (Stepniewska et al., 2005). As a consequence, the same anticipatory feature might also have evolved to serve voluntary object-oriented actions (Gardner et al. 2007; Rizzolatti et al., 1981a, 1981b; Stepniewska et al. 2005; Brozzoli et al., 2014).

To summarize, the accepted view over the years has been that visual body-centred mechanisms should play some general role in the sensory guidance of movements towards objects within reaching distance (Bremmer 2005; Fogassi and Luppino 2005; Graziano 1999; Maravita et al. 2003; Rizzolatti et al., 1997; Graziano and Gross 1998), yet its specific role has not been determined. Within this framework, the first experimental contribution in this thesis is thus to provide support to the hypothesis that PPS is ideally well suited to guide goal-directed actions (see Chapter II).

1.5 Social PPS

It has been extensively argued that the space around us is a sensory-motor interface for interactions with the environment, both for controlling voluntary object-oriented actions and for defending the body against potentially threatening stimuli. Hereafter, I will show that such interactions are not limited to low-level hand-objects contacts, but could also include abstract and cognitive exchanges with other people. Most of the studies previously presented in this dissertation investigated how the representation of the space surrounding the body changes as a function of interaction with an artificial object: by using a tool, for instance, the distinction between a near space - where I can normally act - and the far space – where I can act with the tool - is altered. Critically, in everyday life the distinction between near and far space is meaningful not only in terms of possibility of object interaction, but mainly in terms of social interactions. That is to say, not only the nature of the action one is performing is important in defining the space immediately adjacent to the body, but also the social and emotional valence of the target as well as the interpersonal consequences of the actions.

Accordingly, a new corpus of research has begun to explore how selectively social information can affect how we represent the space around us. A distinction can be made between studies of the role of PPS during social interaction and those investigating how affective information influences PPS coding. While in the first case several investigations have revealed how PPS could be affected by social factors such as presence, morality, or cooperative behaviour of other individuals; only few studies have determined how the emotional (not strictly social) relevance of the stimuli influenced the layout of PPS. Since this latter topic is less relevant for this dissertation, first I briefly will summarize these emotional-related studies before considering the social-related PPS investigations.

A few studies investigated how (perceived) threat affects sensory processing in PPS. For example, clear inter-individual differences in the extension of the defensive PPS, as indexed by distance dependent modulations of HBR, strongly and positively related to the variability in trait anxiety (Sambo and Iannetti, 2013). Other researchers, meanwhile, have reported that the size of PPS is correlated with the extent of claustrophobia, a condition characterised by intense anxiety in relation to enclosed spaces and physically restrictive situations (Lourenco et al., 2011, see Taffou and Viaud-Delmon, 2014, for the relation between cynophobia and PPS). In Lourenco and colleagues' work (2011), the effect of claustrophobia on PPS has been 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, Patanè et al 2015a). The authors 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 PPS. Although it is important to highlight that the extension of the defensive PPS is expected to vary as a function of the threat context in which it is measured, changes in PPS extension correlate with the anxiety similarly to what observed for claustrophobia: figuratively speaking, the greater the fear or anxiety, the bigger the PPS extent. Within the same line of research, a recent study investigated whether visual information in PPS could specifically affect processing of nociceptive stimuli and demonstrated that the interaction between visual and nociceptive stimuli also depends on the region of space in which visual information is presented (De Paepe et al., 2014). Related to this, the proximity of threat also seems to affect distance estimation of stimuli relative to the body (see Tabor et al., 2015) and threatening looming stimuli are perceived as having shorter time to- impact latency as compared to nonthreatening objects moving at the same speed (Vagnoni et al., 2012). More interestingly, the distance from the body at which auditory stimuli starts to affect RTs to tactile targets on the hand is also larger for auditory stimuli with negative compared positive valence. This is a result that could be interpreted as an extension of the defensive PPS for threatening or negative stimuli (Ferri et al., 2015b).

More relevant for this dissertation, PPS representation is shaped both by presence and behaviours of other individuals. The pioneering work by Heed and colleagues (2010) showed for the first time that multisensory integration is modulated as a function of the presence and activities of others located within one’s own PPS. In their behavioural study employing the classic CCE, a group of participants had to respond to the elevation (up or down) of tactile stimuli applied on the hand, and to ignore visual distractor presented concurrently in a congruent or incongruent manner compared to the tactile stimulus. Crucially, participants performed the task both alone and with a partner who responded to the visual distractors. CCE was significantly reduced when the participant performed the task with a partner who sat in front to her and concurrently responded to visual stimuli. Note, however, that the social modulation of CCE required the partner's presence and action within the participant's PPS. When the partner was outside of the participant's PPS, or she did not perform a task on visual stimuli, no modulation of CCE was observed. Such a change of CCE was interpreted as due to top-down modulation, so that knowing that the partner acts upon visual events near to one's body reduces the crossmodal interactions between vision and touch in the space around us. In other words, the possibility exists that the PPS may shrink when other agents act into our vicinity.

Teneggi et al. (2013) extended this intriguing result by describing both that PPS is smaller when facing another individual standing in far space and that the PPS boundary changes as a function of the social experience with the other individual. The size of PPS was assessed in terms of the distance at which approaching sounds started to decrease participants’ detection latencies in response to tactile stimuli delivered to the their face. The first experiment showed that PPS representation shrinks (i.e., PPS boundary move closer to the subject' body) when the far space is occupied by another person, as compared to when it is occupied by an artificial, human-like object (i.e. a mannequin) of comparable size. The fact that the boundary of PPS was closer to the participants seems to indicate that the mere presence of an unknown person shapes PPS representations, as if people automatically and implicitly divide the space between themselves and others. Even more interestingly, in a second experiment the size of PPS was found to increase after playing an economic game with a cooperative individual positioned in front of the participant, as compared to before playing the economic game. Critically, this was not the case when the game was played with an uncooperative individual. In other terms, the shift of PPS boundary when the other individual behaved cooperatively was interpreted as an enlargement of one’s own PPS as to include the space around the other. By contrast, when the other individual failed to cooperate during the economic interaction, the PPS boundaries between self and the other did not change. Thus, this study showed that PPS representation not only responds to the presence of others, but is also shaped by interactions with others and, more specifically, by valuation of other people's behaviour during the social interaction. Lastly, as a further demonstration that PPS representation is sensitive to the social perception of the other, in a recent work adapting the same paradigm in mixed realty, PPS was found to be more extended when participants were facing a moral than when facing an immoral person. This effect was specific for social context, as no change in PPS was detected if participants were facing an object, instead of the person (Pellecin et al., 2017, see also Iachini et al., 2015 and 3.4 session of the present dissertation).

Finally, a recent fMRI adaptation study (Brozzoli et al., 2013) explored whether in the human brain a shared representation of PPS for oneself and another person could exists. Specifically the authors tested if the human brain contains neuronal populations encoding the space near both one's own hand and another person's hand, analogous to what was identified in monkey parietal cortex (Ishida et al., 2010, see previous paragraphs). In this study, participants viewed a ball moving either near to their hand, or to another person's hand, which was positioned with the same orientation of the participants' hand but located in far space. An artificial hand, also located far from the subject, served as a control condition. By employing BOLD adaptation, a pool of neurons was discovered in the left PMv exhibiting mirror-like properties. Namely, a subset of the neuronal populations that displays selectivity for an object near a person’s own hand also displays the same selectivity for representing an object close to another person’s hand rather than close to the artificial hand. This finding fits well with the discovery in the macaque’s brain of visuo-tactile populations of parietal neurons discharging when the monkey sees an object moving close to another individual’s body (the “body-matching neurons” identified by Ishida and others 2010). This mirror-like, embodied simulation mechanism may provide the neural substrate for how the representation of one's own PPS accommodates in the presence of others during social interactions (Lavadas and di Pellegrino, 2015). Consistent with this compelling hypothesis, the last study of this thesis will explore whether a highly social construct might be rooted in such simulative mechanisms.

Chapter II: Action planning modulates peripersonal space

Co-authored by Ivan Patané, Lucilla Cardinali, Romeo Salemme, Francesco Pavani, Alessandro Farnè, Claudio Brozzoli

The first chapter reviewed converging evidence, ranging from non-human primate electrophysiology (Rizzolatti et al., 1981a, 1981b; Colby et al., 1993; Graziano et al., 1993; Duhanamel et al., 1997) to neuroimaging (Sereno and Huaung 2006; Makin et al., 2007; Brozzoli et al., 2011; Ferri et al., 2015a) and behavioural studies in humans (di Pellegrino et al., 1997; Farnè et al., 2000; Spence et al., 2004a; Serino et al., 2015b; Scandola et al., 2016) indicating the existence of a multisensory representation of the space immediately surrounding the body, viz., PPS (see Brozzoli et al., 2014; Ladavas and di Pellegrino 2015; Blanke et al., 2015; van der Stoep et al., 2016 for recent reviews). Because of the properties previously summarised, PPS has been thought to serve defensive purposes, preparing for or boosting motor responses to potential threats approaching the body, such as avoidance movements (Graziano and Cooke, 2006). In line with such a defensive role, PPS boundaries may expand as a function of the speed of approaching objects (Fogassi et al., 1996), thus allowing individuals to respond to objects approaching the body at higher speeds at even further distances. The same dynamic features have also been proposed to serve appetitive actions, such as grasping objects (Rizzolatti et al., 1997). In this regard, a wealth of studies in both human and non-human primates has documented changes in PPS boundaries, namely, the extension following tool-use (Iriki et al., 1996; Berti and Friassinetti, 2000). Most studies in humans have quantified VTI in the space surrounding the hand before and after a short training session with the tool. However, in these studies, the hand was typically immobile during VTI assessment (Maravita et al., 2001; 2002; Farnè et al., 2005b). Consequently, this line of research was unable to probe dynamic changes in PHS boundaries *during action* unfolding.

In contrast to the static approaches described above, initial support for the ‘appetitive function' hypothesis comes from our previous work that assessed the PPS boundary under active conditions, namely, *while* the hand was moving to grasp an object. In particular, by measuring the strength of the interaction between touches delivered to the hand and visual distractors placed on the object that the hand reached for and grasped, we detected an increase in visuo-tactile interaction in real time when the hand moved to grasp the object compared to when the hand was immobile (Brozzoli et al., 2009). In addition, kinematic recordings of hand movements demonstrated that complex grasping movements produced stronger VTI modulation during action compared to simpler pointing movements (Brozzoli et al., 2010). Given the well-known finding that VTI is stronger for targets nearer the hand in humans than for those further away (di Pellegrino et al., 1997; Spence et al., 2004a; 2004b), these results indicated a modulation of PPS boundaries: the target of the action, which was located far from the initial hand position, was 'remapped' as if it were within PHS as soon as the hand moved to grasp it.

However, the question of whether the PPS representation is recruited *before* an upcoming action (i.e., during action planning) remains unanswered, even though it is fundamental to understanding the role of multisensory space representations for action. In the current study, we posited that if PPS supports the control of voluntary actions, an increase in VTI indexing whether a target object is remapped closer to the hand, should occur even when the subject is *planning* to grasp it, i.e., well before the overt motor act. Indeed, it is during planning that the brain initiates the sensorimotor processes that compute both object and hand current states to form an appropriate motor plan that will eventually be realised as a movement (Castiello 2005; Culham, and Valyear, 2006). We therefore predicted that PPS remapping, indexed by an increase in VTI, is triggered by action planning well before movement initiation. To test this hypothesis, we presented the target to be grasped with an unpredictable orientation on a trial-by-trial basis, and we made this visual information available only at the 'go' signal for the action. This design was conceived to force participants to plan the action anew at every trial. Such a procedure ensures the possibility of assessing and comparing the strength of VTI at two critical time-points before movement onset: 50 ms after the 'go' signal, which is immediately after information concerning the target has been made visually available (object vision phase); and 250 ms after the 'go' signal, which is during the planning phase (Koch et al., 2010). In addition, we assessed touch perception alone under the same conditions. Unisensory tactile (hereafter T) and multisensory visuo-tactile (hereafter VT) stimuli were therefore both delivered during the same phases. To note that contrasting multisensory VT and unisensory T performance would allow us to monitor whether VTI changes reflect a mere decrease in tactile perception during movement execution, possibly due to tactile suppression (Chapman et al., 1987; Chapman 1994; Voss et al., 2005). Alternatively, modulation of VTI may reflect interference and/or facilitation driven by the effect of visual stimuli on tactile perception, thus suggesting multisensory processing (Stein and Stanford 2008). Finally, to rule out the possibility that VTI modulation during different action phases was attributable to the multisensory stimulation affecting hand movements, we recorded and analysed the kinematic patterns of grasping movements. Based on previous work using a similar set-up, we predicted that kinematics would differ as a function of object orientation (Brozzoli et al., 2009; 2010) without being critically affected by concurrent sensory stimulation.

2.1 Methods

Participants

Sixteen healthy participants (mean age: 28±5 years) with normal or corrected-to-normal vision and no history of sensory problems took part in the study. The sample size (N=16) was based on an estimate from our previous studies (Brozzoli et al., 2009, 2010). All participants gave informed consent to take part in this study, which was approved by the CEEI (Comité d'evaluation éthique de l'Inserm)/ Institutional Review Board and conducted in accordance with the principles of the revised Helsinki Declaration (World Medical Association, 2013).

Apparatus

The target object was a wooden cylinder (7 cm in height, 1.7 cm in diameter) located at eye level at a distance of 47 cm from the starting position of the participant's hand (Figure 1A). Participants had to grasp the cylinder with a precision grip, such that the index finger touched the top surface and the thumb touched the bottom surface. Two red LEDs (light-emitting diode) were embedded into the cylinder proximal to the contact surfaces of the fingers in the precision grip configuration. Visual stimuli consisted of a single flash (200ms duration) from either the top or bottom LED, delivered concurrently with electro-cutaneous stimulation to the grasping hand. A black dot (1 cm in diameter) in the centre of the cylinder (between the two LEDs) served as a visual fixation (see Figure 2.1A). Disposable electrodes (70015-K, Ambu Neuroline, Denmark) were used to present suprathreshold electro-cutaneous stimuli consisting of square-wave pulses (100 µs, 400 V) delivered by constant-current stimulators (DS7A, Digitimer Ltd., UK) to either the index finger or thumb of the right hand. To ensure that participants could be near to 100% detection of the electrical stimuli during the task, we first estimated thresholds for each of the two fingers and added 20% to the respective intensities that were then kept constant throughout the experiment. Finger threshold was determined via a staircase procedure with manually triggered stimulations (5 on the thumb and 5 on the index finger) in a random order, intermingled with five catch trials in which no stimulation was delivered. Participants were asked to report when and where they felt the tactile stimulus. During the experimental task, participants had to respond to the tactile stimulus as fast as possible by releasing one of two foot pedals (Herga Electric Ltd., UK): the toe pedal indicated stimulation of the index finger, and the heel pedal indicated stimulation of the thumb, according to the classical procedure employed in studies investigating visuo-tactile interaction through the cross-modal congruency effect (CCE, Spence et al., 1998; 2004a; 2004b; Shore et al., 2005; 2006). Participants were therefore required to make speeded location responses, reporting whether tactile target stimuli were presented to the index finger or thumb. Participants were also asked to ignore task-irrelevant visual stimuli embedded in the object. Visual stimuli were presented in a spatially congruent or incongruent arrangement with respect to tactile targets when considering the hand posture (i.e., index finger and top LED or thumb and bottom LED for VT congruent stimulation; index finger and bottom LED or thumb and top LED for VT incongruent stimulation, see Fig. 2.1A). Participants wore a pair of shutter goggles (FE-1 Cambridge Research Systems Ltd., UK) based on ferro-electric liquid crystal (FLC) technology. The liquid crystal lenses of the goggles were configured in either a transparent (open) or a translucent (closed) state; vision was completely occluded in the latter condition and allowed in the former. The brand-estimated switching time from close to open state is 0.1ms. Participants had to move as soon as the goggles opened, making the object visible and constituting the ‘go’ signal.

To vary action plans and execution on a trial-by-trial basis, the cylinder was unpredictably rotated before becoming visible (manually from behind the panel) to one of two different orientations: +36° (clockwise*)* or -36° (counter-clockwise). Accordingly, the object orientation imposed either clockwise (+36°) or counter-clockwise (-36°) wrist rotation. Movements were recorded using an Optotrak 3020 system (Northern Digital, Inc.), with a sampling rate of 150 Hz (0.01-mm 3D resolution at 2.25-m distance) via three infrared emitting diodes (IREDs): two infrared light emitting diodes were attached to the lateral and interior parts of the nails on the thumb and index finger, and one to the interior part of the wrist at the styloid process level. These markers were used to perform on-line registration and subsequent off-line reconstruction of the transport component (the change over time in wrist marker position while the right hand was reaching for the target) and grip component (the change over time in distance between index finger and thumb) for the action. Through MAIN, a software developed in the laboratory Impact for pre-processing and 3D visualization of kinematic data, we identified the following parameters, without applying any filter to the position signals: peaks and relative latencies of wrist acceleration, velocity and deceleration for the transport component of the movement; and peaks and relative latencies of maximum grip aperture (MGA) and velocity of grip aperture (VGA) for the grip component. Movement start was detected on the velocity curve of the wrist IRED with a threshold criterion of 15 mm/s. The velocity was calculated as the first temporal derivative of the position signal relative to the marker placed on the wrist, with a 5-point time window. Its peak was defined as the maximum value between the point when the speed passed the threshold of 15 mm/s and the point when speed went below this threshold again. Peak of acceleration and deceleration were defined respectively as the maximum and the minimum value of the second temporal derivative of the position signal from the wrist marker, before and after the peak of velocity respectively. The grip aperture was defined as the variation in time of the Euclidean distance between index and thumb. Its peak was defined as the maximum value reached after movement initiation and before the end. Velocity of grip aperture was defined as the first derivative of the grip aperture measure. The movement end was set at the first of a series of points showing a stable grip aperture, signalling that the object had been steadily grasped. The latencies of all the parameters correspond to the point in time (ms) of their occurrence with respect to movement onset. All trials were inspected visually to spot accidental failure of the automatic procedure of the software. When necessary, manual detection of peaks and relative latencies was applied following the criteria described above.

Design and procedure

Participants sat at a table with the thumb and index finger of each hand in a closed pinch-grip posture on two switches fixed to the table. They were instructed to perform two concurrent tasks during each trial: the perceptual task (speeded discrimination of tactile stimulus location: index finger or thumb) and the motor task (reaching and grasping the cylinder along its longitudinal axis with the right index finger and thumb). Each trial started with an auditory warning signal. After a variable delay (1500–2200 ms), the goggles opened (i.e., changed to a translucent state), constituting the ‘go’ signal for the motor task (Figure 2.1B). The experiment consisted of 6 blocks of 80 trials: in 2 blocks, only tactile stimuli were delivered, and in the other 4 blocks, visual and tactile stimuli were delivered simultaneously. This design ensured an equivalent number of stimulation trials for the unisensory tactile and multisensory (congruent and incongruent) visuo-tactile conditions. Half of the participants started with tactile blocks, while the other half started with visuo-tactile blocks. In each block, stimulation was randomly delivered across trials at five different latencies (see Figure 2.1B): 1) the object vision phase, beginning 50 ms after the opening of the goggles; 2) the action planning phase, beginning 250 ms after the opening of the goggles; 3) the movement onset phase, where movement initiation was detected by the release of the start switch; 4) the movement execution phase, beginning 200 ms after action onset; and 5) the max grip phase, which was time-locked to the maximum grip aperture of the fingers computed on-line. The choice of stimulation times during the static phases (object vision and action planning) was dictated by the fact that precision grasping planning is typically not initiated earlier than 50 ms after a ‘go’ signal (Koch et al., 2010). We note that both the object vision and action planning phases occurred before movement initiation. Thus, they differ in terms of time elapsed from the moment when visual features of the object become available for the motor program, but they are identical in terms of the motor state of the hand (i.e., immobile in both conditions).

2.2 Statistics

To assess the dynamics of multisensory interactions, we calculated the VTI as the difference between RTs (reaction times) for spatially incongruent and congruent VT trials, as this difference quantifies the strength of the interaction between visual and tactile stimuli. As similar patterns of results were found for accuracy scores, for the sake of brevity I report only analyses and results for RTs. A two-way ANOVA was performed with within-subject factors of object orientation (clockwise vs. counter-clockwise) and timing (object vision phase vs. action planning phase vs. movement onset phase vs. movement execution phase vs. max grip phase). A similar ANOVA was run on tactile RTs to test potential unisensory tactile modulation during action. Newman-Keuls post hoc tests were used when appropriate to explore significant effects.

In addition, we compared VT to unisensory tactile performance. The reasoning behind this choice was twofold. First, we aimed to evaluate the impact of potential variations in unisensory T on multisensory VT perception to ensure that VTI was genuinely affected, independent of any change in unisensory touch perception per se. Second, we aimed to test whether the multisensory integration underlying VTI is due to facilitatory and/or interfering multisensory processes. Thus, for each timing we expressed RTs for congruent and incongruent VT trials with respect to the unisensory tactile performance (i.e., congruent RTs=VT congruent RTs – T RTs; incongruent RTs=VT incongruent RTs – T RTs). Object orientation (clockwise vs. counter-clockwise) conditions were collapsed since this factor did not affect uni- or multisensory performance. Any significant deviation from 0 would thus indicate an effect of the visual event over the perception of touch, in terms of either facilitation (if <0) or interference (if >0). We therefore assessed differences between conditions by running one series of Bonferroni-corrected one-tailed t-tests for the congruent condition and a second series for incongruent RTs against a null hypothesis of zero (i.e., one-sample t-tests).

For the motor task, the primary kinematic parameters for the transport and grip components of the movements were analysed to assess potential differences in the movement profile across conditions. A series of 3-way ANOVAs was conducted on VT trials with stimulus (congruent vs. incongruent), object orientation (clockwise vs. counter-clockwise) and timing (object vision phase vs. action planning phase vs. movement onset phase vs. movement execution phase vs. max grip phase) as within-subject factors. Separate ANOVAs were performed for latency and amplitude of acceleration, deceleration and velocity peaks (transport component) as well as for MGA and VGA peaks (grip component). A similar series of 2-way ANOVAs was conducted on T trials with object orientation and timing as within-subject factors; separate ANOVAs were conducted for the peak and latency of each kinematic parameter. Kinematics analyses were intended to rule out the possibility that VTI increases over time merely reflected a difference in motor performance across conditions. On the contrary, we expected the kinematics of grasping movements to be affected primarily by object orientation in both VT and T trials.

Hereafter, effect sizes are reported in terms of partial eta squared (η^2_p), and averages are reported along with the standard error of the mean (SEM). Unless stated otherwise, only significant results are reported.

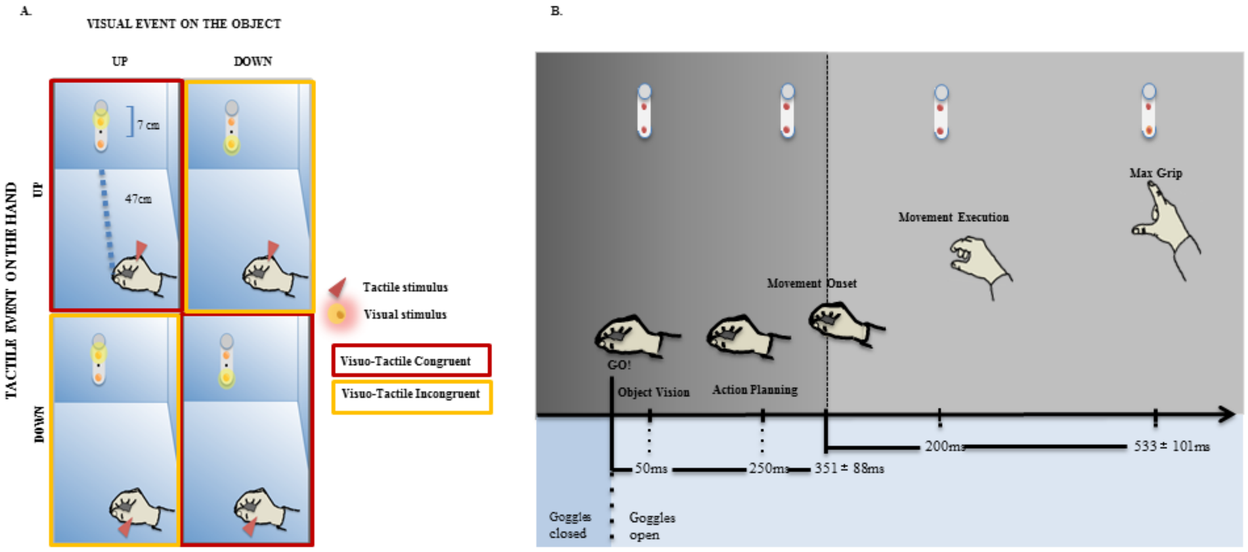


Figure 2.1 Visuo-tactile stimulation during the planning and execution of a grasping movement. (A) Participants were asked to discriminate the location (up or down) of touches (red triangle) delivered to either the thumb (lower panels) or index finger (upper panels) while ignoring visual stimuli embedded in the cylinder to be grasped (upper and lower red circles); these stimuli produced either spatially congruent or incongruent patterns of visuo-tactile stimulation (dark and light grey-framed panels, respectively). (B) Sudden opening of shutter goggles prompted participants to grasp the cylinder in a given orientation; participants' vision was inhibited by the shutters prior to the beginning of each trial. Across blocks, unisensory tactile and multisensory visuo-tactile stimulation were delivered unpredictably, time-locked to crucial phases of the action: the object vision phase (50 ms after the goggles' opening); action planning phase (250 ms after the goggles' opening); movement onset phase (time-locked to individual motor RT); movement execution phase (200 ms after action onset); and max grip phase (time-locked to the maximum grip aperture, available in real time via the kinematics recording).

2.3 Results

2.3.1Visuo-tactile performance

Significant action-dependent modulation of VTI was observed [main effect of timing, F(4,60)=8.69, $p<.0001$, $\eta^2_p=0.37$]. Multisensory performance was enhanced during action planning before any overt movement of the hand occurred. Indeed, even though the hand was still immobile, participants displayed greater VTI in the action planning phase (66±9 ms) than in the object vision phase (36±12 ms, p=.043; Figure 2.2A, upper graph). VTI was further increased in the execution phase (110±13 ms, p=.015) compared to that in the action planning phase. Moreover, VTI was significantly lower in the object vision phase than at all other latencies (p<.001, Figure 2.2A, upper graph).

2.3.2 Tactile performance

Unisensory T perception was affected by action execution [main effect of timing, F(4,60)=11.82, $p<.001$, $\eta^2_p=.44$]. Participants were faster at discriminating which finger had been touched when the hand was moving (movement execution phase: 423±20 ms; max grip phase: 411±14 ms) than when it was not (object vision phase: 485±26 ms; action planning phase: 456±23 ms, p<.001 for all post hoc tests). Crucially, while unisensory T performance was better during action planning than in the movement onset phase (500±30 ms, p<.02), neither phase differed with respect to the object vision phase (p=.07 and p=.37, respectively; see Figure 2.3).

2.3.3 VT performance relative to the tactile baseline

Facilitation of tactile discrimination by congruent visual stimuli occurred selectively at action onset (Bonferroni-corrected p=.042). In contrast, interference with tactile discrimination by incongruent visual stimulation emerged in all remaining phases, from the action planning phase onward (all Bonferroni-corrected p<.001). Neither facilitation nor interference effects emerged in the object vision phase (Figure 2B, lower graph).

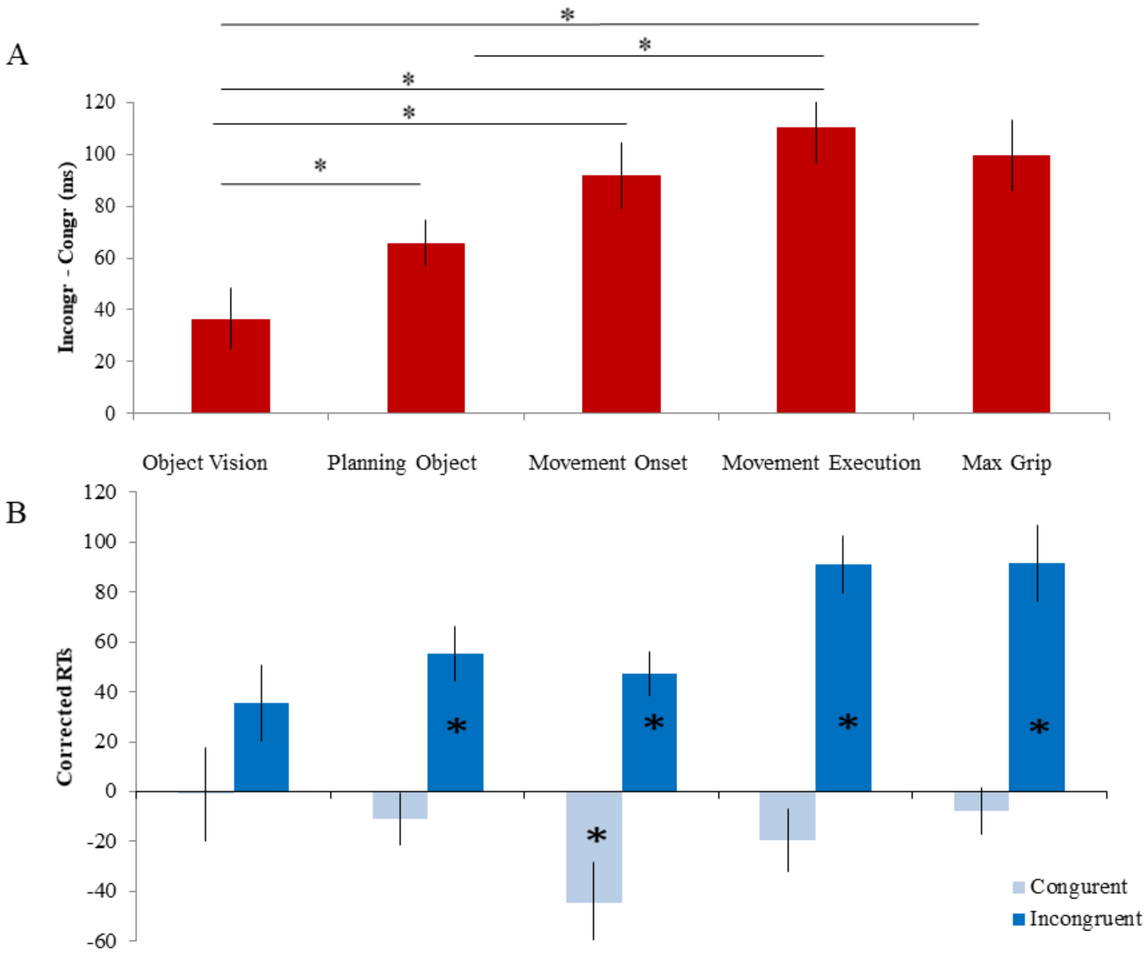


Figure 2.2. Multisensory-motor planning and execution. (A) Bar plots (with SEM) show the modulation of VTI (incongruent minus congruent RTs difference) as a function of timing. Asterisks indicate significant differences among the action phases. **(B)** Bar plots (with SEM) display visuo-tactile RTs relative to unisensory tactile RTs. Asterisks indicate significant deviations from 0 (either facilitation if <0 or interference if >0). The multisensory effect comprised both interference (during all phases from action planning onward) and selective facilitation (in the action onset phase).

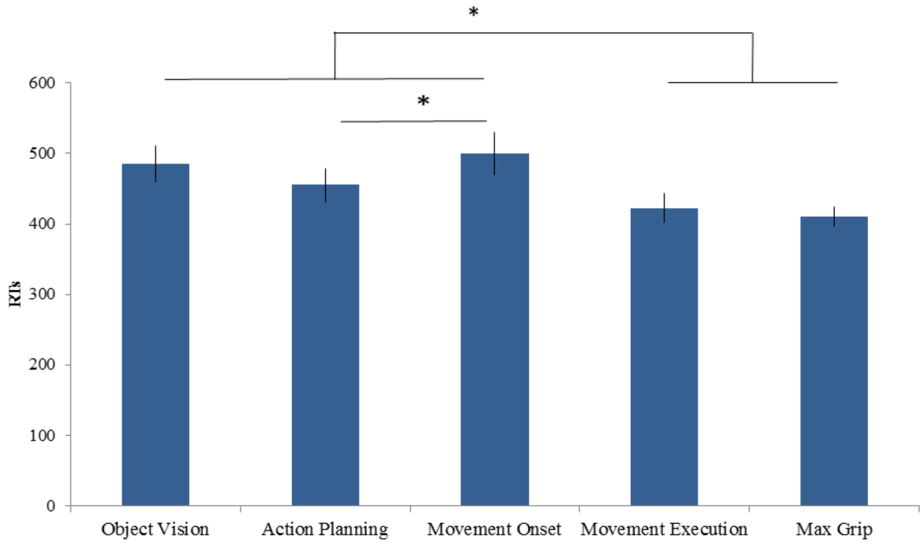


Figure 2.3: Unisensory tactile performance. Bar plots (with SEM) display modulation of tactile RTs as a function of timing. Asterisks indicate significant differences between action phases.

2.3.4 Motor performance

Kinematic analysis of transport component parameters showed that movements required for grasping the counter-clockwise oriented object resulted in larger peaks than movements required for the clockwise-oriented object. Velocity peak latency was accordingly modulated by object orientation (Table 1). This modulation, which was present irrespective of the type of VT stimulation (congruent or incongruent), as expected, was confirmed by kinematic analysis of unisensory T trials, which exhibited similar modulation for peaks of the transport component parameters (Table 1). No major effect of object orientation was found for latencies in unisensory T trials, although velocity peak latency tended to differ according to the clockwise/counter-clockwise orientation of the target object (Table 1, right panel). The effect of object orientation was present across all other independent variables (see Table 2 for an exhaustive report of other statistically significant results). No other significant major effect or interaction was observed.

Kinematic analysis of the grip component parameters revealed that the timing of sensory stimulation affected both latency and amplitude of the MGA and VGA, and this effect was similar for multi- and unisensory trials. Participants tended to open their fingers wider and faster when stimulation was delivered in the static versus the dynamic phases, both under multi- and unisensory conditions and irrespective of the congruency between visual and tactile events. Furthermore, participants displayed longer latencies for these parameters in the dynamic phases of the action (see Table 1), again regardless of the type of stimulation (uni- or multisensory). No other significant effect on the kinematics of the grip component was observed (see Table 2).

Effect of object orientation on the transport component			
Multisensory visuo-tactile trials			
Peak		**Latency**	
Acceleration: F(1,15)=5.34, p=.036*	Counter-clockwise 8517±785 mm/s^2	Acceleration: F(1,15)=0.47, p=.504	Counter-clockwise 114±6 ms
	Clockwise 8358±765 mm/s^2		Clockwise 115±7 ms
Velocity: F(1,15)=14.42, p=.002*	Counter-clockwise 1421±62 mm/s	Velocity: F(1,15)=5.38, p=.035*	Counter-clockwise 310±12 ms
	Clockwise 1397±62 mm/s,		Clockwise 313±12 ms
Deceleration: F(1,15)=20.27, p=<.001*	Counter-clockwise -6745±494 mm/s^2	Deceleration F(1,15)=2.25, p=.154	Counter-clockwise 4483±17 ms
	Clockwise -6452±471 mm/s^2		Clockwise 452±17 ms
Unisensory tactile trials			
Peak		**Latency**	
Acceleration: F(1,15)=4.92, p=.043*	Counter-clockwise 7975±617 mm/s^2	Acceleration: F(1,15)=0.97, p=.369	Counter-clockwise 118±8 ms
	Clockwise 7777±642 mm/s^2		Clockwise 119±9 ms
Velocity F(1,15)=4.74, p=.046*	Counter-clockwise 1403±57 mm/s	Velocity: F(1,15)=3.64, p=.076	Counter-clockwise 325±16 ms
	Clockwise 1378±57 mm/s		Clockwise 328±14 ms
Deceleration F(1,15)=7.79, p=.014*	Counter-clockwise -6673±430 mm/s^2	Deceleration F(1,15)=2.21, p=.157	Counter-clockwise 463±19 ms
	Clockwise -6374±409 mm/s^2		Clockwise 467±18 ms
Effect of timing on the grip component			
Multisensory visuo-tactile trials			
Peak		**Latency**	
MGA F(4,60)=4.11, p=.005*	Object Vision Phase: 114±2 mm	MGA F(4,60)=12.70, p=<.001*	Object Vision Phase: 510±17 ms
	Action Planning Phase: 115±2 mm		Action Planning Phase: 512±17 ms
	Movement Onset Phase: 114±2 mm		Movement Onset Phase: 532±16 ms

	Movement Execution Phase: 113±2 mm		Movement Execution Phase: 550±17 ms
	Max Grip Phase: 111±2 mm		Max Grip Phase: 563±20 ms
VGA F(4,60)=2.80, p=.034*	Object Vision Phase: 570±49 mm/s	VGA F(4,60)=30.39, p<.001*	Object Vision Phase: 266±17 ms
	Action Planning Phase: 587±50 mm/s		Action Planning Phase: 289±18 ms
	Movement Onset Phase: 579±51 mm/s		Movement Onset Phase: 332±17 ms
	Movement Execution Phase: 553±49 mm/s		Movement Execution Phase: 335±19 ms
	Max Grip Phase: 553±52 mm/s		Max Grip Phase: 330±31 ms
Unisensory tactile trials			
Peak		**Latency**	
MGA F(4,60)=6.72, p=<.001*	Object Vision Phase: 114±2 mm	MGA F(4,60)=9.84, p=<.001*	Object Vision Phase: 519±23 ms
	Action Planning Phase: 113±2 mm		Action Planning Phase: 521±23 ms
	Movement Onset Phase: 112±2 mm		Movement Onset Phase: 542±20 ms
	Movement Execution Phase: 110±2 mm		Movement Execution Phase: 568±20 ms
	Max Grip Phase: 113±2 mm		Max Grip Phase: 566±27 ms
VGA F(4,60)=2.74, p=.037*	Object Vision Phase: 555±48 mm/s	VGA F(4,60)=17.11, p<.001*	Object Vision: 287±23 ms
	Action Planning Phase: 563±53 mm/s		Action Planning Phase: 302±22 ms
	Movement Onset Phase: 555±50 mm/s		Movement Onset Phase: 341±26 ms
	Movement Execution Phase: 527±44 mm/s		Movement Execution Phase: 348±26 ms
	Max Grip Phase: 536±50 mm/s		Max Grip Phase: 336±25 ms

TABLE 1: Upper panel: main effect of object orientation on the transport component of grasping movements performed on multisensory VT and unisensory T trials. Lower panel: major effect of timing on the grip components of grasping movements performed on multisensory VT and unisensory T trials. Asterisks denote significant effects. MGA= maximum grip aperture, VGA= velocity of grip aperture.

Kinematic parameter	**Other significant main effects and interactions**	
	Multisensory visuo-tactile trials	
Acceleration latency	Timing F(4,60)=4.97, p=.002	
Velocity latency	Timing F(4,60)=9.53, p<.001	Timing * Stimulus F(4,60)=4.04, p=.006
Deceleration latency	Timing F(4,60)=5.07, p=.001	Timing * Stimulus F(4,60)=3.11, p=.022
MGA latency	Stimulus F(1,15)=7.06, p=.018	
VGA latency	Stimulus F(1,15)=8.33, p=.011	
	Unisensory tactile trials	
Velocity latency	Timing F(4,60)=8.41, p<.001	
Deceleration latency	Timing F(4,60)=3.28, p=.017	

TABLE 2: Other significant main effects and interactions observed for ANOVAs performed on kinematic parameters for multisensory VT and unisensory T trials. MGA= maximum grip aperture, VGA= velocity of grip aperture.

2.4 Discussion

The present study aimed to test whether PPS representation is remapped for action purposes even before overt movement, that is, while planning to execute voluntary grasping actions. We demonstrated that the brain updates the relationship between visual signals from the target object and tactile signals from the acting hand at earlier stages than previously known. Notably, this result indicates that PPS is modified by action planning and is thus temporally suited to ‘remapping’ the (distant) action target into the PPS representation. Such remapping may possibly incur the benefits of the distinctive multisensory processing known to occur within the PPS representation. We suggest that this multisensory-motor processing may contribute to guiding the hand towards a goal during voluntary movements. Contrary to threat-driven defensive actions, voluntary actions afford and actually require a planning step, during which the brain prepares the appropriate sequence of motor commands to achieve the desired goal (Castiello 2005; Culhman and Valyeram, 2006). Our results are in line with the guidance role proposed for the PPS during appetitive hand-object interactions.

We provided previous evidence in favour of the hypothesis that PPS supports the execution of appetitive actions (Brozzoli et al., 2009; 2010). Here, however, we overcame two major shortcomings. First, as mentioned in the introduction, previous work reported VTI increases only after initiation of the reach-to-grasp movement. These reports imply that the hand was physically close to the target object, albeit to a small extent. Therefore, an alternative interpretation is that the VTI increase documented at the action start was actually (at least partially) dependent upon the reduced distance between the hand and target object. Notably, in the current study we found that VTI increased when participants prepared the upcoming movement as compared to a similarly static but earlier phase, with the hand being at the same distance from the target object. This increase in VTI during the planning phase of an action provides the crucial but still missing evidence for functional role of PHS in motor control.

Second, the effect of action on PHS demonstrated in previous studies was compatible with an interaction between action and perception in terms of tactile suppression (Chapman et al., 1987; 1994; Voss et al., 2005). As our data demonstrate, multisensory changes were independent of variations in unisensory tactile perception. In particular, the pattern of VTI modulation reported here is not accounted for by any reduction in unisensory tactile perception, possibly due to concurrent action-dependent tactile suppression. On the contrary, we found that tactile discrimination improved (as evidenced by shorter RTs) during later stages of action execution compared to static phases. This finding aligns with the fact that tactile sensations are enhanced, decreased, or even remain unchanged during movement depending on perceptual task demands (Chapman et al., 1987; Post et al., 1994; Colino et al., 2014; Juaravle et al., 2017). Importantly, unisensory tactile performance during action planning and at action onset did not differ from the earliest stage of object vision, thus ruling out the possibility that either enhanced or decreased tactile performance explains the strengthening of multisensory interactions observed when preparing the action.

Remarkably, another interesting finding of the present study is that multisensory VT performance was characterised by both stronger interference and facilitation, selective for the action start compared to unisensory tactile performance. While most previous studies pointed to differences between VT-congruent and incongruent trials (see Spence et al., 2004a, 2004b), here we additionally examined multisensory VT performance with respect to unisensory T performance (see also Serino et al., 2015b; Shore et al., 2006; Noel et al., 2015). The observation that VTI was enhanced in terms of both facilitation and interference at the onset of grasping movements is in agreement with the hypothesis that visuo-tactile processes may contribute to successfully guiding the hand to its target.

In agreement with previous work, VTI was further enhanced when the hand started moving as well as during execution of the reaching phase (Brozzoli et al., 2009). By monitoring VTI at later action stages than have been investigated in previous works, the present study demonstrated that VTI modulation lasts at least until completion of the finger opening phase, when multisensory remapping appears to plateau (see Figure 2.2A). These results provide the first indication that multisensory PPS boundaries may reflect a continuous process that starts developing during action planning and evolves on-line during action execution to monitor and possibly adjust movements until their completion. From this perspective, we anticipate that VTI undergoes a decrease during later stages of action execution, despite the hand moving closer to the object from which visually interfering information originates.

Finally, hand motion tracking allowed us to further assess whether changes in VTI, and thus in PPS extent, were dependent upon changes in motor behaviour caused by the contingent sensory stimulation. In keeping with previous studies (Brozzoli et al., 2009, 2010), the kinematics of the transport component of the movement showed a consistent effect in terms of object orientation, whereby counter-clockwise orientation of the target object elicited kinematically more-demanding reaching movements than clockwise orientation. Analyses of the grip component of the movement additionally revealed that timing of sensory stimulation affected the aperture of the fingers. Crucially, whenever the perceptual task affected movement kinematic parameters, it did so in the same way in uni- and multisensory trials, thus showing that multi- and unisensory perception were assessed during the planning and execution of comparably demanding grasping movements. Overall, these findings point to a genuine modulation of multisensory interaction processes arising during the preparation of grasping actions.

When considering the possible neural underpinnings of multisensory PPS coding and its action-dependent changes, we note that there may be an intriguing overlap between the two processes. Recent neuroimaging results in humans have shown that a set of brain areas, including the anterior portion of the intraparietal sulcus (aIPS), premotor cortex, and putamen, contains neurons that are selective for the visual presence of an object in the space surrounding the hand (Makin et al., 2007; Brozzoli et al., 2011; 2012; 2013). This series of studies also demonstrated that visual selectivity for space near the hand is anchored to the hand such that when the hand moves in space between two locations, the near-hand selective response follows the hand (Brozzoli et al., 2012). Notably, such visual selectivity remains evident even when near and far locations are both within a reachable distance, indicating that PPS does not coincide with the portion of space that is reachable. This result suggests that human premotor-posterior parietal neuronal populations encode space near the hands in hand-centred coordinates, similarly to non-human primate parieto-frontal areas (Rizzolatti et al., 1997; Graziano and Cooke, 2006; Clery et al., 2015a). These findings, together with previous behavioural studies (Brozzoli et al., 2009; 2010), suggest that multisensory changes originating during action planning may be coded at the level of the PPS representation. Neuroimaging studies investigating brain areas involved in the execution of grasping and reaching movements also point to regions within the parietal and premotor cortices (Culhman and Valyear, 2006; Grol et al., 2007). For example, fMRI studies have demonstrated that action-dependent activity in similar parietal and premotor areas is modulated as a function of the type of action (grasping or reaching) or as a function of the degree of on-line control required by the action, even before overt execution of the movement (Culhman et al., 2003; Grol et al., 2007). Again, this set of results is compatible with neurophysiological research that identifies the neural circuits for grasping and reaching in the macaque brain as residing within a parieto-frontal network (Rizzolatti et al., 1988; Gardner et al., 2002; Fogassi and Luppino, 2005). Solid evidence supports the view that the cortical visuomotor grasping circuit, comprising the IPS, ventral premotor (PMv) and primary motor cortex (M1), allows for transformation of an object's physical properties into a suitable motor command for grasping (Murata et al., 1997; Castiello 2005). Several TMS studies converge in supporting the causal role of aIPS in motor planning. For instance, Davare and colleagues showed that usual muscle-specific PMv-M1 interactions that appeared during grasp planning were significantly reduced following aIPS interference (Davare et al., 2009, 2010; see also Verhagen and colleagues 2012 for a TMS study assessing the causal role of aIPS during planning). Collectively, the literature from human and non-human primates indicates neural and functional similarities. We therefore suggest that modulation of multisensory perception occurring in the planning phase of a grasping action may arise from activity within the premotor-parietal network involved in the multisensory hand-centred representation of PPS. Our findings also point to an interesting prediction: visuo-tactile neurons involved in this representation may not only update their visual receptive field location as a function of the hand position in space but also anticipate the upcoming hand position just before the movement starts. Such remapping mechanisms have been described for visual receptive fields before upcoming saccadic movements (Duhamel et al., 1992). While further studies in human and non-human primates are needed to identify the physiological mechanisms underlying such a behavioural ‘remapping’ of PPS, the current study provides the first evidence that multisensory interactions are dynamically enhanced both before and during action execution. Early multisensory-motor processes that temporally precede and subsequently accompany overt motor execution are ideally suited to planning and guiding our actions.

Chapter III The space between the body: Interpersonal space

"Yes, people do come across the street to say hi, but as they approach and get near, my perception of space begins to dissolve, and a new interest takes over that is primarily emotional, and with it comes a desire to touch, which may be a human interest, but not the interest of my work"

Diego Giacometti

3.1 The social space

The idea that there is a somehow special zone surrounding the body has its roots in animal studies, particularly in the work of ethologists and zoologists from the 20th century. Although the terminology used varies substantially among ethology, zoology, social psychology, and sociology literature, in this context I will refer to "interpersonal space", the space in which distance has a particular meaning in terms of the kind of interaction allowed, as an umbrella term to cover this wide range of concepts used to describe the social and interaction distances between individuals (or animals).

When the interpersonal space (IPS) concept was developed in the 1950s, there was very little published research on distances among humans. The most relevant experimental studies had been done by ethologists using animal species under the rubric of individual distance (Hediger, 1950). Most animals in the wild maintained defined distances from conspecifics, and these distances were influenced by the animal's age, size, sex, and other factors. Particularly relevant were the pioneering theories of the Swiss biologist Heini Hediger, the director of the Zurich zoo, whose work had come directly out of his efforts to improve zoo environments. Based on investigations and observations of animal territorial behaviours, Hediger (1955) noted that animals display different behaviours depending on the proximity of other animals. For instance, when a potential predator is close to the animal entering a critical distance, known as its flight distance, the animal flees or withdraws. Even when the other animal belongs to the same species, there is a distance that, if crossed, the proximity of conspecifics becomes no longer tolerable, what Hediger called the personal distance.

Hence Hediger (1955) proposed an ethological model of space perception that largely influenced literature of human interpersonal space. The author successively divided the animal spacing into inter-species and intra-species distances. For the inter-species distances, Hediger (1955) suggested three different circular categories of space: the attack distance, the critical distance, and the flight distance. For illustrative purposes, let's considerer the example of the dynamic distances between a first animal (*A*) and a second invading animal from another species (*B*). The attack distance is the closest distance for territorial behaviours. If the attack distance boundary of *A* is crossed, such animal will attack the intruding animal *B*. The critical distance is located right between the attack distance and the flight distance. When the intruding *B* animal from another species enters this space, *A* will simply heads towards the intruder to either engage a fight or force it to take flight. Last, the flight distance corresponds to the minimum distance *A* keeps from *B*. In case of an intrusion of its flight space, A will take flight. The bigger an animal is, the further its flight distance will extend, and vice versa. For the intra-species distances, Hediger defined two distinct spaces: the personal distance and the social distance. In order to be able to differentiate areas, the author based this segmentation of space on observations of non-contact species' behaviour. Indeed, some species seek constant physical contact, which complicates the space division, while others do not need to constantly huddle. The personal distance is the minimum distance animals from the same species keep between each other. This distance depends on the social hierarchy: the more dominant an animal is, the further its personal distance will extend. If another animal from the same species enters a first animal's personal space, they will become aggressive. The social distance is, instead, the maximum distance animals from the same species keep between each other. If an animal draws away from the members of its species beyond this distance, it will experience anxiousness of being separated from the group. Hediger believed this separation to be mostly psychological since the visual or hearing contact may still be maintained. This distance depends on the species, the context, and the animal's age (Hediger, 1955).

Subsequent studies expanded this view. Uexkull (1957), for instance, made the famous analogy of individuals surrounded by soap bubble worlds. However, ethology at the time included many descriptive studies where terminology was not used precisely. The concept of a (inter-) personal distance overlapped with several existing concepts and some that came afterward, including the following terms (Sommer 2002):

- *Individual distance*: the amount of space between organisms and their conspecifics.

- *Proxemics*: term introduced by Hall (1963, 1966) for the study of spatial relationships (see below).
- *Distancing*: the act to put physical distance between self and others in order to gain privacy
- *Defensible space*: introduced by Newman (1972) to describe the ways in which well-marked territories and good surveillance can increase the safety of residential housing.
- *Body buffer zone*: term introduced by Horowitz, Duff, and Stratton (1964) with a meaning very similar to that of IPS.

The study of IPS began on this atheoretical basis and continued this way for many years. Thus, some scholar responded to the absence of a satisfactory theory by importing explanatory concepts from social psychology, based either on considerations of protection or communication. Horowitz, Duff, and Stratton (1964) and Dosey and Meisels (1969) depicted the body buffer zone protecting individuals from threat. Altman (1975) described IPS as a boundary regulation mechanism intended to achieve desired levels of privacy. In a similar vein, Aiello (1987) proposed a comfort model based on the (affiliative-conflict) equilibrium model (Argyle and Dean, 1965) in which a person seeks an optimal level of closeness with others. If this equilibrium is disturbed by people coming too close or staying too far away, compensatory behaviors will be used, such as decreased or increased eye contact. Hayduk (1994) explained the results of stop-distance spatial invasions as a dynamic readjustment of the participants. Evans and Howard (1973) suggested that a more thorough understanding of IPS could be achieved by viewing it in functional terms: IPS allows human beings to operate at acceptable stress levels and aids in the control of intraspecies aggression. By maintaining a minimum distance from their fellows, humans are exhibiting adaptive, stress-reducing behavior and this has selective advantages in the evolutionary process.

However, the most prominent and influential model in this field became Hall’s model of proxemics. He noted that the use of social space by both animals and humans is reciprocal with social interaction and can be mapped empirically through measures of proximity. For example, he observed that at 28 inches (approx. 70 cm) separation between self and other participants reported feeling a little uncomfortable; at 20 inches (approx. 50 cm) they felt moderately uncomfortable and at 12 inches (approx. 30 cm) very uncomfortable (Hall, 1966). Basing on these considerations, Hall (1966) introduced the concept of proxemics, the study of IPS, which describes the influence of social interactions on space perception. In his model inspired by Hediger’s (1955), Hall (1966) suggested a division of the interindividual space into four egocentric and circular spaces, each one referring to a certain type of social relationship: the intimate distance, the personal distance, the social distance, and the public distance (see Figure 3.1). Each of these spaces is subdivided into a close and a far phase:

1) The *intimate distance* extends from an individual’s body to approximately 40 cm. The intimate distance is restricted to partners or very close relations; all senses are involved but vision is limited. Since physical contact is inevitable, strangers are not allowed is this portion of space, except for public necessity. The intimate distance close phase extends from an individual’s body to approximately 15 cm. This space is reserved for sexual intercourses, fight, or comfort and communication is predominantly non-verbal. The intimate distance far phase extends from 15 cm to approximately 40 cm and communication predominantly goes through whispers or a very low voice volume.
2) The *personal distance* extends from 45 cm to approximately 125 cm. This space is restricted to close relations. One can see, touch and hear but not smell the other person; physical contacts are no more inevitable but can still occur. Communication in this space predominantly goes through an average voice volume, even if whispers are still audible. The personal distance close phase extends from 45 cm to approximately 75 cm. Instead, the personal distance far phase extends from 75 cm to the point two people can barely touch each other (approximately 120-125 cm).
3) The *social distance* extends from 120 cm to approximately 360 cm. The social distance is opened for acquaintances. People cannot touch each other anymore and an average voice volume is necessary to communicate. Eye gaze, a loud voice and body movements are often present, but an elevation of voice volume in this space may be perceived as an intrusion into the personal space. The social distance close phase extends from 120 cm to approximately 210 cm. This area implies a social interaction since people can hardly ignore each other at such distance. The social distance far phase extends from 210 cm to approximately 360 cm. Social interactions are often more formal in this area (e.g., professional interactions). Moreover, social interactions are not implied at such distance and not talking to each other is not sensed as rude.
4) The *public distance* extends from 360 cm to a distance where communication is no more possible. The individual is not necessarily concerned anymore by an event or situation that occurs in this space. Communication in the public distance space predominantly goes through a higher voice volume. The public distance close phase extends from 360 cm to approximately 750 cm. At this distance formal interactions, such a lecture, are implied; the facial expressions of the lecturer are often more difficult to see, the voice is louder and there are more body movements. The public distance far phase extends from 750 cm to a distance where communication is no more possible unless gestures are intensified in order to convey a message.

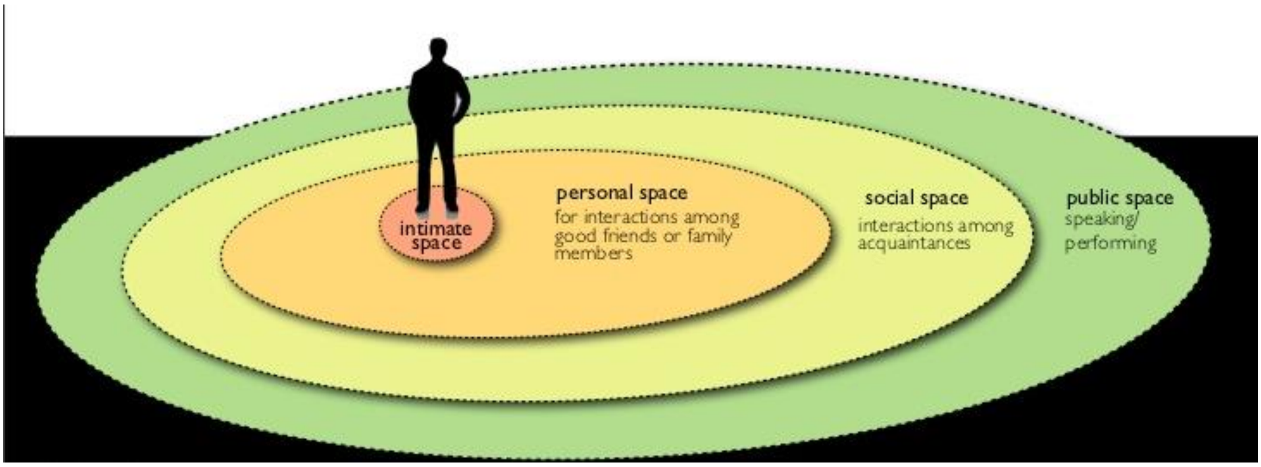


Figure 3.1 schematic view of proxemics according Hall (1966). An intimate zone (or space) is reserved for close friends, lovers, children and close family members. Personal space used for conversations with friends, to chat with associates, and in group discussions. Social space is reserved for strangers, newly formed groups, and new acquaintances. Public space is used for speeches, lectures, and theater; essentially, public distance is that range reserved for larger audiences.

To note, the author advised himself that, even if this space segmentation can be applied to every human being, the given distances were collected from a particular sample (i.e. middle-class Americans) and cannot be applied to each population. Indeed, an individual’s interpersonal space perception depends on his culture, on his personality, and on the context since “[…] each one of us has a number of learned situational personalities. The simplest form of the situational personalities is associated with [different] responses to intimate, personal, social, and public transactions” (Hall, 1966, p.115). It also worth underling here what some scholars seem to neglect: Hall’s theory is a taxonomy which maps interpersonal distances to human social relationships, therefore, it does not aim at analyzing the cognitive structure of the space(s). Likewise, Hall's work remained ambiguous concerning the relative contributions of basic biological factors in defining proxemic distances (Griffin 1991) and later investigations have largely ignored the issue.

Proxemics theory has generated an impressive amount of research and a substantial portion of this literature has investigated the factors that modulate the proxemic “bubbles” surrounding our bodies. Since Hediger and Hall’s work, numerous studies, too many to describe them all in terms of subject population, techniques, and results, explored determinants of interpersonal distance (for extensive reviews see Sommer, 2002; Aiello, 1987; Bechtel, 1997; Burgon 1978; Sundstrom and Altman 1976 ; Hall, 1966;). Here I will report only a non-exhaustive selected list of those findings which seem best substantiated within this copious body of research (Sommer, 2002): attractiveness, friendship, cooperation, similarity, stigma, threat, anxiety, insult, inappropriate staring, family cohesion, age, approach side (side<front in terms of preferred distance and long rear distance particularly marked in studies with violent offenders, see Adams 1997, Bell et al., 1988; Tedesco

and Fromme, 1974; Tesch et al., 1973; Conigliaro et al., 1989; Albas and Albas, 1989; O'Neal et al., 1980; Skorjanc, 1991; Tobiasen and Allen, 1983; DeCarlo et al., 1981; Sigelman and Adams, 1990; Wormith, 1984).

In addition, cultural factors (e.g. people from contact vs. noncontact cultures, Aiello, 1987), environmental variables (e.g. room density, size and shape, location in the room, ceiling height, lightning, indoors vs. outdoors, see Cochran et al., 1984; Evans et al., 1996; Adams and Zuckerman, 1991; Cochran and Urbanczyk, 1982) as well as personality variables (e.g. being aggressive, tolerance of ambiguity, self-acceptance, Pederson 1973) seem to play an important role in shaping IPS. Yet, apart from cultural and situational differences there is evidence for individual trait-like IPS preferences, namely preferences remain more or less stable through life (Patterson, 1995; Andersen and Sull, 1985). These preferences have been related to social attachment styles (Bar-Haim et al., 2002; Kaitz et al., 2004), early child abuse (Vranic, 2003), post-traumatic stress disorder (Bogović et al., 2014), autistic spectrum disorder (Gessaroli et al., 2013; Candini et al., 2017), schizophrenia and depression (Angermeyer, et al., 2004).

Remarkably, all these results stem from the use of different techniques to measure IPS, in part paralleling the different operational definitions employed. Borrowing the methodology and approach from ethology, *field studies* have been carried out in natural settings, whereby the anonymous participants are unaware their behavior was being recorded. Mostly, these investigations were the results of unobtrusive observation or staged invasions in natural settings. More interestingly, in *simulation studies* the participants are aware that they are being observed or tested, although the particular variables of interest, such as space usage, may not be specified. The studies of spatial preference testing how people place themselves under various laboratory conditions (e.g. high vs. low anxiety or cooperative vs. competitive situations) fall into this category. Two ecological paradigms are massively used in this research. In the first, the **Stop distance paradigm**, a confederate approaches the subject who tells the other person to stop when the confederate comes uncomfortably close. In a similar test, the **Approach distance** subjects are asked to move toward another person (showing for instance a specific emotional expression such as happiness or fear), and to stop at a comfortable interaction distance. Finally, in Figure placement tests respondents place surrogate human figure (e.g. silhouettes, photographs, or mannequin) in any social arrangements following the instructions of the task at the hand (figure 3.2, Sommer 2002, Sommer and Iachini 2017).

Figure 3.2 Figure placement tasks. The participant places (or marks the location of) manikins, dolls, or other human surrogates in various social arrangements at various favorite distances. From Sommer and Iachini, 2017.

3.2 Interpersonal space 2.0: a neuroscientific approach

Since late 2000's, thanks to contributions of cognitive neuroscience, the concept of IPS was revived. Within a recent surge of studies examining the neural correlates of social aspects of human behaviour, a new line of research aimed at investigating the neural and physiological mechanisms underlying social space regulation. Yet, it is worth to acknowledge that physiological recording studies had been already conducted, reporting how the subject's eye blink rate, heart rate, electrodermal activity or other physiological measures could vary as a function of interpersonal distance (Omori and Miyata, 1998; Aiello et al., 1977; McBride et al., 1965). Indeed, there is evidence of significant change in autonomic nervous system activity occurring in response to intrusions of IPS. Specifically, women approached by a male stranger have demonstrated significant changes in heart rate (Sawada, 2003), while individuals approached by an android robot have demonstrated significant increases in skin conductance responses (Tanaka et al., 2013). Collectedly, the findings from the physiological correlates of interpersonal distance are consistent with the idea of IPS as a protective safety zone around the body. More recently, the mechanisms underlying the link between affective processes and a defensive safety zone 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. Their result confirmed that proximal social stimuli (i.e. avatars) facilitate defensive responses, as indexed by fear-potentiated startle, relative to distal stimuli. Also, they revealed that interpersonal defensive boundaries increase with aversive learning, as IPS is increased for social stimuli that have become associated with negative consequences.

When considering the neural underpinnings of IPS, the first study that investigated its neural substrates was conducted by Kennedy and collogues (2009). In particular, they identified a candidate brain region crucial in social space regulation: the amygdala. There was already evidence that in nonhuman primates this structure is involved in social approach and avoidance (Emery et al., 2001; Mason et al., 2006), but no investigation on humans had pointed at its involvement in IPS before Kennedy and others' pioneering work (2009). In particular, the authors studied a patient with complete bilateral amygdala damage. In a classic Stop distance paradigm, the patient's preferred distance (around 34 cm from the experimenter) was smaller than that of the comparison group (see Figure 3.3). This highly abnormal pattern was found reliably across a number of additional variables (direct/averted gaze; starting close or far, as well as in the approach distance). Throughout the experiment, the patient demonstrated a striking lack of discomfort at close distances. For example, on one trial she walked all the way toward the experimenter to the point of touching, while remarking she felt comfortable at that distance. When the authors quantified this by asking her to rate her level of discomfort while one of the experimenter stood facing her at various distances, the patient rated the experience as perfectly comfortable, even when nose-to-nose with direct eye contact. Nonetheless, at a cognitive level, the patient completely understood the concept of IPS: she spontaneously stated that she did not want to make the experimenter uncomfortable by standing too close, and she also believed her personal space was smaller than most. Based on these observations, the authors conducted a fMRI study in eight healthy participants to obtain corroborating evidence regarding the involvement of the amygdala in IPS. They accordingly found that the amygdala responded to a greater degree when the participants knew an experimenter was maintaining a close distance to them (standing immediately next to the scanner) compared to when they knew an experimenter was maintaining a far distance. These findings thus showed that the amygdala is differentially activated by proximity to another person, and that complete bilateral damage to this structure results in an abnormally small interpersonal distance preference. From a more theoretical point of view, this intriguing work suggests that the amygdala may help to maintain a minimum distance between people.

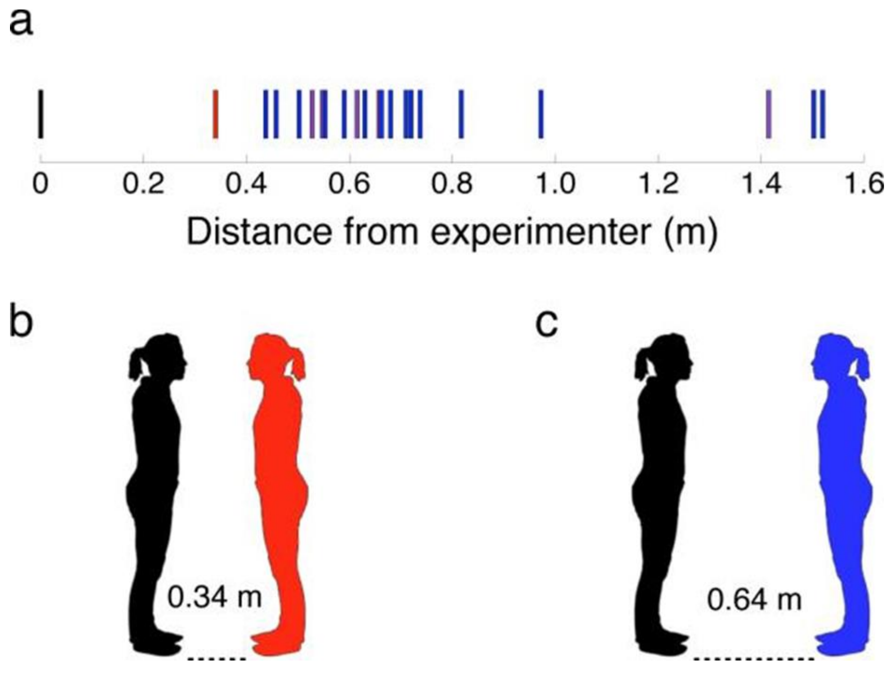


Figure 3.3 IPS in a patient with bilateral amygdala lesion (A) Patient's (red) IPS was the closest distance to the experimenter (black),compared to age-, gender-, race-, and education-matched controls (purple, n = 5), as well as general comparison subjects (blue, n=15). (B) Patient's mean preferred distance away from the experimenter. C) Control participants' mean preferred distance away from the experimenter, excluding the 3 largest outliers. From Kennedy et al., 2009

Relatedly, it is worth mentioning two interesting studies assessing the effect of oxytocin on IPS (Preckel et al., 2012, 2014). Increasing evidence suggests that oxytocin serves as a social hormone in humans and that one of its role may be to alter the perceptual salience of social cues. The prosocial action of this neuropeptide often involves facilitation of approach behaviors (Hurlemann et al., 2010; Striepens et al., 2011) and is known to increase gaze directed at the eyes of others (Guastella et al., 2008). Relevant here, the activity of amygdala is modulated by oxytocin (Gamer et al., 2010, Hurlemann et al., 2010), indicating that this neuropeptide may be a candidate hormone for modulating interpersonal distance. Given this empirical background, in a randomized placebo-controlled trial, Preckel and colleagues (2014) tested how oxytocin influenced the social distance subjects maintained between themselves and either a female or male experimenter. By using an approach-stop distance mixed paradigm, they found that oxytocin decreased the social distance that female participants kept between themselves and an unfamiliar attractive and friendly male experimenter (see also Scheele et al., 2012 for an interaction between oxytocin and relationship status in IPS regulation). Critically, oxytocin did not influence the size of PPS, suggesting that it does not alter perception of space around the body *per se,* but rather that a social element is necessary for oxytocin's effects to become evident. However, it is to note that, as an index of PPS, they used a line bisection task performed at three different distances. All participants, in the control as well as in the experimental oxytocin group, displayed pseudo-neglect (e.i., a leftward bias) in near space and increasing rightward bias in far space (Patané et al., 2016a), revealing therefore no modulatory effect of oxytocin on this task (Preckel et al., 2014).

Amygdala and oxytocin do not seem to be the only biological markers of IPS. A fronto-parietal network appears to be involved in interpersonal interactions and maintenance of a particular “comfort zone” or distance from other people. This finding comes from a recent series of fMRI investigations testing the recruitment of such a fronto-parietal network in healthy and clinical settings. In a first study, Holt and colleagues (2014) measured the neural responses to moving objects (faces, cars, simple spheres) and the functional connectivity of two regions in this network, namely the dorsal intraparietal sulcus (dIPS) and the ventral premotor cortex (PMv). They found that both areas responded more strongly to faces that were moving toward (vs. away from) subjects, but did not show this bias in response to comparable motion in control stimuli, such as cars or spheres (see Figure 3.4). Moreover, these two cortical regions were functionally interconnected. In addition, the magnitude of dIPS and PMv responses was correlated with the preferred level of social activity. More interestingly, the strength of dIPS-PMv connectivity was correlated with the interpersonal distance that subjects chose to stand from an unfamiliar person. Indeed, the authors used both an out-of-scanner behavioral task (i.e., Stop distance paradigm), measuring individual differences in IPS involving actual intrusion by a conspecific, and a within-scanner virtual task, designed to stimulate IPS intrusion through the apparent approach or withdrawal of a conspecific's face or inanimate objects. The adopted version of Stop distance paradigm involved in study provides measures of IPS size, which refers to the moment the subject expresses that he/she feels “slightly uncomfortable,” and IPS permeability, which refers to the subject's ability to tolerate personal space intrusion, measured as the ratio of when the subject says he/she feels “slightly uncomfortable” and to when he/she feels “very uncomfortable”. Holt et al. (2014) compared thus the behavioral data from the Stop distance paradigm with the neural data during the virtual approach withdrawal task, finding a positive correlation between IPS size and connectivity between the dorsal intraparietal sulcus and ventral premotor cortex activity during virtual approach and a negative correlation between IPS permeability and connectivity. However, while the Stop distance paradigm involves active indication by the participant of when they feel uncomfortable with intrusions into their space, the virtual paradigm is a passive task where participants view approaching and withdrawing faces or objects. This makes it difficult to relate the data from the virtual task to the behavioral paradigm to determine whether the virtual task is indeed acting as a personal space intrusion rather than just approach or withdrawal (Smith and Faig, 2014). Despite these limitations, the task designed by Holt and colleagues was largely used in following research. For instance, gender differences (approaching men vs. women) were tested directly in two fMRI studies by Schienle and colleagues (2016, Wabnegger et al., 2016). A first fMRI investigation with exclusively male participants replicated previous finding by showing that approaching faces generally provoked activation of a fronto-parietal network, as well as the insula. More interestingly, amygdala recruitment was only seen when the approaching person was male (Schienle et al, 2016). In a subsequent study by the same group, investigating the hemodynamic responses of 30 women, reported similar results. Approaching faces generally provoked activation of a parietal network (e.g., intraparietal sulcus, superior/inferior parietal cortex). When the approaching person was male additional amygdala activation was detected. Because the amygdala is a central structure for the initiation of defense responses, the heightened activation might reflect that male intrusion was decoded as potential threat (Wabnegger et al, 2016).

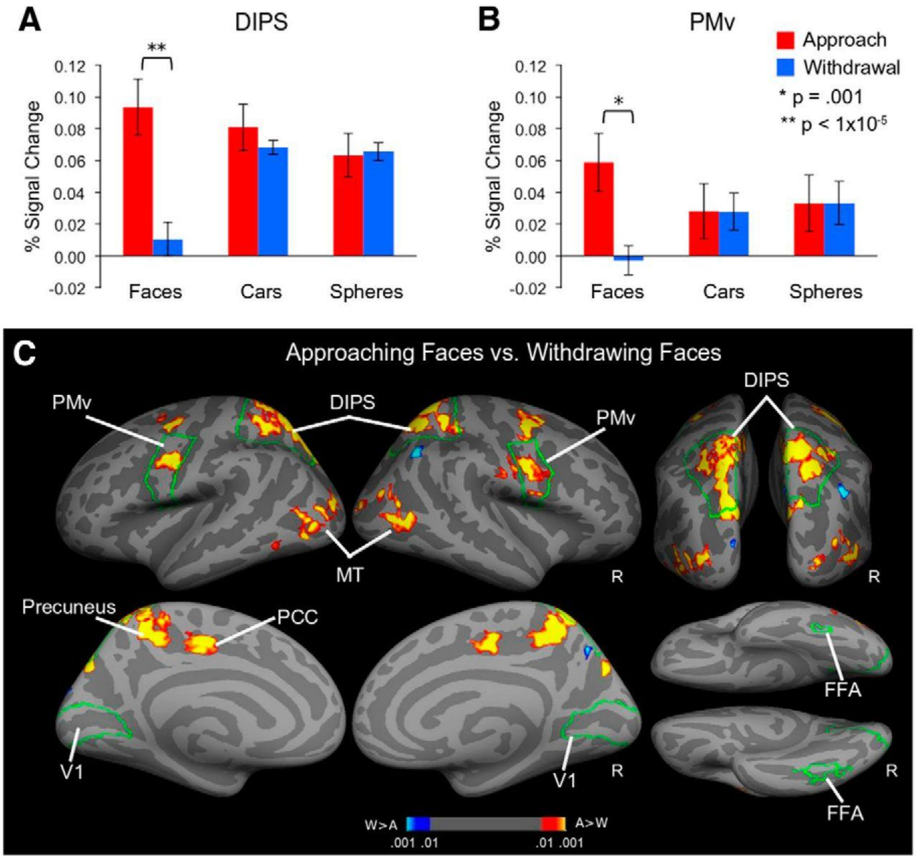


Figure 3.4 Functional MRI responses to approaching and withdrawing faces, cars, and spheres. The results of the analysis conducted using the dIPS (***A***) and PMv (***B***) anatomical ROIs are shown. DIPS and PMv show a significant approach bias to faces, but not to cars or simple spheres. ***C***, Lateral, medial, superior, and inferior views of cortical surface maps of activation to Approaching versus Withdrawing faces are shown. The outlines of the anatomically defined DIPS and PMv ROIs are shown in green, as well as the outlines of primary visual cortex (V1) and the face fusiform area (FFA). These maps reveal that although dIPS and PMv show approached-biased responses, as well as a number of other regions, such as the PCC, precuneus, dorsal premotor cortex, and MT, lower-level visual areas, such as V1 and FFA, do not show this bias. W, Withdrawal; A, Approach; R, right. From Holt et al., 2014.

The same approach was used to explore the neural basis of IPS abnormalities in clinical population. Findings of enlarged or inflexible personal space have been consistently reported in schizophrenia (Duke and Mullens, 1973; Deus and Jokic-Begic, 2006; Nechamkin et al., 2003; Park et al., 2009; Srivastava and Mandal, 1990). Using fMRI, Holt's group found that the dorsal intraparietal sulcus was hyper-responsive in schizophrenic patients to face stimuli appearing to move towards the subjects, intruding into IPS. This hyper-responsivity was predicted by the severity of negative symptoms (Holt et al., 2015). In another fMRI study, neural activity of high-risk violent offenders was assessed with a similar task. Offenders responded with greater insula activation to approaching faces, especially when the person was a male. Such an increased activity of violent offenders was interpreted as a result of their hostile attribution bias (Schienle et al, 2017). Finally, another region associated with complex social behaviors and tightly connected with the amygdala, that is the orbitofrontal cortex (OFC), is accordingly critical for maintaining appropriate interpersonal distance. Indeed, patients with OFC damage show abnormal interpersonal distance preferences, significantly different from both healthy and patients controls with dorsolateral prefrontal damage (Perry et al, 2016).

Overall, these findings suggest that within a large (and maybe non-specific) fronto-parietal network proposed to be involved in IPS representation, insular and amygdala activation have been recognized as neuronal correlates of potential threat and harm detection in IPS. In fact, although informative, these studies don’t reveal the mechanism underling IPS regulation. Only a recent contribution has tried to provide a unitary “biological” account of IPS. Perry and others (2015) suggested that, though there are multiple factors contributing to IPS variance among both healthy and clinical samples, an important factor that may contribute to this variance is one’s level of sensory sensitivity, i.e. how sensitive one is to nearby visual stimulation, noise, touch or smell (Dunn, 2001). The idea behind this hypothesis is the following: if one is more sensitive, for example, to touch or smell, s/he would prefer further distances from others, to avoid being over stimulated and uncomfortable. Given this rationale, the study sought to characterize IPS preferences in terms of their hormonal, behavioral and electrophysiological basis, specifically in relation to levels of sensory sensitivity. Salivary cortisol was measured as an indication of baseline stress in general and social stress in particular. Indeed, cortisol levels have been shown to be affected by physical proximity. For example, commuters on public transport showed elevated self-report stress levels and increased salivary cortisol when sitting in close proximity to other commuters (Evans and Wener, 2007). Hence, Perry and colleagues (2015) measured salivary cortisol levels before and after the Stop distance paradigm. Following the Stop distance task, the same participants participated in an EEG study, in which IPS was assessed using a modified computerized version of the Stop distance paradigm (Duke and Nowicki, 1972; Duke and Kiebach, 1974). In the computerized task the authors employed, participants were instructed to imagine themselves in the center of a room visualized on a computer screen with a virtual friend or stranger approaching them. Results showed that levels of sensory sensitivity, as measured the Sensory Profile questionnaires (Dunn, 2001, Brown et al., 2001), predicted IPS preferences. Note that levels of baseline cortisol behaved as moderators of IPS, interacting with sensory sensitivity levels such that the higher one’s initial cortisol level, the less effect sensory sensitivity has on IPS. Such an interaction highlights the importance of both trait (sensory sensitivity) and state (hormonal levels, stress) conditions on social behavior. The importance of sensory sensitivity levels in IPS was further supported by neural differences in alpha between high and low sensory sensitivity groups performing the modified IPS task. Electrophysiological evidence revealed that individuals with higher sensory sensitivity show more alpha suppression suppression (which is related to sensory, mostly visual attention, Klimesch, 1999) for approaching stimuli. These results also relate to previous findings linking IPS with attention and with the N1 event related potential (ERP) component (Perry et al., 2013). Notably, the N1 has been shown to correlate with alpha suppression (Ergenoglu et al., 2004; Sauseng et al., 2005) and it is thought to be the result of phase synchronization between alpha and other frequencies (Gruber et al., 2005). To conclude, these findings have important implications for social cognition, stressing how ‘low level’ physiological mechanisms, such as sensory sensitivity, affect ‘high level’ social decisions such as where one feels comfortable when talking to another.

3.3 In a nutshell

To sum up, despite different theoretical underpinnings, techniques for its measurement, research findings, the term IPS describes the socially and emotionally tinged zone around the body that people feel is “their space” (Sommer, 1959). The boundaries of such a space are not fixed but vary according to internal states, culture, and context. Since the introduction, IPS has become a common term in the social psychology literature, and a chapter heading in environmental psychology and communications textbooks. Nevertheless, after four decades of considerable research with no signs of disappearing, the topic lost its popularity, maybe because of the lack of a unitary theory attempting to explain why people maintain distance from others (or why people seek privacy, comfort, reduced arousal, or equilibrium to cite several of the social-psychological theories). Yet, the advent of cognitive neuroscience in social science gave a fresh boost to research in the field of interpersonal spacing. This recent flourishing research has identified insular and amygdala structures as two areas critically involved in IPS, within a large neural circuit encompassing frontal and parietal regions (Kennedy et al, 2009; Holt et al, 2014; Schienle et al, 2016). Related to the activity of these areas, oxytocin and cortisol levels have been found to exhibit a modulatory effect on space regulation. As a further demonstration of the inherently social and emotional nature of IPS, a recent lesion study revealed that orbitofrontal cortex, but not dorsolateral prefrontal cortex, is associated with impaired interpersonal distances (Perry et al, 2016).

3.4 How many spaces around the body?

The use of space by both animals and humans is inherent in social interactions, which have been most effectively mapped through observing the behaviour of the individual and through measuring proximity and factors that mediate its use. In the social psychology literature, the space around the body has been defined as the ‘area individuals maintain around themselves into which others cannot intrude without arousing discomfort or even withdrawal’ (Hayduk, 1983; Sommer, 1969). Once intruded the person may experience a perception of threat of psychological or biological integrity (Horowitz et al., 1964), which clearly emphasises the important influence that emotional and motivational factors can have on the use of space between people. At this point, this claim should sound familiar. In fact, the idea of *body buffer zone* and the proposed link between surrounding space and defence of the body come from IPS literature, but it has been recycled in the neurocognitive field as one of the functions assigned to PPS.

Graziano and Cooke were perhaps the first who formalized this hypothesis: “One possibility is that this nearby attentional space is related to the protective personal space described by Hall and others and the defensive flight zone described by Hediger. […] Neurons in cortical areas VIP and PZ are multimodal, responding to tactile, visual, and sometimes auditory stimuli […]. The receptive fields are usually though not always confined to the space near the body. These receptive fields are like bubbles of space anchored to the body surface. […] We speculate that these body-centred receptive fields in VIP and PZ could also form the neural basis for the psychological phenomenon of personal space and the ethological phenomenon of a flight zone” (Graziano and Cooke, 2006, pp.848-9).

Successively, Lloyd (2009) extended this view and claimed that the mechanisms and principles underlying the individual representation of the space surrounding the human body also mediate the space between interacting human partners. The purpose of her review was to bring together evidence from the disparate fields of cognitive neuroscience and neuropsychological studies of PPS, which typically focus on the behavioural and neural factors underlying the spatial coding of a single individual (or single body parts), with more ecologically valid studies of interpersonal behaviour. Aware of the two isolated fields of neurocognitive study of PPS and research on IPS behaviour, through a phenomenological approach Lloyd proposed a framework that aimed at investigating and interpreting the "neural mechanisms of ’social space’" (p. 298).

Hence, scholars from cognitive neuroscience and social psychology have looked with ever-growing interest at the possibility that IPS may emerge from lower level sensorimotor processing of PPS. Both representations, indeed, emphasize the importance of the body and are thought to serve a protective function in response to possible threats approaching the body. Crucially, both are highly flexible and their plasticity depends on the dynamic relationship one is stabling with the surroundings: PPS is modulated to adapt to the constantly changing action requirements of our environment, while IPS is adjusted to maintain a comfortable distance from other individuals. Last, as previously reviewed, social interactions as well as other social and affective cues can also modulate the boundary of PPS (and, by definition, the boundary of IPS).

In this regard, Iachini and Coello (2015) stated that "social interactions require accurate control of interpersonal distances, and this would suggest that the encoding of peripersonal space is crucial, not only for the regulation of interactions with objects, but also for our social life" (p.208). They offered the thesis that the two spaces share a common motor nature and pushed forward their speculations by going as far as to state that "From a theoretical perspective, […] the motor nature of space perception plays a crucial role in complex social processing, as peripersonal space encoding represents a key element in the regulation of distances in social interaction situations." (Quesque et al., 2017, p.11), defining such motor nature as a "common underlying causal factor" (Quesque et al., 2017, p.2). In a more attenuated and testable form of such hypothesis, one might propose that the two representations are, at least, similarly sensitive to social aspects. In support of this, in a series of experiments the authors jointly assessed PPS and IPS in a virtual environment to investigate whether the two representations refer to a similar or different physical distance. To this aim, Iachini and Coello's group compared PPS and IPS by means of two standard paradigms: reachability and comfort distance judgments. In the first case, participants had to evaluate if visual stimuli presented at various distances from the body were reachable or not; in the second case, participants had to stop the visual stimuli at the point where they felt still comfortable with the other's proximity (a combined version of the Stop distance and Approach distance paradigms). More interestingly, in first study participants, immersed in a virtual scenario, had to provide reachability distance and comfort distance judgments towards human (male and female avatars) and nonhuman (cylinder and robot) virtual stimuli while standing still or walking towards stimuli (Iachini et al., 2014). Results showed that comfort distance was larger than reachability distance when participants were passive, being approached by the virtual stimuli. Nevertheless, reachability and comfort distances did not differ when participants could actively move towards the stimuli. This finding was interpreted as evidence that the same motor processes subtending reachability judgments and the encoding of PPS also contribute to specify comfortable social distances. The other finding that should suggest communality between the two spaces is that both distances are modulated by human versus nonhuman stimuli. Somehow in line with previous data (Teneggi et al., 2013), distances were expanded with virtual objects and reduced with virtual humans. In addition, there was a contraction of distance with virtual females as compared to males and an expansion with cylinder as compared to robot. In a subsequent examination, the same group replicated these patterns of results showing how distances are affected by the gender of the confederates: distance was smaller for female than male confederates. This effect was actually evident for comfort distance and as long as participants had to remain passive. In the latter case, i.e., when participants were passive and approached, both reachability and comfort distances were larger for the male than the female confederate. On the other hand, when participants could actively approach the confederates, they chose similar reachability distance for both female and male confederates. By examining age effects, it was also demonstrated that the comfort distance was larger when facing a virtual old adult than a young adult or child, in line with previous findings in social psychology (Iachini et al., 2016).

Not only “demographical” variables, but also contingency factors such as moral evaluation and facial expressions have been tested to explore the relationship between PPS and IPS. It was observed an increase of distance when seeing angry rather than happy virtual human, regardless of who was moving (i.e., whether the participant was approaching the virtual human or vice versa). The effect also appeared in reachability distance, but only if participants were passive and approached by the virtual human (Ruggiero et al., 2016). In the case of the manipulation of perceived morality, comfort distance was modulated according the negative (immoral), positive (moral), and neutral description of the virtual human facing participants, with largest comfort distance found in the negative and the smallest comfort distance in the positive condition. In contrast, in reachability only the moral – immoral comparison was significant (Iachini et al., 2015).

Highlighting the similar rather the different modulations, these findings were interpreted as providing support to the view that peripersonal and interpersonal spaces share a common motor nature and are endowed with finely tuned mechanisms for processing social information (Coello and Iachini 2016). Despite the fact that the analogy between such different construals developed within such separate domains is a very interesting approach, I would like to stress here that the lack of difference neither indicates the two construals are actually the same one nor implies they underlie a common psychological entity. Before concluding I wish also highlighting that, although it is an important issue that is currently the object of a very lively debate, it would be premature to draw any conclusions on the outcomes of these first studies. Keeping this in mind, one of the aims of this dissertation is thoroughly testing the possible relationships between PPS and IPS.

3.5 IPS=PPS?

The material summarized above indicates that during the past decades, cognitive neuroscience and social psychology have been independently generating remarkably similar results regarding the representational domain of space perception. In particular, these two fields have been converging on the view that there is an intimate relationship between action, social interaction and spatial processing.

The concepts of PPS, as defined by cognitive neuroscience, and IPS, as defined by social psychology, refer to approximately the same spatial area surrounding our bodies. The aim of this series of studies is thus to assess experimentally whether PPS and IPS represent the same psychological entity. Were this held true, they should share some functional features. In order to test this experimental hypothesis, we took advantage of both sensorimotor and social manipulations to probe for the plasticity of both spaces. Results showed that the plastic changes induced by a "typical" (see Chapter IV) and a new "social" tool-use-paradigm (see Chapter V) display a behavioural double dissociation between PPS and IPS.

Chapter IV: Tool use differently shapes the space around us

This study is co-authored by Ivan Patanè, Tina Iachini, Alessandro Farnè, Francesca Frassinetti

4.1 Experiment 1

All the studies so far reviewed converge in indicating PPS as an action space that offers a multisensory interface for body–objects interactions (Brozzoli et al., 2014; Lavadas and di Pellegrino, 2015) somewhat overlapping the reaching space (Maravita and Iriki, 2004; Ocelli et al., 2011). Yet, in everyday life we interact not only with inanimate objects, but also with more "social" stimuli, namely our con-specifics. Typically, we maintain a distance around our bodies, any intrusion into which by others may cause discomfort (Hall, 1966; Hayduk, 1983) i.e., IPS. As previously recalled, both PPS and IPS are plastic: PPS is, for instance, can be extended by tool use (Iriki et al., 1996; Berti and Frassinetti, 2000), whereas IPS can be modified by emotional and socially relevant interactions (Sommer 2002, Tajadura-Jimenez et al., 2011). In this regard, it has been shown that social interactions between confederates can also modulate the plastic boundary of PPS (Teneggi et al., 2011). After an economic interaction, for example, PPS boundary can extend to include a partner at a distance, only if she had behaved cooperatively. In fact, merely knowing that the seen partner acts upon events near one's body has been found to influence the visual-tactile integration in the PPS (Heed et al., 2010). This "social" influence was thus interpreted as due to a top-down modulation on the sensorimotor representations of PPS.

In the light of this recent evidence revealing that PPS is sensitive to some social factors, the question has been raised as to whether PPS and IPS may share some functional features (Iachini et al., 2014). As described in the previous chapter, the idea is emerging that functional links, or maybe even functional identity, may exist between the two spatial representations. Our rationale for testing this hypothesis is the following: were this is the case, any sensory-motor plastic change induced in the "low-level" PPS representation should concurrently modulate the "higher" level IPS one. For this purpose, here we applied a tool-use paradigm, well known to modify both near-body space perception and arm length representation (Maravita et al., 2001; Serino et al., 2007; Cardinali et al., 2009; Sposito et al., 2012; Miller et al., 2014) to assess whether PPS and IPS are similarly affected, or not. In order to easily compare tool-use effects onto the two representations, we adopted two classical measures taken as index of the extent, or "size", of PPS and IPS, respectively. On the one hand, the reachability judgement task was here borrowed from the neuro-cognitive domain as an index of PPS boundary (Bourgeois et al., 2014). In this task, participants are required to estimate whether stimuli presented at various distances are reachable or not by their limb (without moving), thereby stressing the sensorimotor and potential action aspects of spatial perception. Because in this work we rather focused on individual-to-individual relationships, a modified version of the reachability task was applied whereby subjects were asked to estimate the reachability distance towards an unfamiliar person. On the other hand, the comfort-distance task was adopted from the social psychology field, to estimate IPS. Similar to Iachini et al. (2014), this task is a combined version of the approach and stop distance paradigms: subjects were asked to stop the confederate at the point where they still feel comfortable with the other's proximity (Sommer 2002; Aiello 1987), stressing thus the social aspect of spatial perception. Importantly, participants performed the two tasks during both Passive and Active approach conditions. In the former case, the confederate walked across the room towards the participant, whereas in the latter case, the participant walked towards the confederate. Since it has been documented PPS and IPS seem to share a similar size in the Active approach (Iachini et al., 2014, 2015), we asked whether plastic effects of tool-use on spatial processing are modulated by the active or passive way of interacting with the environment.

4.1.1 Materials and method

Ethics Statement

Participants gave written consent to take part in the study, which was approved by the Ethics Committee of the University of Bologna and carried out in accordance with the 2008 Helsinki Declaration.

Participants

Twenty-four participants (9 females, mean age=22 years, age range 19-27 years), naïve to the experimental hypothesis, volunteered for the study. Participants had no self-reported history of neurological or psychiatric diseases, and were all right-handed as assessed by administration of the Edinburgh Handedness Inventory (Oldfield 1971). We calculated our target sample size using an estimated effect size, f, of 0.2, which would require a sample of 24 participants for the study to be powered at 80%. The a priori established sample size was also used as data-collection stopping rule, i.e. when 24 volunteers were administered with the tasks in a fully counterbalanced design, no more participant was recruited for this study.

Procedure

All participants were tested individually in the same room (7.5 x 6.5m) by one experimenter and two confederates. The experimental protocol consisted of two tasks (i.e., Reaching- and Comfort-distance, Figure 4.1A), designed to respectively measure PPS and IPS, which were performed in both active and passive approach conditions. Testing began with a participant positioned at a fixed location in the room and one confederate standing at a distance of four meters (starting position). In the active conditions, participant approached a confederate and had to comply with either of two instructions: “stop yourself at the distance you think you can reach the confederate” (active Reaching-distance), or “stop yourself at the shortest distance you feel comfortable with" (active Comfort-distance). In the passive conditions, the confederate approached the participant who had to either: “stop the confederate at the distance you think you can reach the confederate” (passive Reaching-distance) or “stop the confederate at the shortest distance you feel comfortable with" (passive Comfort-distance). In each task, subjects could fine-tune the distance by moving slightly further backward or forward. Then they closed their eyes and the chest-to-chest distance at the sternum level was measured with a digital laser meter (Agatec, model DM100, error ±0.3 cm).

This procedure was repeated twice in separate blocks of five trials per each condition: before and after 15 minutes of tool-use. Two different male confederates, unknown to participants, were involved in pre and post-tool sessions. One of the confederates approached and was approached by the participant for the entire duration of the first session before tool-use, whereas the second confederate was introduced in the experimental session after tool-use. The confederates had to wear the same neutral casual clothes and to maintain a neutral expression and same speed in walking throughout the experimental session. Confederates’ gaze was kept looking straight ahead at participants’ eye-level. Furthermore, to avoid any confounds due to aesthetical or idiosyncratic features of the two confederates, the order of the confederate facing the participant in the pre and post tool-use session was also counterbalanced between subjects. A standardized appearance of both confederates was ensured across all sessions and all subjects: the confederates had to wear the same neutral casual clothes and to maintain a neutral expression. Participants and the confederates were not allowed to speak to each other for the whole experiment. Before starting the experiment all participants received an explanation of the task and had one practice trial with the experimenter for each task. Then the first confederate was introduced.

During tool-use, subjects stood still in front of a table and were required to use a 70 cm long rake to reach and to retrieve, one at a time, a total of 36 tokens, located out of the reaching space, at a distance of ≈85cm from the participants' sternum. Tokens were randomly positioned by the experimenter at different azimuthal and radial locations in order to cover the whole participant's action space. There was no time constraint; participants were required to be as accurate as possible by making a continuous, fluid movement to retrieve the targets and to move them close to their body midline.

Immediately after 15 minutes of tool-use, participants were asked to perform the Comfort-distance and Reaching-distance tasks in both active and passive approach conditions. Throughout the experimental sessions before and after too-use, the participants stood with their arms extended along their trunk and were instructed to close their eyes between each trial.

4.1.2 Data analysis and results

To test whether tool-use may extend either the Reaching-distance or the Comfort-distance estimate or both, the mean distances (in cm) obtained in the different experimental conditions were compared through a three-way ANOVA taking Session (Pre and Post tool-use), Task (Reaching and Comfort distance), and Approach (active and passive approach) as within-subject factors. Newman-Keuls post-hoc test was used to analyse significant effects. For all mean values reported, standard error (SE) is indicated. Partial eta squared (η^2_p) and Cohen's *d* were used to report effect size. Additional variables included as covariates in exploratory analyses were age, sex, handedness and years of formal education. Since inclusion of these covariates in the analyses did not modify the results, they were left out of the final analyses.

Statistical analysis revealed a significant effect of the approach variable, $F_{1,23}$=6.84, p=.015, η^2_p=0.23, due to overall participant-confederate distance being larger in the passive approach (M=65.45±2.87) than active approach condition (M=61.95±2.72). More importantly, the significant Task by Session interaction, $F_{1,23=}$6.25, p=.020, η^2_p=0.21, showed that only the Reaching-distance, but not the Comfort-distance, was significantly extended after tool-use as compared to before (Post Reaching M=63.79±1.94 vs Pre Reaching M=59.75±1.80, p=.018; Post Comfort M=64.85±3.65 vs Pre Comfort M=66.42 ±4.72, p=.333). The Reaching-distance before tool-use was the shortest distance as compared to all other conditions (all ps<.05). The ANOVA also found a statistically significant interaction between Approach and Task, $F_{1,23}$=16.08, p<.001, η^2_p =0.41. In the active approach, Comfort (M=62.31±3.89) and Reaching distances (M=61.59±2.02) did not significantly differ (p=0.797), whereas in the passive approach the Comfort-distance (M=68.96 ±4.46) was larger than the Reaching-distance (M=61.95±1.75, p<.001). The passive Comfort-distance condition was significantly larger as compared to all other conditions (all ps<.001).

Since the three-way interaction was not significant, $F_{1,23} < 1$, p=.56, η^2_p=0.08, the effect of tool-use in Reaching-distance was present both in the active (Pre Reaching M=59.72±1.95 vs Post Reaching M=63.46±2.21, two tailed *t*(23)= 3.35 p=.002, d=0.71) and in the passive condition (Pre Reaching M=59.77±1.81 vs Post Reaching M=64.12±1.85, two tailed *t*(23) = 4.12, p<.001, d=0.83), but was not evident in the Comfort-distance task for either approach (active Pre Comfort M=62.93±4.39 vs Post Comfort M=61.68±3.62 two tailed *t*(23) <1, p=.475; passive Pre Comfort M=69.91±5.38 vs Post Comfort M=68.02±3.93 two tailed *t*(23) <1, p=.539, Figure 1B). Moreover, in line with previous studies (see Iachini et al., 2014), at baseline in the active approach no significant difference between Comfort and Reaching-distance appeared (two tailed *t*(23) < 1, p=.388, d=0.18). Overall, these results reveal that tool-use modifies the reaching space, but not the comfort space.

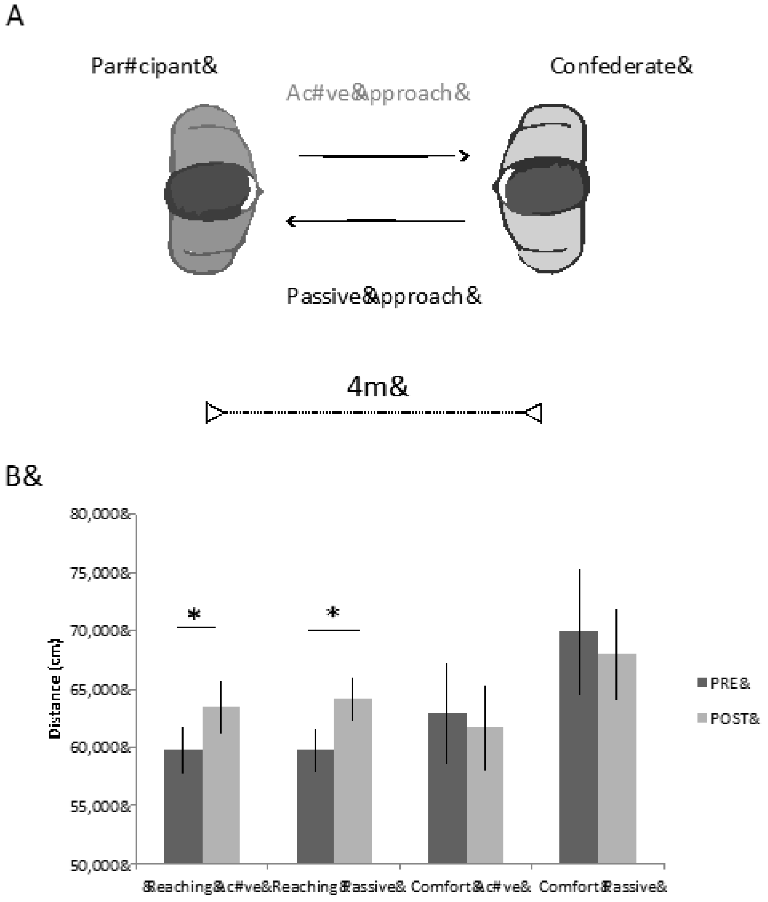


Figure 4.1 Experimental procedure and results. Participants performed Reaching-distance and Comfort-distance tasks in the active and passive-approach conditions (A). Participants were told to stop a confederate (passive condition) or themselves (active condition) when they could

either reach the confederate, in the Reaching-distance, or feel comfortable with their interpersonal distance, in the Comfort-distance task. The graph (B) shows the average group distance (in cm) as a function of task, condition, and session. Error bars indicate standard errors of the mean. Asterisks indicate significant differences in Reaching-distance before (PRE, dark grey) and after (POST, light grey) tool-use.

4.1.3 Interim discussion

In this first experiment we investigated changes of PPS and IPS after tool-use by measuring the spatial distance between the participant and another person in a Reaching- and a Comfort-distance task. Two main results emerged from the first experiment. First, we replicated previous findings, indicating PPS and IPS seem to refer in some circumstances to a similarly sized sector of space. Indeed, Reaching- and Comfort-distances had a similar extent when participants walked toward stimuli (i.e., active approach). By contrast, the Comfort-distance was larger than the Reaching-distance when participants stood still while being approached by the confederate (i.e., passive approach, Iachini et al., 2014, 2015). More interestingly, the second result of this experiment goes beyond previous findings: tool-use manipulation was effective in selectively shaping the perceived reaching space (PPS), both during the active and passive approaches, but not the perceived comfort space (IPS).

In this first experiment, the rake wielded during tool-use session allowed participants to reach targets located beyond the natural reaching distance of their arm, significantly extending their action space. In agreement with earlier works on tool-use (Iriki et al., 1996; Berti and Frassinetti, Farnè et al., 2005b; Cardinali et al., 2009), it is therefore likely that an extension of the sensorimotor representation of the arm length was critical to determine such an extension of action space. Nevertheless, a possible alternative interpretation may be that the mere act of reaching repetitively for objects placed in the space in front of the participant, regardless of the length of the used tool, may have affected the estimated reaching distance. In order to control for this potential alternative explanation, we conducted another study (Experiment 2), where as a control, participants used a short rake that did not offer effective extension of their arm length (Farnè et al., 2005b; Serino et al., 2007; Sposito et al., 2012). In experiment 2, we anticipated that only using a tool that elongates the arm length would remap PPS, as measured by the Reaching-distance task, whereas using a short tool should be ineffective.

Concerning the lack of a significant effect of tool-use on the comfort space estimation, one could argue that participants may have used non-spatial (e.g., temporal) strategies during the task, since the two confederates were positioned at a constant distance from the participant prior and following tool-use. To avoid this potential confound, in Experiment 2 confederates were therefore positioned at one of three different initial distances from participants.

4.2 Experiment 2

By analogy with previous investigations estimating reachable distance from objects (Bourgeois et al., 2014), Experiment 2 tested the hypothesis that tools that increase the natural range of action, as compared to those which don't, may extend the reachable space estimate toward another individual. To this aim, participants performed the same tasks as in the previous experiment, but they wielded either a long or a short tool. Since in Experiment 1 tool-use dependent changes were observed both in passive and active approaches, and the reaching and comfort distances were similar only in the active one, in Experiment 2 we focused on the active approach. Besides, the confederate was randomly located at three different positions, thus preventing participants from using a non-spatial strategy to stop themselves in front of the confederate. We predicted an increased distance in the estimated reaching space after use of the long, but not the short tool. Finally, we should expect no change in the estimated comfort space after either long or short tool use.

4.2.1 Materials and method

Ethics Statement

All participants volunteered and provided written informed consent. The study was approved by the Ethics Committee of the University of Bologna and was performed in accordance with the ethical standards laid down in the Declaration of Helsinki.

Participants

Forty-eight healthy volunteers (12 females, mean age: 22.47 years, age range: 18-27) naive to the purpose of the study participated in this experiment. All participants had normal or corrected-to-normal vision, no history of neurological or psychiatric diseases, and all but two were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971).

Procedure

The experimental setting and procedure were similar to those of Experiment 1, with the following exceptions. Participants were randomly assigned to one of two groups: Long tool or Short tool group. In the former group, the rake was the same as in the previous experiment (70 cm long). In the latter group, the tool was a 10 cm-long weight-matched rake and the distance at which target objects were placed during the tool-use session was adapted at around ≈25 cm from the participant's body. Participants performed the Reaching- and Comfort-distance tasks in separate blocks, under Active approach only, prior to and following the tool-use session. As in experiment 1, each participant faced a different confederate before and after the tool-use sessions. In each condition the position of the confederate, and thereby the initial distance from participant, could be either 3.5 m, 4 m, or 4.5 m from the participant. Each different confederate position was randomly administrated four times, yielding a total of twelve trials per each condition.

4.2.2 Data analysis and Results

Statistical analyses consisted on a three-way ANOVA with Session (Pre-Post tool-use) and Task (Reaching-Comfort distance) as within-participant factors and the Tool group variable (Short-Long tool group) as between-participant factors. Because preliminary analyses of variance failed to reveal any significant effect of the different confederate positions, this factor is not considered further here.

The ANOVA revealed a significant Task by Session interaction, $F_{1,46}=6.64$, $p=.013$, $\eta^2_p=0.13$, explained by the fact that the pre-tool Reaching-distance (M=62.82±1.08) showed the shortest amplitudes as compared to the post-tool Reaching-distance (M=65.00±1.27 p=.024) and to the Comfort distance before (M=65.97±2.93 p=.012) as well as after tool-use (M=64.67±2.76 p=.024). Crucial to the present investigation, a significant Task by Session by Tool group interaction emerged, $F_{1,46}=7.25$, $p=.001$, $\eta^2_p=0.14$. The interaction was driven by an increased Reaching-distance estimation following the use of the long (M=67.74±1.79), but not the short-tool, with respect to before tool-use amplitudes (M=62.74±1.52 p=.001). Post hoc tests revealed no other significant differences (all ps ≥ .062, see Figure 4.2). None of the other terms in the ANOVA reached statistical significance (all *F*s ≤ 2.62). In other terms, the critical Task by Session by Tool group interaction witnesses that only the use of a long tool affects the reachable space estimation. In sharp contrast, neither the short nor long tool modulates the comfort space estimation, as participants maintained similar distances between themselves and the confederates before and after either tool-use sessions.

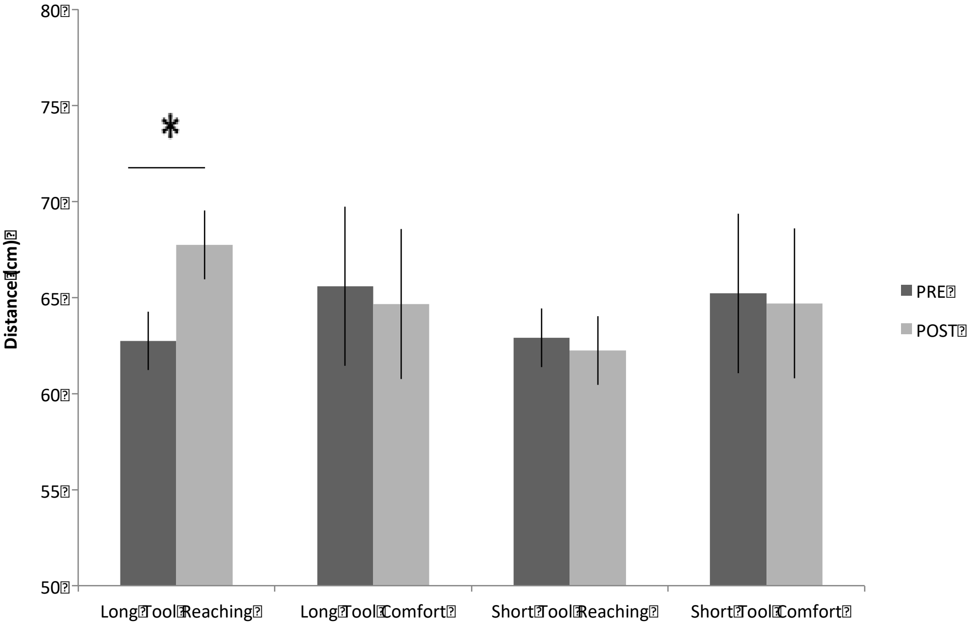


Figure 4.2. Results of Experiment 2. The graph shows the average distance (in cm) as a function of group, task, and session. Error bars indicate standard errors of the mean. Asterisk indicates a significant difference between Reaching-distance before (PRE, dark grey) and after (POST, light grey) long tool-use session.

Experiment 2 replicates previous findings in showing the tool-use-dependent plasticity of PPS (Berti and Frassinetti 2000, Farnè et al., 2000, Canzoneri et al., 2013) In particular, only after using the 70 cm-long tool that extends the arm reachable space was the PPS extended, a measured by the Reaching distance-task. As predicted, and also in keeping with previous findings (e.g., Farnè et al., 2005b, Bourgeois et al., 2014), using a shorter tool that provides no functional extension to the arm did not influence PPS. As far as the question of whether the IPS representation may be shaped plastically by the use of tools, the second experiment confirms the lack of effect of tool-use on the Comfort-distance task.

4.3 Discussion

This first investigation brings two major new findings. The first important result is that tool-use can modify the reachability estimate toward another person, a potentially relevant social stimulus. At odds with previous tool-use studies, by focusing on individual-to-individual spatial relationships, i.e., the interpersonal distance (Lloyd 2009), we provide here, to the best of our knowledge, the first demonstration that tool-use affects the estimated reaching-distance between two conspecifics.

So far, several studies have demonstrated that the extent of PPS representation is dynamically shaped by use of tools that increase the arm length (Cardinali et al., 2009, 2012; Canzoneri et al., 2013; Maravita et al., 2011; Longo and Lourenco, 2007), as using short tool, which does not extend action potentiality, is not sufficient to "elongate" PPS (Farnè et al., 2005b; Serino et al., 2007; Costantini et al., 2011). Noteworthy, most if not all studies on PPS have mainly tested participants while facing objects in absence of conspecifics, although people around us often represent the most behaviorally relevant stimulus in everyday life. In this respect, the findings from the present study indicate that extending the arm action capability also affects the perceived reaching distance from another individual.

The second, but most important result is that tool-use extends PPS, as measured by the Reaching-distance task, but not the social IPS, as measured by the Comfort-distance task. This dissociation is particularly interesting as the estimated Reaching and Comfort space had similar size before tool-use, specifically in the Active approach, that is when participants moved toward the confederate (for similar findings see also Iachini et al., 2014). In light of such a similarity, and I might add, in spite the hypothesized common nature of PPS and IPS, it might appear surprising that tool-use does not influence the social space surrounding the body, but only the space representation for action.

Before considering the theoretical implications of this finding, consistently observed across two experiments, we wish to emphasize that the experimental design was aimed at controlling for potentially confounding variables, such as repeated contact with the same individual and non-spatial response biases, that could account for the lack of effect of tool use on the social space representation. Indeed, several pieces of evidence from social psychological studies indicate that repeated contact with individuals affect interpersonal distances (e.g., Tedesco and Fromme 1974; Pedersen and Shears, 1974). In order to avoid this possible confound, here participants were not exposed to the same person in the session prior to and following tool-use: confederates' identity differed between pre- and post-tool use sessions. In addition, since in the second experiment the confederate was not located at the same initial distance from the participant, it is unlikely that the internally replicated finding concerning the comfort-distance may be due to any response/strategy bias. In Experiment 2, in fact, participants could not use non-spatial cues, such as the time spent while walking or the number of walking steps, or other cues in the room.

Although some previous studies have suggested a communality between peri- and interpersonal spatial representations, the results of both experiments converge in indicating that social and action space representations do not fully share the same functional properties. Moreover, but fundamental to the present study, this tool-use-dependent dissociation actually fits well some differences between PPS and IPS. Their anatomo-functional underpinnings seem indeed to not perfectly overlap. The fronto-parietal regions associated with IPS have been reported by a functional neuroimaging study to be more sensitive to approaching social stimuli (i.e. faces), than to approaching objects. Indeed, greater bold responses were found in the dorsal intraparietal sulcus and the ventral premotor cortex for approaching than receding faces (Holt et al., 2014, see also Schienle et al., 2016, Wabnegge, et al., 2016). By contrast, in these regions no differences were found between approaching and receding objects (i.e., cars and spheres). Instead, when regions involved in the PPS coding are probed by fMRI adaptation, allowing to isolate functionally selective neuronal populations, the premotor and parietal cortices (inferior parietal lobe and anterior intraparietal sulcus), and the putamen were reported to be involved in the coding for approaching, non-socially relevant objects (Colby et al., 1993; Grazino and Gross, 1993; Sereno and Huang, 2006; Makin et al., 2007; Brozzoli et al., 2011, 2013)

To conclude, whilst it has been shown that PPS plasticity may be sensitive to top-down influences coming from social experiences with the individual facing us (Heed et al., 2010; Teneggi et al., 2013; Maister et al., 2015; Pellecin et al., 2017), here we report that the sensorimotor plasticity induced by tool-use on the action space does not influence the social space between individuals. Critically, this finding was observed while concurrently demonstrating that the very same tool-use manipulation was effective in extending PPS also when measured from a more social perspective, namely by asking to estimate the reachable distance with respect to a person, instead of an object. Therefore, these findings provide novel insights to the current debate, spanning from cognitive neuroscience to social psychology about some critical functional features of action and social space representations, notably their plasticity.

Chapter V: Cooperative Tool use reveals periperisonal and interpersonal space are dissociable

This study is co-authored by Ivan Patanè, Alessandro Farnè, Francesca Frassinetti

The previous study hinted at the possibility that there may not be full overlap between action and social space: the tool-use-dependent changes of the peer-referred PPS, as indexed by a Reaching-distance task, do not modify the IPS toward the same peer, as indexed by a Comfort-distance task (Patané et al., 2016b). Yet, one may argue that IPS modulation was not observable because the classical tool-use manipulation was not ‘‘social” enough, since participants were left alone and required to reach for objects by themselves (e.g. Farnè et al., 2005b). Stressing the sensorimotor body-objects interaction by the means of “classical” tool-use might have thus endorsed only PPS plasticity, whereas IPS plasticity may require a more social context to emerge. Here we have overcome this limitation to more directly address the question of whether PPS and IPS may be considered as the two faces of the same coin, or not. As we frequently engage in cooperative behavior to coordinate our actions in space with those of conspecifics, we introduced a ‘‘social” tool-use setting, in which tools are not only bodily extensions, but become instruments for social cooperation. Similarly to what we hypnotized in the first study, If PPS and IPS represent the same psychological entity, then cooperative tool-use should similarly impact reachable (PPS) and comfort space representations (IPS). More specifically, if a social dimension is necessary to unveil IPS changes, adding a social context to a conventional long-tool-use manipulation known to extend PPS could increase not only the reachable, but also the comfort space. The finding of a similar tool-use dependent remapping of both spatial representations would thus support the idea that PPS and IPS share common functional mechanisms. Alternatively, if the social dimension of long-tool-use triggers plasticity of two functionally distinct representations, a different scenario would be predicted: PPS estimates should increase because of tool-use-dependent *sensorimotor* plasticity, whereas IPS estimates should decrease because of tool-use-dependent *social* plasticity. This finding would instead support the alternative hypothesis that the two spatial representations are independent from each other. We tested these predictions in Experiment 1. Participants were engaged in a

Reaching-distance and a Comfort-distance task to estimate respectively their PPS and IPS toward a male confederate, before and after having used a 70 cm-long tool to cooperate with the confederate. After finding evidence for differential changes of PPS and IPS following the use of a long tool in a social context, in Experiment 2 we investigated the effects induced by the use of a short tool in the same cooperative set. We predicted that plasticity due to the cooperative use of a short tool, which does not expand one's action capability, should affect perceived IPS, but not perceived PPS. Finally, to further assess the selectivity of social too-use effects, we also ran a control experiment. The question we addressed in Experiment 3 was whether cooperative interaction with another person is critical for any sensorimotor or social modulations of both spatial representations. In particular, neither PPS nor IPS changes were expected to occur when short tool-use is not cooperative. A final goal of the present work was to explore the relationships between PPS and IPS and a series of factors potentially involved in the sensorimotor and social regulation of the space surrounding the body. An overview of the state of the art of cognitive neuroscience and social psychology literature led us to select two variables of interest: actual length of the arm (Linkenauger et al., 2015; Longo and Lourenco, 2007) and familiarity with the other individuals (Hayduk, 1983; Pedersen and Shears, 1974). Accordingly, we hypothesized the perception of PPS to be influenced by actual arm's reach, whereas the perception of IPS should be influenced by the degree of perceived familiarity of the interacting person.

5.1 Experiment 1: cooperative long tool use

This experiment was conducted to assess the plastic effects of a novel version of a long-tool-use paradigm from a more social perspective. To this aim, we adopted two tasks to measure the individual-to-individual spatial relationships before and after a cooperative long-tool-use session. Participants were therefore engaged in a Reaching-distance and a Comfort-distance task, administered in two separate blocks, to estimate respectively their PPS and IPS toward a male confederate, before and after having used a 70 cm-long tool to cooperate with the confederate.

5. 1.1 Method

Sample size estimation

A statistical power analysis was performed for sample size estimation, based on data from our previous study, where we compared effects of short- and long-tool-use on the Reaching- and Comfort-distance tasks in two groups (N=48), with a partial eta squared for the highest-order within-between interaction =.14. With an alpha = .05, power = 0.80 and correlation among repeated measures = -0.32, the projected sample size needed with this effect size (GPower 3.1.9) was N = 34 (17 for each group), whilst with power=0.90 the estimated sample size was N=46 (23 for each group). Thus, we chose a sample size N=40 (20+20) for the first two experiments that would be more than adequate for the main objective of this study and should also allow capturing any possible effect of the social interaction. The a priori established sample size was also used as data-collection stopping rule, i.e. when 20 volunteers were administered with the tasks in a fully counterbalanced design, no more participants were recruited for either experiment.

Participants

Twenty healthy volunteers (9 women) were recruited for this experiment (mean age=23 years, SD=2.03 years, education=15.90, SD=1.17). They were all right-handed but three ambidextrous as assessed by the Edinburgh Handedness Inventory (mean = 58.72, SD = 20.24; Oldfield, 1971), and provided written informed consent before participating. The protocol was approved by the institutional ethics review board and conformed to the principles of the Declaration of Helsinki.

Procedure

All subjects were tested individually in the same room. They performed a Reaching- and a Comfort-distance task to measure the estimated PPS and IPS between the participant and a male confederate actor. Next, participants underwent a cooperative tool-use session by using a 70-cm long rake, i.e., *long-tool,* to perform a task with the confederate. Then, the Reaching- and the Comfort-distance tasks were repeated with the same confederate. After completing the experimental post tool-use tasks, participants were asked to rate their perception of the tool-use session on several dimensions (i.e., easiness, pleasantness, positivity, cooperation, competition) and the perceived familiarity with the confederate. Moreover, the experimenter recorded the participant’s length of the right arm (acromion to middle fingertip, with both arms outstretched at shoulder height). At the very end of the experiment, subjects were debriefed and thanked. None of the participants was suspicious about the real goal of the study.

Experimental tasks

The experimental tasks were similar to those of previous study described in Chapter IV. At the beginning of each trial, participants were positioned at a starting position with their toes on a line that was marked on the floor, while the confederate was located in front of them. The confederate looked straight at the participant's chin, avoiding any direct eye contact. Through the experimental tasks, participants stood with their arms extended along their trunk and were instructed to close their eyes between each trial. In the Reaching-distance task, participants were required to move at a natural gait speed toward the confederate and stop themselves at the distance they thought they could reach the other person by extending their arm. Instead, in the Comfort-distance task they were asked to move toward the confederate and to stop themselves at the shortest distance they would feel comfortable with the other's proximity. In either task, subjects could fine-tune the distance by moving slightly further backward or forward. Finally, they closed their eyes and the chest-to-chest distance at the sternum level was measured with a digital laser meter (Agatec, model DM100, error ±0.3 cm). Then participants opened their eyes and came back to their initial position for the following trial. The Reaching- and Comfort-distance tasks were administered in separate blocks of 10 trials per task. The order of blocks was counterbalanced between participants. Within each task, the initial distance between the two partners varied randomly across trials. In half of the trials the confederate was located at a distance of 3.5 metres from participant, whereas in the remaining half of the trials the confederate was positioned at a distance of 4 metres (see Figure 5.1A). This experimental manipulation served to prevent the use of any response strategy based, at least partly, on non-spatial cues in both tasks. Participants completed a practice trial before starting each task.

Cooperative tool use session

During long-tool-use session, both the participant and the confederate, facing each other, stood still along either side of a table (60 x 180 cm). As a cover story, the experimenter justified the presence of the same confederate during the long-tool-use session by explaining that the study aimed at demonstrating how collaborating with another person enhances the motor performance in speed and accuracy of both agents. Participants were indeed informed that, compared to their performance when alone, individuals tend to perform better when working in pairs. They were instructed to retrieve all the objects placed on the table (i.e., plastic poker chips and domino tiles) by means of the long rake and put them, one at a time, into a basket located along either the right or the left side of the table, according to the participant's position. The right and the left basket position were alternated across subjects. Notably, both the participant and the confederate had to collect together all the items, regardless of the type and position on the table, in the common basket. The plastic chips and domino tiles were randomly located by the experimenter outside the reaching space, at a distance of ≈90 cm from the participant' and confederate's trunks (see Figure 5.1B). Participants were also required to be as accurate as possible and there was no other constraint.

Moreover, in order to promote the joint completion of the task, from time to time the confederate would encourage cooperative play by facilitating the task, passing or moving some items closer to the participant to engage her in cooperative activities. As a stopping rule for deciding whether to continue or stop the tool-use session, we decided to end the session when one of the two following criteria was met: the participants performed 250 movements, even before 15 minutes of tool-use, or the participants used the long tool for 15 minutes, even before performing 250 movements. These two criteria were established on the basis of data from a pilot study to have comparable amount of movements performed, as well as comparable time spent with tools and the confederate across experiments.

Ratings

In order to assess how participants perceived both the long-tool-use session and the confederate himself, we administered several questionnaires at the end of the experiment. Participants were asked to rate the tool experimental session using a 7-point bipolar scale on the following dimensions: easy versus difficult (1 = easy, 7 = difficult), pleasant versus unpleasant (1 = pleasant, 7 = unpleasant), positive versus negative (1 = positive, 7 = negative), not cooperative versus cooperative (1 = not cooperative at all, 7 = highly cooperative), and not competitive versus competitive (1 = not competitive at all, 7 = highly competitive). Finally, participants rated the familiarity perceived throughout the experiment with the other person on a 7-point scale (1=not familiar to me, 7=very familiar to me). To avoid potential test-retest effects, all the questionnaires were collected only after the end of the post-tool experimental tasks.

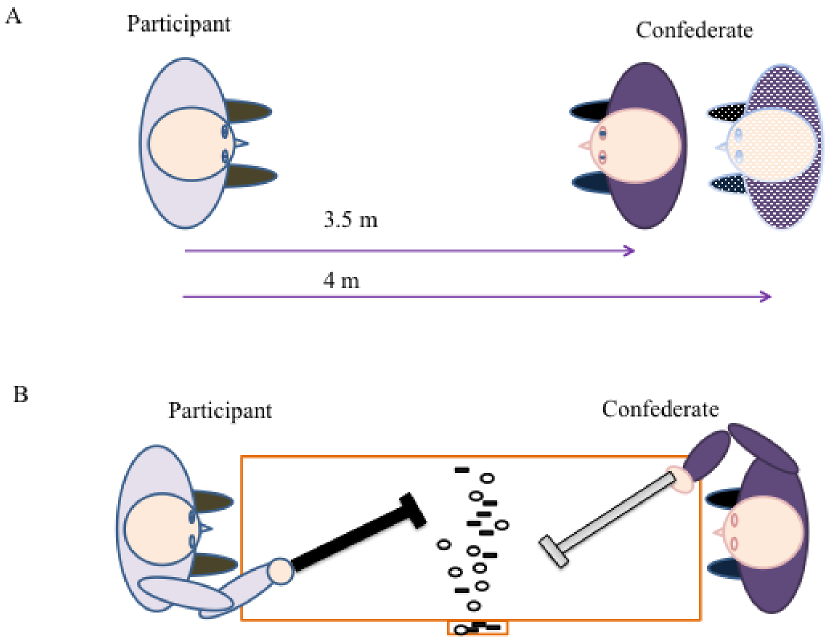


Figure 5.1A) Experimental Tasks: Participants performed Reaching-distance and Comfort-distance tasks, designed to respectably measure PPS and IPS. Participants approached the confederate and had to either: “stop yourself at the distance you think you can reach the other person” (Reaching-distance) or “stop yourself at the shortest distance you feel comfortable with the other person" (Comfort-distance). Across trials, the confederate was randomly positioned at 3.5 m or 4 m from participant. **B)** Long-tool-use session: The participant and the confederate, facing each other, stood still along either side of a table (60 x 180 cm). They were instructed to retrieve plastic all the poker chips and domino tiles (depicted by circles and rectangles) by means of a 70 cm-long rake and put them, one at a time, into a common basket located to the left or to the right according to the participant’s position (here depicted on the right). Plastic chips and domino tiles were randomly presented outside the reaching space, at a distance of ≈90 cm from the participants’ trunk.

5.1.2 Statistical analysis and results

For all mean values reported, standard error is indicated. Partial eta-squared and Cohen’s *d* were calculated as measures of effect size. The mean distances in cm recorded in each condition were contrasted by analysis of variance (ANOVA) with Task (Reaching- and Comfort-distance) and Session (pre- and post-tool) as within-subject factors. Significant interactions were followed by Bonferroni post-hoc test.

A significant main effect of Task, F(1,19)=6.73, p=.018, η^2_p=.26, showed generally larger distance in the Reaching-distance (M=67.87±2.02) than in the Comfort-distance task (M=57.80±4.71). The main effect was qualified by its interaction with Session, F(1,19)=60.76, p<.001, η^2_p=.76. Bonferroni post-hoc comparisons revealed the Reaching-distance was significantly extended after cooperative long-tool-use (M= 70.97±2.22), as compared to before (M=61.49±4.56, p<.001, d=0.87), whereas the Comfort-distance following the cooperative use of long-tool (M=54.11±4.95) was reduced with respect to before (M=61.49±4.56, p<.001, d=1.19). In addition, before tool-use no significant difference between Reaching and Comfort-distance amplitudes appeared (p=.09, d=0.19). Yet, such difference was found to be significant after cooperative tool-use (p<.001, d=0.91, see Table 5.1 and Figure 5.2).

As complementary evidence for the efficacy of the cooperative interaction, participants reported that long-tool-use session was easy, pleasant, positive, cooperative and not competitive. Furthermore, the confederate was rated as mildly familiar (See Table 5.2).

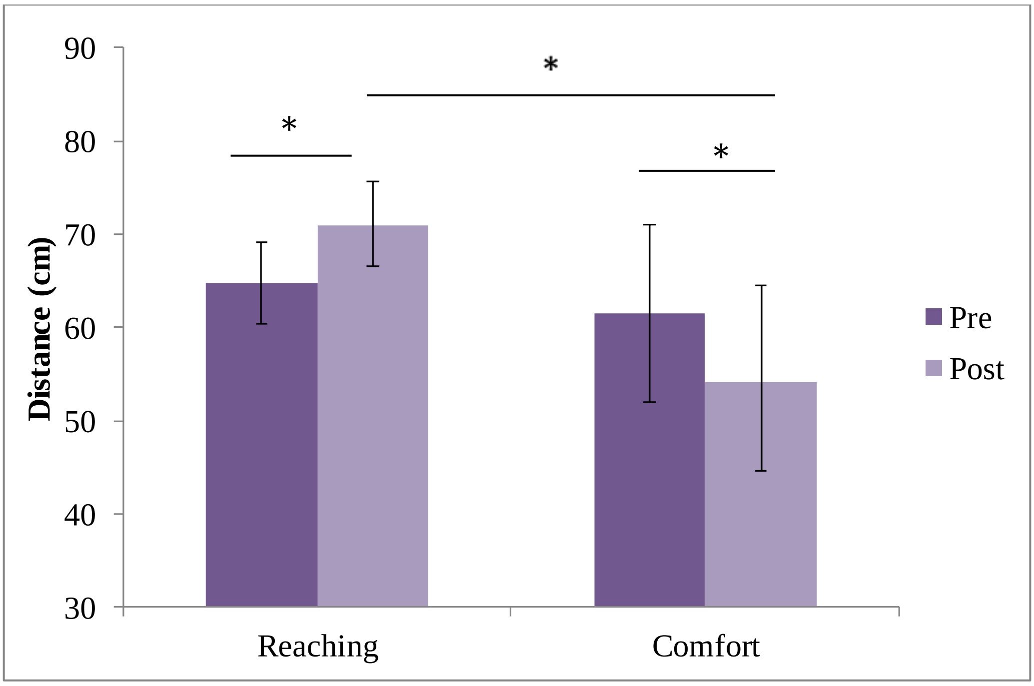


Figure 5.2 The graph shows the average distance (in cm) as a function of task (Reaching- and Comfort-distance) and session (prior to and following cooperative long-tool-use session). Error bars indicate 95% confidence intervals. Asterisks indicate significant differences in Reaching and Comfort-distance estimates before (PRE, dark purple) and after (POST, light purple) long tool-use.

Consistent with recent findings (e.g., Iachini et al., 2014), replicated in previous experiments (see previous study, chapter IV), before long-tool-use reachable and comfort space estimates did not differ, supporting the idea that PPS and IPS could refer, in some circumstances, to a similarly sized sector of space. More interestingly, despite the fact that the reaching and comfort pre-tool amplitudes were comparable, the cooperative long-tool manipulation revealed an opposite pattern in the plastic properties of PPS and IPS. Indeed, we observed a plastic change of PPS representation in the direction of extension, due to the tool-use effects on the perceived reachable distance. This is of particular interest in light of the plastic contraction of IPS representation, due to the cooperative social interaction on the perceived comfort distance between conspecifics.

As previously argued, even though several pieces of evidence have shown tool-use effects to vary with the functional length of the tool, it could be argued that the mere act of reaching repetitively for objects may alter the PPS estimation, regardless of the length of the tool used to retrieve them. In addition, it has been disclosed that social interactions (i.e., an economic exchange) may expand one's own PPS boundaries to incorporate the space surrounding the cooperative confederate (Teneggi et al., 2013). Thus, either repeated reaching movements or the cooperative interaction per se could have extended the PPS estimates. In order to control for these alternative hypotheses and to parallel the previous study, we conducted a control study using a short tool, which did not increase action potentialities and, thereby, should not impact on PPS estimates. Nonetheless, short tool-use in a cooperative context should still reduce the IPS estimates.

5.2 Experiment 2: Cooperative short tool use

This second experiment was run to further explore the role of tool-use-dependent plasticity in a social setting by measuring the perceived PPS and IPS before and after a cooperative short-tool-use session.

5. 2.1. Method

Participants

Twenty new healthy adults (10 women) were recruited (mean age=22.75 years, SD=2.57 years, education=15.95, SD=1.32). They were all right-handed but four ambidextrous as assessed by the Edinburgh Handedness Inventory (mean = 62.20, SD = 20.41; Oldfield, 1971), and provided written informed consent. The protocol, approved by the institutional Ethics Committee, was performed in accordance with the standards of the Declaration of Helsinki.

Procedure and tasks

The procedure was the same as in Experiment 1, except that in the tool-use session participants used a short tool to cooperate with the confederate. Both the participant and the confederate used a rake with a 10 cm-long handle (i.e., not extending the sensorimotor representation of the arm length) to reach and move the same objects into the same basket. The distance at which target objects were placed was adapted at around ≈30 cm from either member of the dyad (see Figure 5.3A).

5.2.2 Results

The mean distances in cm were entered in a two-way ANOVA with Task (Reaching- and Comfort-distance) and Session (pre and post-tool) as within-subject factors. A significant main effect of Session appeared, F(1,19)=21.86, $p< .001$, $\eta^2_p=.54$, with participants keeping a shorter distance in the post (M=58.15±2.74) than in the pre tool-use session (M=65.53±3.54). Also, a significant interaction between Task and Session emerged, F(1,19)=7.93, $p=.011$, $\eta^2_p=.29$, due to the fact that the distance in the Comfort-distance task was reduced after (M = 53.73±4.69) as compared to before cooperative short tool-use session (M = 64.51±6.35 $p<.001$, d=0.92). Crucially, no significant difference between before and after tool-use estimates was found in the Reaching-distance task (M = 64.51±6.35, M= 62.56±2.10 respectively, p=.187, d=0.89). Furthermore, at baseline Comfort- and Reaching-distance amplitudes prior to cooperative short-tool-use did not differ from one other (p=0.99, *d*=0.07). However, after tool-use distance amplitudes were significantly smaller in the Comfort- than in the Reaching-distance task ($p<.001$, $d=0.41$, see Table 5.1 and Figure 5.3A). Moreover, participants perceived the cooperative short-tool-use session as being easy, pleasant, positive, cooperative, but not competitive. They also rated the confederate as moderately familiar (see Table 5.2).

Once again, at baseline no difference in terms of distance emerged between the two tasks designed to measure PPS and IPS. Noteworthy, the cooperative interaction was effective in reducing the comfort distance from the confederate after the short-tool-use session. By contrast, no significant difference in pre vs. post-tool estimates was observed in the reachable distance toward the confederate.

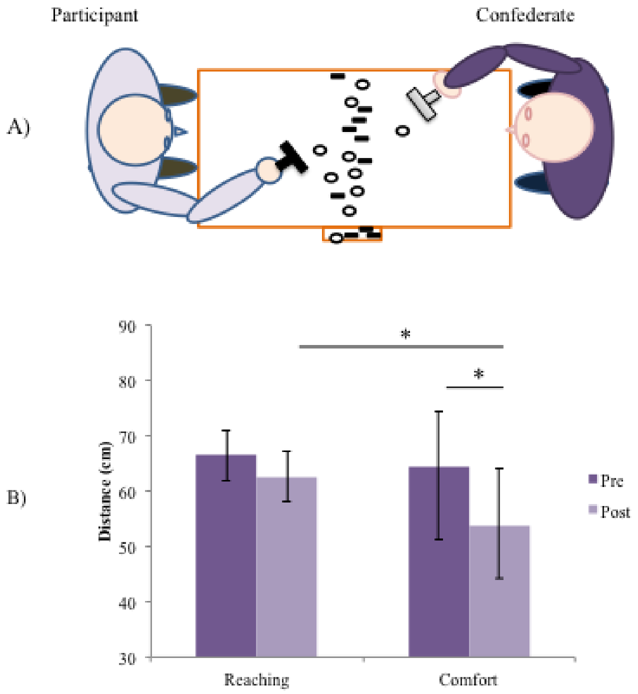


Figure 5.3 A) Short-tool-use session: The participant and the confederate used two 10 cm-long rakes to retrieve plastic poker chips and domino tiles randomly located by the experimenter at ≈30 cm from both the confederate and the participant. The goal of the task was to put the objects into the same basket, located at the right or left edge (randomly varied across subjects) of the table. B) The graph shows the average distance (in cm) as a function of task (Reaching- and Comfort-distance) and session (prior to and following short-tool-use session). Error bars indicate 95% confidence intervals. Asterisks indicate significant differences in Comfort-distance estimates before (PRE, dark purple) vs. after (POST, light purple) short-tool-use and in Reaching vs. Comfort-distance estimates after short-tool-use.

Experiment 1: Cooperative Long-tool-use	Pre Reaching-distance M= 64.78 SE=2.12 95% CI=[60.34, 69.22]	Post Reaching-distance M= 70.97 SE=2.22 95% CI=[66.32, 75.62]
	Pre Comfort-distance M=61.49 SE=4.56 95% CI=[51.95, 71.03]	Post Comfort-distance M=54.11 SE=4.95 95% CI=[43.74, 64.47]
Experiment 2: Cooperative Short-tool-use	Pre Reaching-distance M= 66.55 SE=2.25 95% CI= [61.84, 71.26]	Post Reaching-distance M= 62.56 SE=2.10 95% CI= [58.17, 66.98]
	Pre Comfort-distance M = 64.51 SE=6.35 95% CI = [51.21, 77.80]	Post Comfort-distance M = 53.73 SE=4.69 95% CI = [43.91, 63.55]
Experiment 3: Test-retest control	Pre Reaching-distance M = 64.12 SE=1.73 95% CI = [60.26, 67.98]	Post Reaching-distance M = 64.80 SE=2.12 95% CI = [60.07, 69.53]
	Pre Comfort-distance M = 67.04 SE=6.56 95% CI = [52.43, 81.65]	Post Comfort-distance M = 64.78 SE=4.78 95% CI = [54.12, 75.44]

Table5 .1. Descriptive statistics for the participant-confederate distances obtained in the experimental conditions.

Experiment 1 Cooperative long-tool-use	Familiarity with the candidate: 1=not familiar to me, 7=very familiar to me	M = 3.95 SE = 0.25 95% CI=[3.44,4.46]
	Easiness of tool-use session: 1 = easy 7 = difficult	M = 2.65 SE = 0.24 95% CI=[2.14, 3.16]
	Pleasantness of tool-use session: 1 = pleasant 7 = unpleasant	M = 3.35 SE = 0.24 95% CI=[2.84, 3.86]
	Positivity of tool-use session: 1 = positive 7 = negative	M = 2.50 SE = 0.21 95% CI=[2.06, 2.94]
	Cooperation of tool-use session: 1 = not cooperative at all 7 = highly cooperative	M = 5.15 SE = 0.17 95% CI=[4.80, 5.50]
	Competition of tool-use session: 1 = not competitive at all 7 = highly competitive	M = 1.15 SE = 0.08 95% CI=[0.98, 1.32]
Experiment 2 Cooperative short-tool-use	Familiarity with the candidate: 1=not familiar to me, 7=very familiar to me	M=3.85 SE=0.26 95% CI=[3.30, 4.40]
	Easiness of tool-use session: 1 = easy 7 = difficult	M = 2.50 SE = 0.28 95% CI= [1.92, 3.08]
	Pleasantness of tool-use session: 1 = pleasant 7 = unpleasant	M = 2.60 SE = 0.20 95% CI= [2.19, 3.01]
	Positivity of tool-use session: 1 = positive 7 = negative	M = 2.30 SE = 0.22 95% CI= [1.84, 2.76]
	Cooperation of tool-use session: 1 = not cooperative at all 7 = highly cooperative	M = 5.40 SE = 0.21 95% CI= [4.62, 5.84]
	Competition of tool-use session: 1 = not competitive at all 7 = highly competitive	M = 2.00 SE = 0.29 95% CI= [1.39, 2.61]

Table 5.2 Descriptive statistics for rating scores.

Overall, these results indicate that the use of a short tool to collaborate with another individual did not modify the estimated reachable distance. At the same time, the very same manipulation selectively shrank the estimated comfort distance. Thus, by replicating previous work showing the lack of effect of short tool-use on reachable space (e.g., Bourgeois et al., 2014; Costantini et al., 2011), the results of this further investigation provide strong support to the finding the PPS and IPS representations can be shaped differently and, more importantly, they may be even directionally dissociated.

5.3 Relationships between participant-confederate distances, arm length and familiarity

Finally, we tested for the relationships that may exist between the distance at which the participants stopped themselves according to the task (Reaching- or Comfort-distance) in Experiment 1 and 2 and some independent variables of interest. In particular, we focused on the actual arm's reach (here measured in terms of arm length) and the degree of familiarity with the other person (here assessed by judging on a Liker-like scale the perceived familiarity with confederate during the whole experiment).

Preliminary analyses revealed a linear relationship between the reachable or comfort distances and the two additional measures, which are not part of the main experimental manipulation but have an influence to some extent on the distances being measured. To assess the influence of arm's length and familiarity on PPS and IPS estimates before and after the social tool manipulations, we pooled the data of all the experimental conditions from the two experiments in a single analysis. We thus fitted a linear model (ANCOVA) to submit the pooled data to inferential analysis. Assumptions for an ANCOVA model were met. A Repeated Measures ANCOVA was conducted on the reachable and comfort distances prior and following the two cooperative tool-use sessions taking Task and Session as within subject factors and Tool (short and long) as between subject factor. To control for the influence of the actual arm's reach and the perceived familiarity, we entered arm's length and scores of the familiarity rating as covariates. Finally, we also included in the model the appropriate two-way and three-way interactions. Results revealed a significant main effect of Task, F(1,35)=6.50, p= .015, η^2_p=.15, and a significant interaction Session by Tool, F(1,35)=10.91, p=.002, η^2_p=.23. More relevant to the purpose of the present study, these three factors (i.e., Task, Session, Tool) interacted, F(1,35)=5.09, p= .030, η^2_p=.12, even after taking into account the effect of the covariates. As far as the arm's length, the analysis found only a significant interaction with Task, F(1,35)=4.26, p= .046, η^2_p=.11 (Figure 5.4A and 5.4B display the effect of the covariate against the Reaching and Comfort-distance amplitudes). Finally, there also was a significant main effect of familiarity, F(1,35)=10.28, p= .003, η^2_p=.22, qualified by its interaction with Task, F(1,35)=13.35, p= .001, η^2_p=.27 (see Figure 5.4C and 5.4D). To summarise, this analysis fully replicated the pattern of results described above, with the additional benefit of offering a more powerful and stringent approach. The critical Task by Session by Tool interaction witnesses again the differential changes induced by the cooperative use of a long or short tool on the reachable and comfort space estimations. Here we wish to emphasize that this effect is significant even after controlling the influence of the covariates being considered. Most interestingly, specific correlations of the arm's length and familiarity rating were observed with the Reaching and Comfort-distance tasks, respectively. The positive relation between the arm length and the reaching estimates revealed that participants with longer arm kept a larger distance in the Reaching-distance task, whereas no influence of the arm length was found on the comfort estimates. When looking at the perceived familiarity with the confederate, the negative relation between this covariate and the comfort estimates indicates that the more participants perceived the other individual as familiar, the shorter the distance they kept with him. In sharp contrast, no influence of the familiarity rating was found on the reaching estimates. Therefore, these findings support the view that PPS and IPS can be specifically influenced and functionally dissociated.

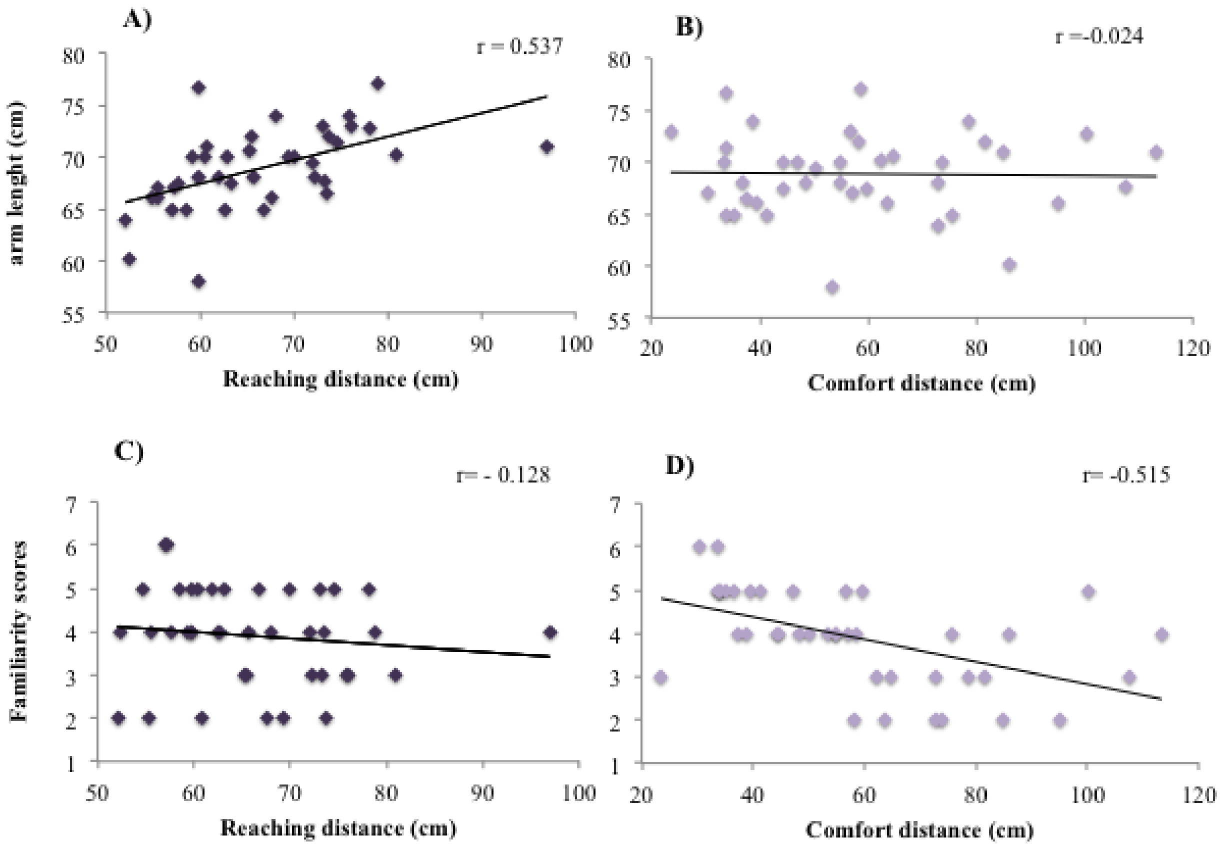


Figure 5.4 Scatter plots (with best-fitting regression lines) showing confederate-participant distances, separately for the Reaching- (A and C) and Comfort-distance tasks (B and D), as a function of the length of the participants' arm (upper panels) and as a function of the ratings of perceived familiarity with the confederate (lower panels)

5.4 Experiment 3: control tool use

Taking into account the evidence that familiarity with another person is associated with the extent of the estimated IPS, one could wonder whether the mere fact of being exposed to the same social stimulus (i.e., the confederate) throughout the experiment can have an effect either on reachable or comfort distance. It is indeed important that the results of the two experiments are controlled for potential confounds, such as the repeated contact with the other, familiarization with the tasks, or any test-retest effects. As a control, novice participants were submitted to the same procedure previously described in Experiment 2 with the only difference that during the short tool-use session they simply performed the classical (i.e., non-cooperative) task while the confederate was observing the participants using the short rake. Participants therefore underwent the Reaching- and Comfort-distance tasks prior to and following a classical tool-use session in the presence of the confederate, who was simply observing the completion of tool session.

5.4.1 Method

Sample size estimation

H_0 implies that mere repeated contact could account for similar changes in IPS and PPS estimates, regardless of the social interaction with the other person. We therefore based the population effect size estimation on the empirical effect that we found in the previous experiment. The effect size, which we would detect with this control study if the prolonged contact was sufficient to explain the pattern of result of Experiment2, is approximately $\eta^2_p = .54$ or Cohen's d=1.05 (i.e., the effect size of the main effect of Session on pre and post Reaching- and Comfort-distances). With such an effect size and an alpha of .05, we would need N=10 with a power of .80 and N=12 with a power of .90. To parallel the first sample size analysis and to obtain a powerful enough test, we chose a sample size N=11 and ceased data collection when our minimum sample size was reached.

Participants

Eleven female healthy volunteers (mean age 21.55; SD = 1.12 years, mean education =16, SD=0.94) took part in this control experiment.

Procedure

Participants were required to estimate their reachable and comfort distances toward another person, in the Reaching- and Comfort-distance tasks respectively, before and after a tool-use session. During the tool-use session participants used a short-tool in front of an immobile confederate. They were also asked to pay attention at the same time to the presence of the confederate who observed participants completing the tool task. Therefore, in this non-cooperative social setting the short-tool-use session was expected not to alter either the perceived reachable or the perceived comfort distance estimates. Throughout the whole experiment, participants faced the same person and were led to believe the confederate actor was also another participant. As a cover story, they were told that the researcher was interested in investigating how people perform a motor task in the presence of on observer.

5.4.2 Statistical analysis and Results

The mean distances in cm recorded in each condition were contrasted by analysis of variance and a series of paired-sample t tests. The Repeated Measures ANOVA was conducted with Task (Reaching- and Comfort-distance), Session (pre and post tool) and within-subject factors.

As predicted, the ANOVA found neither significant main effects nor interaction (all *F*s<1, all *p*s $\geq .386$, $\eta^2_p \leq .08$, see Figure 5.5). To inspect whether there was at least a tendency towards decreased post-tool amplitudes due to any test-retest effect or repeated contact, we computed a series of uncorrected t tests contrasting before vs after tool-use values in each experimental task for each starting position. Again, there was no hint of difference ($|t|$s≤ 0.89, *p*s $\geq .392$, Cohen's $d \leq 0.36$). In sum, data from this further control study revealed no significant difference between pre-tool vs. post-tool amplitudes in either Reaching- or Comfort-distance task.

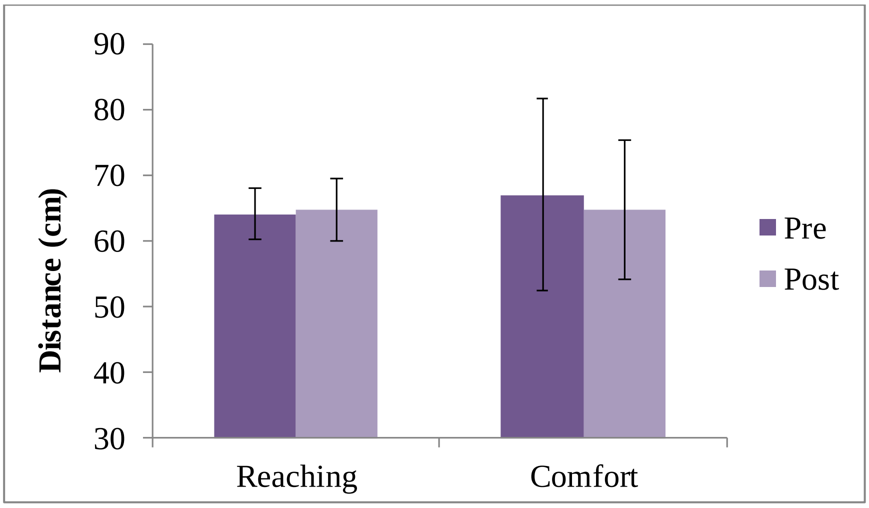


Fig. 5.5. The graph shows the average distance (in cm) as a function of task (Reaching- and Comfort-distance) and session (per and post control short tool-use). Error bars indicate 95% confidence intervals.

Results from this additional experiment showed no significant difference in pre vs. post estimates, ruling out any role for unspecific effects potentially coming from repeated administration of the tasks, habituation of the experimental context, or increased contact with the confederate. Although the interaction with the confederate was not cooperative in the control tool-use experiment, one result is worth noticing here: ratings of perceived familiarity with the confederate during the whole study did not differ across experiments (see Manipulation check questionnaires below). This interesting comparison reveals that the mere presence of the same individual throughout the experiment cannot account for the selective modulations induced by cooperative tool-use. These findings therefore suggest that the differences in reachable and comfort distance estimates observed after cooperative tool-use in Experiment 1 and 2 reflect genuinely our variables manipulation.

5.5 Manipulation check questionnaires

Finally, we assessed the effectiveness of the cooperative tool-use manipulations in the three experiments. To this aim, we analysed the self-report measures of participants' social perception of the confederate and tool-use session by comparing the scores of the questionnaires collected in the first two experiments with those collected in the control experiment. By contrasting the scales across experiments, we should predict the cooperation ratings from the Experiment 1 and 2 to be significantly different from those from the Experiment 3. Indeed, in the control Experiment 3 the procedure was the same as in Experiment 1 and 2, except that during the tool-use session only the participant wielded a short rake and no cooperative interaction with the confederate was required. Moreover, we should not find any significant difference in terms of familiarity with the confederate across the experiments, as participants were exposed to the same person from the beginning to the end of each experiment.

A series of two-tailed t-tests showed that participants perceived not only as more cooperative, but also as positive the social use of both a long (p<.001, Cohen's *d*=2.05 and p=.035, Cohen's *d*= *0.84*, respectively) and a short tool (p<.001, Cohen's *d*=2.14 and p=.011, Cohen's *d*=1.03 respectively) with the interacting confederate, as compared to the non-social tool-use. No other significant contrast emerged in all comparisons (p>.05). In addition, we performed numerous bootstrapping and resampling procedures for each of the comparisons. In every case, this bootstrapping procedure supported the inferences derived from the *t* tests, so we report only the standard parametric tests in this manuscript.

To summarise, these findings confirm the effectiveness of social tool manipulations as participants from the experimental groups explicitly judged tool-use activities as cooperative. The comparisons of familiarity ratings additionally showed that perceived familiarity did not vary across the three experiments, so we can infer that the contact with the social stimulus (the confederate) was not significantly different among the three experiments.

5. 6 Discussion

The eventuality of a multiplicity of the spaces surrounding the body becomes increasingly debated (see, for a review, de Vignement and Iannetti, 2015). We suggest a fruitful strategy to inform theoretical models of near space representation would consist in testing PPS and IPS for their dynamics. As a first contribution, we reported that a classic tool-use session enlarged the action-related PPS representation, but not the social-related IPS representation (see chapter IV). Here we make a substantial step forward: by transforming the most typically employed tool-use paradigm into a socially cooperative tool-use paradigm, we disclose a full dissociation between IPS and PPS. The findings of Experiment 1 reveal that a completely opposite modulation of the extent of IPS (reduced) and PPS (enlarged) may result when introducing a social dimension to an otherwise classical tool-use task. Experiment 2 and 3 show the selectivity of this dissociation: social cooperative use of a short tool, which provides no functional extension of the individual's arm reach, shapes the IPS estimates only, while the same short tool used in a neutral, non-cooperative setting has no effect in modulating either spatial representation.

It should yet be noted that the distance at which the participants and the confederate performed the social tool-use tasks varied across experiments. Indeed, that distance was larger in Experiment 1 than Experiment 2 and 3 because both members of the interacting dyad had to use a 70 cm-long rake in the cooperative long-tool-use session. Since IPS is, by definition, sensitive to the distance at which the social stimulus is located, the different location of the confederate could differently affect the perceived comfort space after tool-use. One may predict that the closer the confederate is facing the participants during the cooperative interaction, the shorter comfort distance they maintained with him. In spite of such a possibility, when comparing results from the two experiments we observed similar Comfort-distance estimates after cooperative long and short tool-use (t(38)=.05, p=.957). As a consequence, we consider unlikely that the different confederate-participant distance during social tool-use session could have an important effect on our measures. To corroborate this point, one must also consider that the reduction of IPS after cooperative tool session is comparable, as indicated by the effect size of the contrasts pre vs. post Comfort-distance estimates in the first and the second experiment.

Results from questionnaires importantly add to these behavioural findings, in that they support the effectiveness of the novel social version of our tool-use task. The ratings administrated to assess perception of tool-use manipulations indicated that, when comparing the three experiments, participants explicitly judged the quality of the tool sessions as different (see Manipulation check questionnaires in the supplemental materials). Indeed, the social tool-use paradigm in Experiment 1 and 2 was perceived as more cooperative and more positive than the “less social” manipulation in the control Experiment 3. Conversely, the social perception of the other individual in terms of familiarity appeared comparable: familiarity ratings collected in Experiment 1 and 2 were not significantly different from those collected in third control experiment. Hence, as the familiarity of the social stimulus (i.e., the confederate facing the participants throughout the study) was similarly perceived across experiments, we deem unlikely that the results of the present study could be explained in terms of different degree of familiarity with the confederate. We suggest instead that the crucial variable that selectively affected spatial regulation is the social dimension (cooperative vs. non-cooperative) of tool-use (see also Candini et al., 2017 for a recent study showing a differential modulation of IPS depending on the type of interaction, cooperative or non-cooperative, in children).

Before arguing the theoretical implications of these findings, we would like to point out that our design was aimed at controlling for potentially confounding variables, such as gender effects, that could account for the potentially different modulations of cooperative tool-use on the social space representation. A wealth of studies from social psychology has indeed shown the influence of gender on interpersonal spatial relationships (Aiello, 1987; Hayduk, 1983 and Sommer 2002 for reviewers). In this regard, a recent study investigating how reachability and comfort distances were moderated by gender differences reported that the critical determinant of this effect was not the participants’, but the confederate’s gender: larger distances were indeed chosen in front of a male than a female confederate (Iachini, et al., 2016). In the light of these findings, here participants were exposed to the same male confederate. In addition, to limit potentially spurious effects driven by participants’ gender, we recruited balanced samples in Experiment 1 and 2. Thus, even if gender was not the focus of our investigations, care was taken to ensure that this social variable could have not masked the effects being assessed in our study.

When considering other social variables influencing the representation of the space around the body, previous work (Teneggi et al., 2013) reported a PPS modulation as a function of the interaction with a partner. By using an audio-tactile paradigm to estimate the PPS boundary, the authors showed there was no longer detectable PPS boundary between the participant and the confederate when the latter had behaved cooperatively. This finding was thus interpreted as a social extension of PPS. As suggested by an anonymous reviewer, if we consider the differences between previous and the present results, one could argue that they may emerge from different definitions/functions of PPS. In their work, Teneggi et al (2013) relied on the audio-tactile facilitation effect as a proxy for the location of the PPS boundary from the participants’ face, while here we used the perceived reachability toward another person as a proxy of PPS. These two different paradigms to assess PPS extent could therefore focus on two different metrics of the same representation: on the one hand PPS as the portion of space where multisensory integration is facilitated; on the other hand PPS as reachable space where hand-object interactions occur. In the light of this definition, one may argue the perceived reachability as an index of the extent of PPS could be less sensitive to social factors. Following this alternative account, one might think that we disclose a dissociation between PPS and IPS because the reachable space is modulated only by low level sensorimotor manipulations such as tool-use. However, several reports concur in demonstrating that PPS, as operationalized by reachability measures, is actually affected by social and emotional factors (e.g., perceived morality and facial expressions, Iachini et al., 2015; Ruggiero et al., 2016). For instance, when participants are being approached by a confederate they perceive as immoral, both comfort and reaching distances were modulated. Although this impact of the (im)moral evaluation was more prominent on IPS, there was a significant expansion not only of the comfort zone, but also of the perceived reachable space, allowing to dismiss an alternative account of the present findings in terms of resilience of reachability to social modulations.

Before concluding, another point we would like to mention here is that the same direction of the PPS modulation (i.e., expansion) might be driven by the different functional features of the PPS. Even when PPS is assessed by audio-tactile interaction tasks to capture its multisensory nature, the same directional effect can observed after manipulations of seemingly opposite emotional valence. Unlike the reaching estimates (Iachini et al., 2015), the audio-tactile paradigm as a proxy of PPS might not differentiate between the positive and negative valuation of social-emotional factors: a larger PPS was found after both *positive* valuation of a fair confederate (Teneggi et al., 2013) and *negative* valuation of sound-mediated emotions (Ferri, et al., 2015b). These apparently conflicting results might be reconciled if interpreted in the light of the different functions of PPS recently proposed by de Vignemont and Iannetti (2015). They suggested a distinction between PPS functions defining a protective space and a working space: the former functional role would be protection of the body, while the latter would serve goal-directed actions. Each function would correspond to a specific set of actions: appetitive and protective actions. Indeed, working space interface is more often associated to voluntary movements, while the protective space interface to automatic movements. Following this suggestion, we would argue that the same outcome (i.e., expansion) can be elicited by opposite functions subserved by PPS and that the different nature of the interactions with the surroundings would privilege one target function over the other. Positive valence of the interaction may induce an “extension” of PPS, an effect compatible with the appetitive function of the working space interface, while negative valence may induce an extension, compatibly with the defensive function of the protective space interface. As quality or valence of body-objects interactions might represent a possible confounding variable, we wish to emphasize that here we investigated PPS and IPS plasticity within the same (positive) social context: the use of a tool to cooperate. To this aim, we capitalized on reaching estimates as a measure of PPS, which are selectively and reliably sensitive to social variables (Iachini et al., 2015; Ruggiero, et al., 2016). The double dissociation reported here emerged from a social set with a similar positive valence, but only following cooperative use of a long tool. In sharp contrast, the neutral nature of the non-cooperative tool-use turned out to have no effect on IPS and IPS plasticity.

In line with the hypothesis that the functional properties of PPS and IPS may differ, the complementary pooled analysis indicated that reachable and comfort space are based upon different action-related (i.e., the actual arm's length) and socio-emotional (i.e., the perceived familiarity) factors, respectively. Indeed, the results revealed that perception of the space between conspecifics is selectivity influenced by different factors (namely, the arm length and the familiarity with the other) according to the spatial representation examined (namely PPS and IPS, respectably). It is reasonable to expect that body-related factors, and thereby possibilities for reaching, may modulate PPS extent, which in some situations may remain immune to some social-related factors, such as the perceived familiarity with the person facing us. If the arm length role in modulating the perceived reachable distance fits with previous findings and confirms a close relationship between body-action capabilities and PPS (e.g., Longo and Lourenco, 2007), one may have expected this factor to be involved also when regulating interpersonal social distances. On the contrary, here we disclose that only the perceived familiarity with the confederate correlated with IPS, a result consistent with prior evidence reporting that stimulus familiarity can influence social distance (e.g., Pedersen & Shears, 1974). This is particularly interesting given that PPS and IPS were measured from a social perspective by asking to estimate the reachable and comfort distance toward the same peer. Indeed, one important difference with respect to our previous study (Patané et al, 2016) is that here participants were being exposed to the same person in the session prior to and following tool-use. Nonetheless, the feeling of familiarity with the interacting individual influenced differently the extents of PPS and IPS: another important piece of evidence indicating that the two spatial representations are not completely overlapping dimensions.

To summarize, these findings converge in bringing support to our suggestion that the putative role of PPS for the guidance of interpersonal motor interactions (e.g., Brozzoli et al., 2014; Ambrosini, et al., 2014) does not legitimate the assumption of its functional identity with IPS. In conclusion, we would like to remark that although PPS and IPS can be influenced similarly by some high-order social manipulations, our results based upon testing for their potential dissociation calls for a distinction between them.

Chapter VI: Mine, Thine, Ours

> *“We feel and act about certain things that are ours very much as we feel and act about ourselves. Our fame, our children, the work of our hands, may be as dear to us as our bodies are, and arouse the same feelings and same acts of reprisal if attacked”*
>
> William James

As described in the first and third chapter, in everyday life we do not act in a “social vacuum”: sensorimotor and social interactions with objects take place in social contexts. In such contexts manipulable objects, however, are not defined solely by their physical characteristics. Indeed, targets of our daily actions are also specified by nonphysical (i.e., conceptual) features such as aesthetic qualities, value, and ownership status. To date it has been demonstrated that the physical and functional features of objects (e.g. short vs long-tool) differently affect PPS, yet, the potential impact of *social features* of objects has never been tested. Yet, the importance of personal property, belonging, in human personal and social life is undoubtable (see below). In In this chapter, I will specifically focus on ownership, a psychological construct that pervasively biases our cognitive processes. In this respect it has been shown, for instance, that self-owned objects enjoy elevated importance with regard to a number of psychological variables, including attention (Turk et al., 2011a), memory (Cunningham et al., 2008) and language (Abbi, 2011).

Hence, the first purpose of the current research is to generate a new and more ecologically valid understanding of how the ownership status of objects and one’s own or other people’s action influences the perception of space. From a more theoretical point of view, the ultimate purpose of this dissertation is to provide first evidence of the involvement of PPS in the guidance of motor inter-actions toward socially relevant objects. Before doing so, I will briefly present an *up-to-date* review about ownership as a theoretical framework to ground the last investigation of this dissertation. Then, I will present a novel examination of this construct within the neurocognitive investigation of PPS.

6.1 Mine is special: the pervasive psychological advantage of self-owned objects

The concept of ownership is inherently social. We can claim ownership not only of accumulated material wealth, but also of ideas and places, as well as other people (i.e., my husband, our daughter). Potentially, the feeling of ownership extends to just about anything for which the terms mine, my, or our(s) (for shared ownership) can be applied. It can be founded in the laws of society (i.e., legal ownership) being recognized foremost by society, and hence the rights that come with ownership are specified and protected by the legal system. Yet, ownership can manifest in the feelings toward an object that is owned by the individual (i.e., psychological ownership) without any legal claim to title (Pierce et al., 2003).

Rousseau (1762) suggested that "civil society" began when a person fenced off a plot of ground and took it into his or her head to claim "This is mine," and other people accepted this assertion. Recognizing the importance of possession, Sartre (1943/1969) noted that "to have" is one of the three categories of human existence (along with "to do" and "to be") and that "the totality of my possessions reflects the totality of my being. . . I am what I have . . . . What is mine is myself" (pp. 591–592). Hence, scholars from various disciplines have tried to understand what ownership over an object really implies, and the conditions under which it manifests itself. Particularly informative were the works by James (1890) and Prelinger (1959) on objects perceived to be part of the self.

James (1890) made seminal observations about the nature of the self, noting that it extends beyond the boundaries of one's own body. The self can indeed "incorporate" many other possessions, including those that one is frequently in physical contact with (e.g., clothing, jewellery, sentimental objects, etc.) and those that one is tightly bound to in other ways (e.g., family members, reputation, creative accomplishments, etc.). As James (1890, pp. 291–2) put it, ''a man's Self is the sum total of all that he CAN call his, not only his body and his psychic powers, but his clothes and his house, his wife and children, his ancestors and friends, his reputation and works, his lands and yacht and bank-account. All these things give him the same emotions'.'

The most widely accepted view is that psychological ownership reflects a relationship between an individual and an object (material or immaterial) in which the object is experienced as having a close connection with the self (Furby, 1978a, 1978b; Litwinski, 1942) and becomes part of the "extended self" (Belk, 1988; Dittmar, 1992). As Isaacs (1933) noted, "what is mine becomes (in my feelings) a part of ME" (p. 225). Moreover, the state of psychological ownership (i.e., "mine-ness" or "our-ness") is composed of a cognitive and affective core that results in different behaviors. It is a condition of which one is aware through and reflects an individual's awareness, thoughts, and beliefs regarding the target of ownership. This cognitive state, however, is coupled with an emotional or affective sensation: feelings of ownership are said to be pleasure producing per se (Beggan, 1992; Furby, 1978a; Nuttin, 1987; Porteous, 1976) and are accompanied by a sense of efficacy and competence (White, 1959). As a result, feelings of ownership toward various objects have important and potentially strong psychological and behavioural effects.

Because of their association with the self, owned objects are believed to enjoy a special psychological status (as being viewed as extensions of self, Beggan, 1992; Sartre, 1943; James, 1890). For example, people ascribe more value to things merely because they own them, phenomenon known as the "endowment effect". In one of the first demonstrations of this effect in literature, Knetsch (1989) presented three groups of undergraduates with coffee mugs and chocolate bars. The participants in Group 1 could choose any item before completing a questionnaire, and they displayed roughly equal preferences for the two types of objects. The participants in the other two groups were initially endowed with either a mug (Group 2) or a chocolate bar (Group 3), and then, after completing the questionnaire, they were given the opportunity to exchange the item for an object of the other type. The main finding was that nearly 90% of these participants retained the item they were endowed with. Several different explanations of such behaviour have been offered (e.g. Morewedge and Giblin, 2015; Plott and Zeiler, 2003, 2007; Tversky and Kahneman, 1991). However, what mostly matters for the present purposes is the general point that the endowment effect seems to reveal a strong propensity not just to over-value one's own possessions, but to treat them as elements of one's extended self.

This is further illustrated by the classical "mere ownership" effect, a tendency for objects arbitrarily assigned to self (i.e., owned but not chosen by self) to be imbued with more positive characteristics (Beggan, 1992; Belk, 1988, 1991). Beggan examined how individuals rated their preference for objects of varying ownership statuses. Participants were presented with different objects and asked to rate how much they liked the object, as well as the value of receiving the object as a gift. In the ownership condition, prior to rating the items, each subject read that she would receive the object as a gift for her participation. The participants rated self-owned objects more favourably than the other participants who did not own the object. The mere ownership effect was obtained even when there was no time delay between when participants were informed they owned the target object and when they were asked to rate its attractiveness. Because the participants still showed a preference for self-owned compared to other-owned objects, this preference could not be attributed to familiarity with self-owned objects (Beggan, 1992). This is a striking example of an influence of ownership: people prefer and give significantly more positive evaluations to trivial items they own compared to those they do not. Remarkably, this effect does not appear to be due to the amount of time spent, attention paid, increased contact, familiarly with owned objects (Beggan, 1992). Likewise, numerous subsequent studies have shown that, compared to unowned objects, owned objects are attended, remembered, and valued more strongly, even when the experience of possession is only imaginary or very brief (e.g., Belk, 1988, 1991; Cunningham et al., 2008; Gray et al., 2004; Shi et al., 2011; Turk, van al., 2011a, 2011b; van den Bos et la., 2010; see Morewedge and Giblin 2015 and Kemmerer 2014 for recent reviews).

It is interesting to note that the assignment of items as mine does not have to be self-generated. Cunningham et al. (2008) asked participants to sort images of objects based on an arbitrary assignment to an ownership category ("mine" or "other"). Subsequent recognition was higher for self-owned objects in comparison with other-owned objects, regardless of whether the participant or a confederate had sorted the items. What Cunningham et al.'s (2008) findings reveal is that self-item associations forged through psychological ownership yield a similar mnemonic advantage to that generated through the explicit, evaluative encoding of trait adjectives describing the self (Turk et al., 2008; Symons and Johnson, 1997). The link between possessions and the self may help to explain why we provide higher valuations (the endowment effect) and positive attributes (mere ownership effect) to owned items. This skewing of value and valence may reflect the operation of positivity biases that distort the evaluation of material possessions that comprise an important element of self (Beggan, 1992; Belk, 1988, 1991; Kahneman et al., 1991; Knetsch and Sinden, 1984). That is, our tendency to have a positive bias towards ourselves (e.g. Koole, et al., 2001) also extends to our property (Gawronski et al., 2007). Hence, the self-relevance of our property may give rise to stronger memory representations of our possessions relative to unowned objects (Cunningham et al., 2008; van den Bos et al., 2010).

In line with the view that the sense of possessing certain inanimate objects is related to self-referential processing, further insight into the basis of the relationship between the self and the extended self comes from TMS and fMRI and investigations. Salerno and colleagues (2012) found similar increase in similar corticospinal motor excitability induced via TMS while participants watching pictures of one's own hand and phone. Using Cunningham et al.'s paradigm (2008), Turk et al. (2011b) asked participants to categorize everyday items as either self-owned or other-owned in the scanner. They showed that the recognition of self-owned items uniquely engaged the medial prefrontal cortex as well as the insula and supramarginal gyrus. This suggests that cortical midline brain areas previously associated with self-referential encoding (for instance the medial prefrontal cortex, see Northoff et al., 2006) and regions that have been shown to support hedonic aspects (for instance the insula) might play an important role in forming associations between self and owned objects. Similarly, the medial prefrontal cortex was found to be involved in the endowment effect and even when ownership is processed implicitly (Kim et al., 2010; Kim and Johnson; 2012; 2014;

Kim et al., 2015; Krigolso et al., 2013). Taken together, these data ‘‘provide neural evidence for the idea that personally relevant external stimuli may be incorporated into one’s sense of self’’ (Kim and Johnson, 2014, p. 1).

6.2 Our-ness: our objects are special too?

Psychological ownership, therefore, offers an alternative route to study self through its association with objects. Indeed, when objects become grounded psychologically, they become for the individual ‘‘mine’’ as the individual finds him/herself present in them (Kline and France, 1899), and they become a part of the ‘‘extended self’’ (Belk, 1988; Dittmar, 1992). Although psychosocial ownership is mainly established by a social relationship between an individual and his/her object, recognized (and legitimated) by at least another person, it is worth noticing that virtually all of this literature has treated feeling of ownership as an individual-level phenomenon. This scholarship has indeed examined mostly the somehow special processing of self-owned objects (vs other-owned or unowned objects) and the feeling of “mine-ness” (Etzioni 1991) associated with such a psychological ownership. However, this represents only one of the ownership categories, being mine vs non-mine juxtaposition simply one of the possible combinations of ownership we deal with in our environment.

Another category is “ours”, that can be considered as a shared ownership. As noted by Peirce et al (2003, 2009), from a Western and individualistic cultural tradition, *our* is a double possessive in form. It implies that the object of possession has a connection with the self (*my*) while simultaneously having a possessive relationship with one or more other individuals. “She is *our* daughter” quite simply means that she is *my* daughter as well as the daughter of my partner. Thus, “our” is a dual possessive, since a person can recognize that not only is she/he psychologically tied to the object, but so are others. This can create a new emergent property. While personal feelings of ownership emerge through interactions between target and one person, the emergence of a shared sense of ownership (i.e., “our-ness”) on the other hand is seen as dependent upon person-object, other-object, and person-to-person interactions (Pierce and Jusilla 2010). More specifically, two or more individuals have to interact with the same target so that they need to be aware of one another’s interaction and that they together are psychological owners of the target in question. The object can thus become a part of the ‘‘extended sense of ‘us’”.

Further, cross-cultural psychology has highlighted differences in the conceptualization of the self across people and regions of the world (Markus and Kitayama, 1991). At the same time, differences in socialization practices might potentially result in more collectivistic than individualistic feelings of ownership. Theoretically, it could be argued that the more the self is tied to the collective entity (as in collectivistic cultures such as China), the more psychological ownership will be defined as a collective, shared feeling. In contrast, in individualistic cultures (e.g., the United States), the feeling of ownership could be experienced more at the individual level. Yet, there is no empirical evidence in support of such propositions. Related to this, Pierce and Jussila

(2010) defined collective ownership as a “collective held sense (feeling) that this target of ownership (or a piece of that target) is collectively ours”. However, to date no empirical work has been undertaken to test whether ownership can be aggregated to the interpersonal or group levels. Noteworthy, the same authors also stated that collective ownership is distinguished from group identification in general. Preliminary empirical support for the existence of two distinctive individual and collective-oriented dimensions of ownership has been obtained in the field of the organizational psychology (Henssen et al., 2014). Nevertheless, shared (i.e., interpersonal) or collective (i.e., in-group) ownership remain emergent constructs without empirical support.

6.3 In a nutshell…

Ownership refers to the classification of a physical or mental object as belonging to self and is a core facet of human experience (James, 1890). Philosophers (Rousseau, 1762; Sartre, 1943), psychologists (Csikszentimihalyi and Rochberg-Halton, 1981; James, 1890; Winnicott, 1953), and researchers (Belk, 1988; Beggan, 1992) converge in interpreting such valuation as a tendency to represent objects as extensions of the sense of one's self (or of 'us' in the case of shared ownership).

A sense of ownership over an object gives it a pervasive psychological advantage over other objects. When everyday objects are conceptualized as *mine* (vs. *not mine*), even when arbitrarily assigned, we pay more attention to them, remember them better, implicitly prefer them, and even assign them higher value and favorability ratings (Gray, et la.; 2004; Turk et al., 2011a; Cunningham et al., 2008; van den Bos et al.; 2010; Huang, et al., 2009; Morewedge, et al., 2009; Beggan, 1992). The psychological construct of the self and the cognitive and affective relationship between the self and one's possessions represent the heart of these ownership effects. Objects become physical manifestations of one's, or others', personal identities, values, and characteristics, such that we become the objects that we own. Research has so far focused only on individual property, by comparing the effects due to attributing objects to the category "mine" vs. "not-mine". Critically, no study has tested the possibility of shared "our" ownership and whether such a feeling may induce effects similar to those observed for the items categorized as "mine". Another critical point is the lack of a heuristic mechanism explaining how and when one may establish an (inter)individual sense of object ownership relevant for the self.

6.4 Tracking and controlling owned objects

Self–object associations form the basis for the concrete self-construct developed in early childhood. Several developmental studies show that tracking the ownership status of, and regulating interactions with, objects that are owned by other individuals is critical to social cognition. Hood and Bloom (2008) showed that when children (3-6 years old) are presented with an object that is perceptually identical to a favourite toy, they prefer to keep the original toy than accept the replacement. This suggests that children rapidly learn to detect the cues of ownership and conform to the given societal norm of one's culture. Accordingly, they learn possessive pronouns by the age of 16 months (Fenson et al., 1994). By the age of two years, they understand when someone owns an object even though a third person may be in possession of it (Fasig, 2000). By age four, children infer an object's owner as the individual who controls permission of use (Neary et al., 2009). Last, 6–8-year-old children use cues of ownership to predict the likely winner in third-party contests (Pietraszewski and Shaw, 2015).

It should be fairly clear that cues to ownership are themselves intrinsically social, involving possession (Friedman and Neary, 2008), investment of labor (Kanngiesser et al., 2010), and economic or social exchanges (Blake and Harris, 2009). Thus, the ownership relationship is not inherent in an object itself, but rather in the network of relations between an object and the agents that interact with it. So how could young children easily and rapidly detect such cues? To answer to this question, it has been proposed that we are endowed with a powerful disposition to track the actions and possessions of agents (Gelman et al., 2014). Tacking and establishment of individual physical control over targets could therefore be required for the ownership status to emerge.

Gelman, Manczak, and Noles (2012) conducted a series of experiments in which children (ages of 2–4 years) were shown sets of objects and learned novel ownership information about a subset of these objects. Then, children were tested to see if they had spontaneously tracked the owned objects. By 3 years of age, children tracked individual objects that were designated (by the experimenter) as their own, even when such objects had little value or distinctiveness. Furthermore, they showed a preference for the owned objects, liking them more than objects that had not been tagged as their own. Also, already at 3 years of age, they do not lose track of the owned objects even when the objects were subtly different instances of the same kind or indistinguishable, or after receiving a distracter task that drew their attention away from the target objects (Gelman et al., 2014).

These findings therefore would suggest that tacking object in order to control it could be a possible mechanism that could account for ownership-related effects, as previously proposed by non-experimental work. In her control model of ownership, Furby (1978a) argued that the greater the amount of control a person can exercise over certain objects, the more they will be psychologically experienced as part of the self. McClelland (1951) developed the idea that, much like parts of the body and control over them, objects that can be controlled become part of the self. Prelinger (1959) provided support for the proposed relationship demonstrating that objects over which the participant had control or could manipulate were more likely to be perceived as parts of the self than objects for which was not the case. Merely touching an object, in absence of any ownership instructions, increases one’s perceived ownership and valuation of objects by providing an increased sense of control (Peck and Shu 2009). Likewise, the endowment effect is significantly influenced by the amount of tactile contact that participants have with them (Wolf et al., 2008, see also Newman and Bloom, 2014).

Consistent with these views, Scorolli et al. (2014) assumed that tracking object ownership can be influenced by any cue that predicts the establishment of individual physical control over objects. As a consequence, spatial proximity (being spatially close to the object), temporal priority (being the first to find it), and touch (being in bodily contact with it) can all be used, possibly with different reliability, as cues of ownership. To test this hypothesis, in Experiment 1 participants were shown a neutral object located on a table, in the reaching space of one of two characters. In Experiment 2 one character was the first to find the object then another character appeared and saw the object. In Experiments 3 and 4, spatial proximity, temporal priority, and touch were pitted against each other to assess their relative weight. After having seen the scenes, participants were required to judge the sensibility of sentences (i.e.; whether semantically sensible or not) in which ownership of the object was ascribed to one of the two characters. Responses were faster when the objects were located in the reaching space of the character to whom ownership was ascribed in the sentence and when ownership was ascribed to the character who was the first to find the object. When contrasting the relevant cues, touch cue was stronger than temporal priority cue in modulating the ascription of object ownership. The advantage of spatial proximity and touch over temporal priority reveals that cues that are more reliable to predict who is going to establish control over an object are more relevant to track its ownership status. In addition, this may also point to the possibility that the conceptual representation of ownership is, at least partially, constrained by the body.

In keeping with this notion, recent evidence has started to identify potential body-related constraints and modulations of the cognitive effects of object ownership, suggesting that such an abstract social feature is possibly grounded in the body (corporeal) self.

6.5 Embodied object ownership?

As outlined above numerous studies have examined owned objects as material aspects of the extended self. Yet the self is not *just* a psychological construct. It also has a physical counterpart: the body. In this paragraph I will try to argue that the sensorimotor body processes and the spatial relationships with objects may contribute to the cognitive effects of object ownership.

First insight into the neurocognitive basis of the relationship between the core (corporeal) self and the extended (extracorporeal) self comes from the literature on somatoparaphrenia (Vallar and Ronchi, 2009). So far only a few studies have carefully investigated whether—and if so, to what degree—this disorder goes beyond body parts to encompass other possessions. In some patients, complex bidirectional interactions have been reported between the affected limb and possessed items that are frequently in contact with it. In a fascinating report, a patient described by Sandifer (1946, p. 123) falsely believed that her left hand belonged to the doctor, but then she recognized a ring on one of the fingers and said, ‘That’s my ring; you’ve got my ring, doctor.’ This example illustrates how non-corporeal elements of the extended self can influence corporeal elements of the core self. Even more interesting is that the opposite pattern has also been documented by Aglioti et al. (1996) in a patient who denied possession of her left hand. In one of the experiments, an examiner asked her to indicate whether she owned hand-related objects, including rings, watches, combs, brushes, scissors, and holy icons. When the objects were placed in her normal right hand, all of her judgments were accurate. On the contrary, when the same objects were placed in her repudiated left hand, she incorrectly denied possessing the ones that did in fact belong to her, while correctly rejecting ownership of the others. For example, when one of her rings was placed in her good right hand, she immediately recognized it as her own and recalled many autobiographical details about it (e.g., ‘I remember quite clearly that this ring was given to me by my late husband’). However, when the same ring was placed in her affected left hand a few minutes later, she maintained that, although it looked similar to the one she had seen earlier, it was not hers. Thus, in this particular case, because the left hand was no longer treated as ‘‘mine’’, the associated objects were likewise disowned, at least when viewed and evaluated in the context of the now-denied body part. More generally, Aglioti et al. (1996) suggest that these results bolster James’s (1890) original proposal that there is a tight link between the body and the representation of closely related, personally significant possessions.

A further demonstration of the special relationship between body and “embodied ownership” comes from recent investigations aimed at examining whether object-directed actions modulate the ownership bias (Truong et al., 2016). The authors investigated whether the location of owned objects relative to the body would interact with recall performance for those objects. To emphasize the dynamic spatial relationship between the participant's body and the objects, participants were required to move and sort objects from a start position to a location close to or far from themselves. After the sorting task they examined participants' recognition of the objects via a surprise memory test. Results revealed an enhanced object processing when the object was both self-related and self-moved toward the self. Specifically, self-owned objects moved to a location close to the body were subsequently remembered significantly better than self-owned objects moved to a far location, as well as other-owned objects moved to either location. Importantly, the modulatory effect was absent when the participant did not physically move the objects closer or farther from the body but instead watched them appear in either location as a result of a key press. These findings reveals therefore the contribution of physical actions to the sense of ownership: 1) moving self-owned objects closer to the body enhanced memory for those objects; 2) an active manual interaction seems to be necessary for memory benefits to emerge (Truong et al., 2016).

Similarly, Oakes and Onyper (2017) found a memory advantage for pictures and words categorized via a motion in the direction of the physical body. Interestingly, also movements toward one's cell phone increased memorability of stimuli when compared to the same movement toward an unfamiliar phone (see also Salerno et al., 2012). This would appear to indicate that both a self-relevant frame of reference and a movement indicative of approach are required for the memory advantage to emerge. Taking all these findings together, it seems that acting on an object through bringing it toward the body may enable the body to "embody" the object.

In addition, ownership status of objects influences visuomotor processing. For instance, verbally acquired knowledge that a mug is owned by someone else directly modulates its affordances by eliminating the automatic potentiation of action towards a graspable object. When participants judged orientations on the handles of mugs assigned to either themselves or the experimenter, standard stimulus–response compatibility effects were abolished when they belonged to the experimenter. The finding that the object affordance compatibility effect emerged for a self-owned object only, but not experimenter-owned one, may suggest that there is a distinction between how self-owned and other-owned objects are represented in the visuomotor system (Experiment 2 in Constable et al., 2011).

The high-level concept of ownership has also been shown to affect physical movement towards objects when individuals act alone on with a partner. For example, Constable et al. (2011) focused on the influence of ownership in individuals' daily lives by examining the movement trajectories of people moving mugs with different ownership statuses (i.e., the participant's mug, the experimenter's mug, and an un-owned mug). Ownership was established by having the participants to paint their mug to create their own design, and to take the mug home to use daily for approximately two weeks before returning to complete the second half of the experiment. During testing participants were presented with one of the three mugs, and were asked to perform a simple natural lifting movement with the mug. Kinematic data such as movement trajectories and acceleration were measured. Participants lifted their own mug more forcefully (i.e., with a greater acceleration) and drew it closer to their own body, while they lifted the experimenter's mug with greater care and moved it slightly more towards the experimenter. The authors discussed that this pattern of results is consistent with a general reticence to interact with other people's objects and that it may reflect a reluctance to interact with other people's possessions. They also speculated that the reduced acceleration exerted upon the experimenter's mug may be an indication that the participant was attempting to develop and maintain a positive social relationship with the experimenter.

In a second investigation the same authors investigated whether object ownership status influenced motor behavior in joint action (Constable et al., 2016). Participants were instructed to pass mugs that differed in ownership status to a partner. It was shown that participants oriented handles less toward the partner when passing their own mugs than when passing mugs owned by the partner or by the experimenter. Because the objects were physically identical (aside from color), the difference in rotation is driven by top-down modulation of motor commands associated with ownership status, rather than bottom-up factors associated with the low-level perceptual properties of the mugs. Collectivity, these results indicates that individuals implement joint actions that assist less the partner if they intend to manipulate own objects (Constable et al. 2016).

6.6 In a nutshell…

In sum, the material summarized above indicates that during the past few decades, cognitive neuroscience and social science have been generating remarkably similar results regarding the representational domain of personal possessions. Simple act of deeming an object as one's own bestows it with special status as the object in question becomes part of the extended (body) self. Such feeling of object ownership would indeed appear to share some neural and cognitive mechanisms with the feeling of body ownership.

The sensorimotor system of the body self seems to have developed, both at collective and individual level, elegant solutions to the core problems of efficiently interacting within a social world. Object ownership can accordingly bias the perception of self-relevant objects as well as the execution of motor plans. That is, the perception of ownership influences the way in which an individual interacts in a given environment, suggesting an intricate relationship between action and perception. Given that PPS is a multisensory-motor representation of the space immediately surrounding the body, taking the body as spatial reference for encoding near objects, the ownership status of an object might shape PPS in social interactions.

Chapter VII: Our peri-personal property: Exploring the effect of object ownership on the space around us

This study is co-authored by Ivan Patané, Claudio Brozzoli, Eric Koun, Fancesca Frassinetti, Alessandro Farnè

The concept of possession is central in the development of the person in social contexts. Given the ubiquity of object-oriented actions in our daily life, knowing ownership status is essential to deal with others successfully. Accordingly, the verbally acquired knowledge of ownership can affect even deep-seated aspects of visuomotor processing, indicating that the motor system seems to be highly tuned to detecting interaction with self - or other-owned objects (Constable et al. 2011, 2014; Throung et al., 2016). The property status could thus play an important role in shaping the dynamic spatial relationships between the body and the way it acts on target objects, that is on PPS.

Here I will present a novel contribution to the examination of the relationship between action, space and ownership, by exploring the modulations induced by object ownership on the representation that guides hand-object interactions, i.e., PPS. As previously outlined, this body centered coding of space is involved in the motor control of goal-directed actions, inasmuch as voluntary acting on objects triggers online remapping of PPS boundaries (Brozzoli et al 2009, 2010). It therefore stands to reason that the conceptual socially based feature of personal possession may modulate multisensory-motor interactions between the body and the target object. More specifically, as grasping one's own or somebody else's object has been recently reported to alter movement kinematics (Constable et al. 2011, 2014), here we tested whether the concept of object ownership may differentially shape the PPS boundaries when grasping one's own or the other person's object.

Furthermore, in the light of ample evidence that the observation of an action can result in the activation of the corresponding motor plan in the observer (di Pellegrino et al., 1992, Fadiga et al., 1995, Grezes and Decety, 2001; Brass et al., 2001; Blakemore and Frith, 2005; Brass and Heyes, 2005; Keysers and Gazzola, 2009; Rizzolatti and Sinigaglia 2010; Naish et al., 2014), we hypothesized the PPS boundaries could be shaped not only by actual execution, but also by mere of somebody else's observation action. Given that action observation leads to a representation of both the motor aspect of an observed action (motor simulation) and its somatosensory consequences (action-based somatosensory simulation) in the observer's brain (Deschrijver et al., 2016), the second aim of the study is to examine online remapping of PPS during observed goal-directed actions. Specifically, we tested whether PPS visuo-tactile updating could occur when actively executing a grasping action upon self- or other-owned object, as well as when merely observing another person executing the same action of grasping toward the very same objects.

To this aim, dyads of participants took turns to reach and grasp with their right hand a glass-shaped object. Object ownership was determined by verbal instructions (e.g., the yellow glass is yours) and followed by self-contact. To assess PPS remapping, visuo-tactile interactions (VTI) were probed either before or at movement onset by a task known to modulate tactile perception on the acting hand. The strength of the interaction between touches on one’s hand and visual distractors from the target object that the hand would grasp is taken as a behavioural proxy of PPS boundaries. Importantly, VT stimulation was also delivered during grasping observation: prior to or at the onset of an action performed by the participant sitting in front (hereafter the peer). This experimental design allowed us to examine whether visual and tactile information interact strongly at the beginning of, rather than before, the overt movement as a function of the execution or observation of grasping actions towards the objects owned by participants. Likewise, hand motion tracking allowed us to test whether movement execution was differentially modulated by attributed ownership. To test the effects of different property conditions, in the first experiment the participants interacted with one’s own or peer’s object. Based on previous evidence, we predicted that on-line strengthening of VTI, as a proxy of PPS remapping, should be elicited by executing a voluntary action directed towards one’s own object. In contrast, simply knowing that an identical glass-shaped object belongs to the other person should reduce such on-line updating of VTI during actions. Lastly, a similar action-dependent VTI modulation could arise not only during actual execution of actions, but also during mere observation.

After revealing selective modulations of PPS during overt execution or mere observation of goal-directed moments toward self- or other-owned items, we investigated a virtually so-far-neglected instance of ownership: ours. We disclosed that our-ness, or shared ownership, is perceived as a hybrid instance of propriety that simultaneously is experienced as ‘‘mine’ and “someone else’s”. This dual feeling of ownership reflects in similar VTI modulations when voluntary acting upon the object owned by the two participants, no matters who performs the movements.

7.1 Experiment 1

In the first experiment we investigated whether an arbitrary assignment of two identical objects (aside from color) to an ownership category (“mine” or “other”) could affect action-dependent modulation of PPS. We therefore expect the relative increased of VTI during action unfolding, as compared to before, to be modulated as a function of object ownership. Moreover, we expect a relative increased of VTI at the onset of the other’s action, as compared to before, while the participant is simply observing the other grasping his/her target. We tested also for possible parallels between the motor and perceptual performance by analyzing how ownership object affects VT performance as well as pattern kinematic movements. Finally, we explored the relation between modulation of PPS during observed action and empathy.

7.1.1 Methods

Participants

On the basis of power analysis, we set a target of 16 same-sex pairs. The a priori established sample size was also used as data-collection stopping rule. Thirty-two healthy participants (16 men, 16 women, mean age= 22.39 years, SD=2.91 years) with normal or corrected-to-normal vision took part in the study. Data from one participant (whose mean accuracy was 2.5 SD below the overall mean of the group) were excluded from analyses because of low accuracy (i.e., 6%, 25%, and 56%) in several experimental conditions of the VTI task. All participants were right-handed as assessed by the Edinburgh Handedness Inventory (mean score= 76. 37, SD=19.65 years) and had no history of neurological or psychiatric disorders. All participants were naive as to the experimental hypotheses being tested and provided written informed consent. The procedures were approved by the Inserm ethics board and complied with the ethical standards outlined in the Declaration of Helsinki (World Medical Association, 2013).

Procedure

Two same-sex participants were tested in a pair. Each person received one of two glass-shaped objects from the experimenter. The two objects were physically identical, aside from the (blue or yellow) color of a band placed on the upper part that served to mark the grasp landing positions required for the tips of the thumb and index fingers. Participants were told they each owned one of the two glasses for duration of the whole experiment. The mapping of color to attribute ownership of the objects was counterbalanced between participants. After explicitly assigning either object, the experimenter asked participants to bear object ownership in mind throughout the experiment. Then participants seated in front of each other on the opposite side of a table. The experimental protocol consisted of a VTI task, a modified version of the crossmodal congruency effect (CCE) task (see Spence et al., 2004a, 2004b) adapted by Brozzoli et al., (2009, 2010), whereby visual stimuli were embedded in the to-be-grasped object and tactile stimuli were delivered to only one acting hand. In the current version of VTI task adapted in this study, participants took turns to grasp one of the two objects in separate sessions. At the same time, both participants had to discriminate the location of a tactile target delivered to thumb or the index finger, while ignoring visual distractors from the object that could produce either congruent or incongruent patterns of VTI stimulation. After the two sessions, each subject completed the Inter-personal Reactivity Index scale (IRI; Davis, 1983) to measure various facets of dispositional empathy.

Visuo Tactile Interaction Task

Apparatus

The two target objects were two identical plastic glasses (5 cm in diameter and 10 cm in height). They only differed from a yellow or blue (2 cm high) band located on the upper part of each object. One of the two objects at a time was located on a support at a distance of 47 cm from the starting position of the two participants' hand (Figure 7.1). Two (1.5 x 1.5 cm) squares drawn on the coloured band marked the grasp landing positions required for the tips of the thumb (on the front surface of the object) and index fingers (on the rear surface of the object) in a precision grip configuration. The virtual line connecting these two points of contact determined an opposition axis of the precision grip of 45° with respect to both subjects' trunk. Two red LEDs were fixed at the front and the back of the superficial border of the glass-shaped object, proximal to the respective contact surfaces of each finger. Visual stimuli consisted of a single flash (200-ms duration) from either the back or front LED, delivered concurrently with electro-cutaneous stimulation to the grasping hand. Disposable electrodes (700 15-K, Ambu Neuroline, Denmark) were used to present suprathreshold electro-cutaneous stimuli consisting of square-wave pulses (100 µs, 400 V) delivered by constant-current stimulators (DS7A, Digitimer Ltd., UK) to either the index finger or thumb of the right hand of the two subjects. Electro-cutaneous target intensities were set out individually for each subject and stimulated location, so that participants could detect 100% of the stimuli in a series of ten trials for index finger and thumb [thumb mean current (s.e.m.) = 7.71mA (0.3); index finger mean current 7.78mA (0.3)]. During the experimental task, participants had to respond to the tactile stimulus as fast as possible by releasing one of two foot pedals (Herga Electric Ltd., UK). The toe pedal indicated stimulation of the index finger, and the heel pedal indicated stimulation of the thumb, according to the classical procedure employed in studies investigating visuo-tactile interaction through the cross-modal congruency effect (CCE,). Participants were therefore required to make speeded spatial discrimination responses, reporting whether tactile target stimulus was presented to the index finger or thumb. Participants were also asked to ignore task-irrelevant visual stimuli embedded in the object.

Hand movements were recorded using an Optotrak 3020 system (Northern Digital, Inc.), with a sampling rate of 200 Hz (0.01-mm 3D resolution at 2.25-m distance) via three infrared emitting diodes (IRED) for each of the two participants. Two infrared light emitting diodes were attached to the lateral and interior parts of the nails on the thumb and index finger, and one to the interior part of the wrist at the styloid process level, for either member of the experimental pair. These markers were used to perform on-line recording and subsequent off-line reconstruction of the transport component (the change over time in wrist marker position while the right hand was reaching for the target) and grip component (the change over time in distance between index finger and thumb) for the action of the two participants. We computed the following kinematic parameters: peaks and relative latencies of wrist acceleration, velocity and deceleration for the transport component of the movement; peaks and relative latencies of maximum grip aperture (MGA) for the grip component; Movement reaction time (the release of the starting position switch from the GO signal) and Duration (from the movement start detected by the release of the starting position switch up to the closing of the fingers on the object to be then lift from its saucer to complete the required action).

Design

Two participants sat in front each other at a table with the thumb and index finger of participants' right hands in a closed pinch-grip posture on the two starting position switches fixed to the table. Before starting the VTI task, the experimenter explicitly told the participants to take turns in performing a motor task, while responding to a visuo-tactile stimulation. In the motor task either participant was required to grasp and lift the target object up to a height of about 5 cm above its original position with the right hand. They were instructed to grasp the object using a precision grip by placing their thumb onto the front of the object and their index fingertip onto the back of the object, in correspondence of the marked landing position. After lifting the object, the participants had to put it down on the support and get the right hand back to starting position.

Regardless of who grasped the target object, in each trial both participants were instructed to discriminate location of the tactile stimulus. Both participants had to respond as fast as possible to the administered tactile stimulus, ignoring a task-irrelevant (congruent or incongruent) visual stimulus from the target object. Therefore, each participant had to report the tactile stimulus during trails in which s/he had to perform him/herself the action (Action execution) as well as during trials in which the peer had to perform the action (Action observation). Simultaneous visual-tactile stimulation was delivered randomly between trials: (1) before the movement onset phase, i.e., when the grasping hand is still immobile at the starting position switch, or (2) at the moment onset phase i.e., at the beginning of the grasp movement, where movement initiation was detected by the release of the starting position switch. Before the beginning of each trial, a recorded voice randomly called the participant who had to perform the motor task (TAH or TOH for participant 1 or 2, counterbalanced across subjects). Each trial started with an auditory warning signal after a random delay (800-1200 ms). After a further variable delay (1500–2200 ms) a second auditory signal constituted the GO for the motor task.

The task consisted of two VTI blocks of 128 trials each, where spatially congruent (in half of the trials) or incongruent (in the remaining half) VT stimulation was randomly delivered. For each type of (congruent and incongruent) spatial arrangement, VT stimulation was given in half of the trials prior to or, in the other half at the beginning of, one's or the peer's action. In the first block participants took turns to grasp one of the two objects assigned to one of the participants (Mine condition), while in the second block they took turn to grasp the other object assigned to the other participant (Other's condition, counterbalanced across subjects). After the first block they took a break (5 min). All subjects underwent a practice session with each object.

Assessment of empathy

After the VTI session, each subject completed the Interpersonal Reactivity Index (IRI; Davis, 1983). IRI measures on a 5-step Likert-type scale various facets of dispositional empathy through four scales of 7 items each (two cognitive scales, namely perspective-taking and fantasy, and two affective scales, namely empathic concern and personal distress):

1) The perspective-taking scale (PT) measures the reported tendency to adopt spontaneously the psychological point of view of others (e.g. 'I sometimes try to understand my friends better by imagining how things look from their perspective');

2) The fantasy scale (FS) measures the tendency to imaginatively transpose oneself into fictional situations (e.g. ‘When I am reading an interesting story or novel I imagine how I would feel if the events in the story were happening to me’);

3) The empathic concern scale (EC) assesses the respondents’ feelings of warmth, compassion and concern for others (e.g. ‘I often have tender, concerned feelings for people less fortunate than me’);

4) The personal distress stress scale (PD) assesses self-oriented feelings of anxiety and discomfort resulting from tense interpersonal settings (e.g. ‘being in a tense emotional situation scares me’).

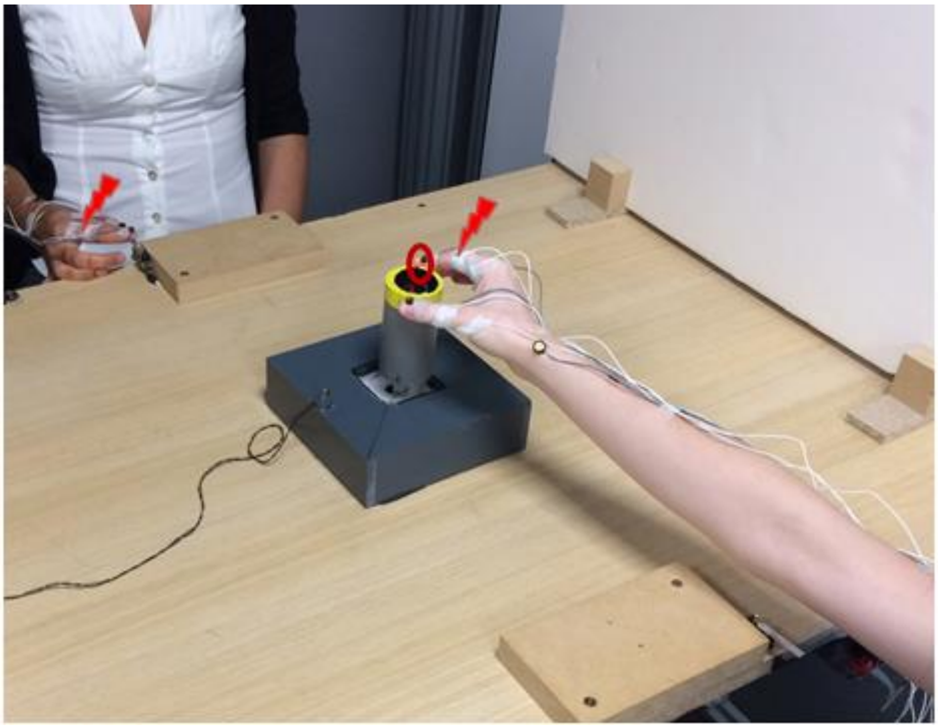


Figure 7.1 Experimental setup: view of one participant grasping the target object with a precision grip configuration in front of the other participant. Electro-cutaneous targets (red zaps) were delivered to the index finger (as shown in the picture) or thumb of both participants, while a visual distractor (with red circle emphasizing the LED locations) could be presented from either the same (congruent) or different (incongruent) location.

7.1.2 Statistics

To assess the effects of object ownership on the PPS dynamics, we calculated the VTI on corrected trials as the difference between RTs for spatially incongruent and congruent VTI trials, as this difference quantifies the strength of the interaction between visual and tactile stimuli. A three-way ANOVA was conducted with within-subject factors of Phase (before vs. onset movement), Action (execution vs observation), and Ownership (mine vs. other's).

For the motor task, the primary kinematic parameters for the transport and grip components of the movements were analysed to assess potential differences in the movement profile across conditions. A series of three-way ANOVAs was conducted with Spatial congruency (congruent vs. incongruent), Phase (before vs. onset movement), and Ownership (mine vs. other's) as within-subject factors. Separate ANOVAs were performed for both latency and amplitude of acceleration, deceleration and velocity peaks (transport component) as well as for MGA and VGA peaks (grip component). Two further ANOVAs were run for movement reaction time and the duration of the grasping movement. Hereafter, effect sizes are reported in terms of partial eta squared (η^2_p), and averages are reported along with the standard error of the mean (SEM). Newman-Keuls post hoc tests were used when appropriate to explore significant effects.

Lastly, as a final goal of the present study was to explore the relationships between empathy and PPS remapping during observed actions, we computed a series of separate Pearson product moment correlations between each IRI scale and VTI in action observation conditions.

7.1.3 Results

Visuo-Tactile Interaction (VTI)

Overall, a significant action-dependent modulation of VTI was observed, as revealed by the main effect of phase, $F(1,30)=8.83$, $p=.006$, $\eta^2_p=.23$. Participants displayed greater VTI at the onset (26±5 ms) than before movement (11±3 ms). Crucially, this effect was modulated by ownership during execution and observation of action, as witness by the significant highest order interaction, Phase by Action by Ownership $F(1,30)=15.78$, $p<.001$, $\eta^2_p=.35$. Post hoc test showed that, as compared to before the initiation of the overt movement (4±5 ms), VTI was enhanced when the participant's hand started moving to grasp one's own object (35±9 ms, p=.013). In sharp contrast, such a VTI modulation during action execution was not found when the target was instead the object assigned to the peer (before 11 ±5 ms vs. onset 19±9 ms, p=.64). During action observation, an increased VTI emerged at the beginning of the observed movement (37±6 ms) with respect to before (5±6 ms, p=.008), but only when the peer's hand started to grasp his/her own object. Conversely, no action-dependent change in VTI was detected when the participant observed the peer interacting with participant's object (before 23 ±6 ms vs. onset 12±6 ms, p=.40; Figure 7.2).

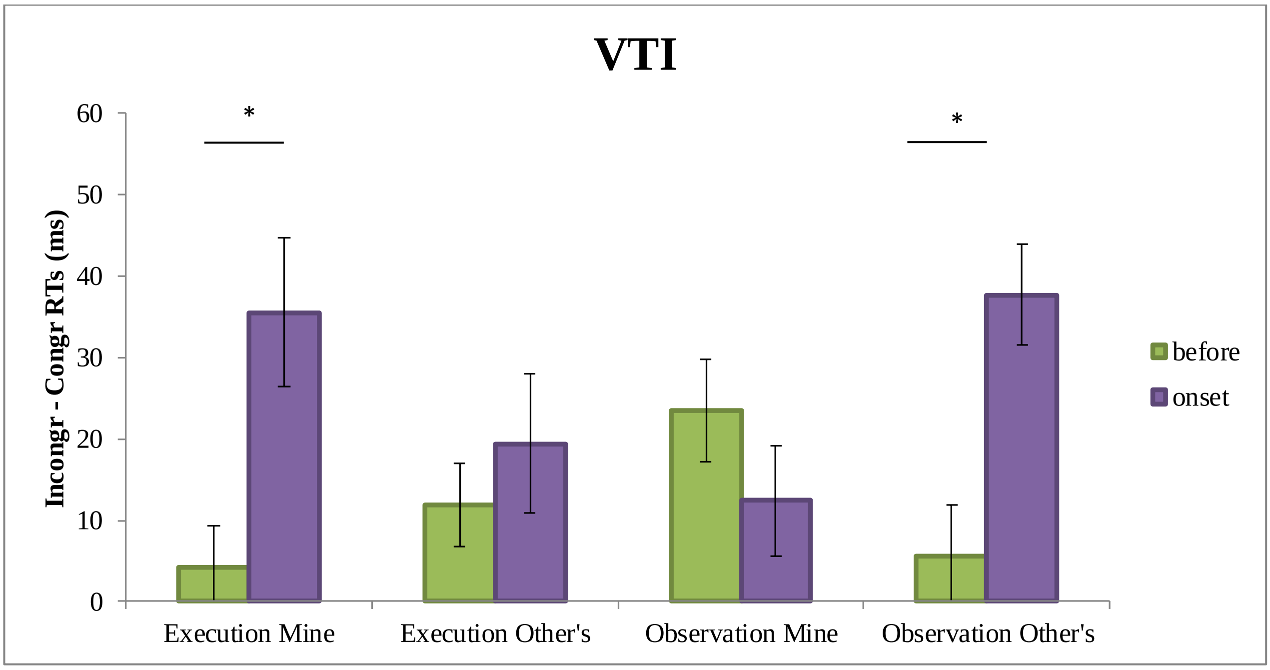


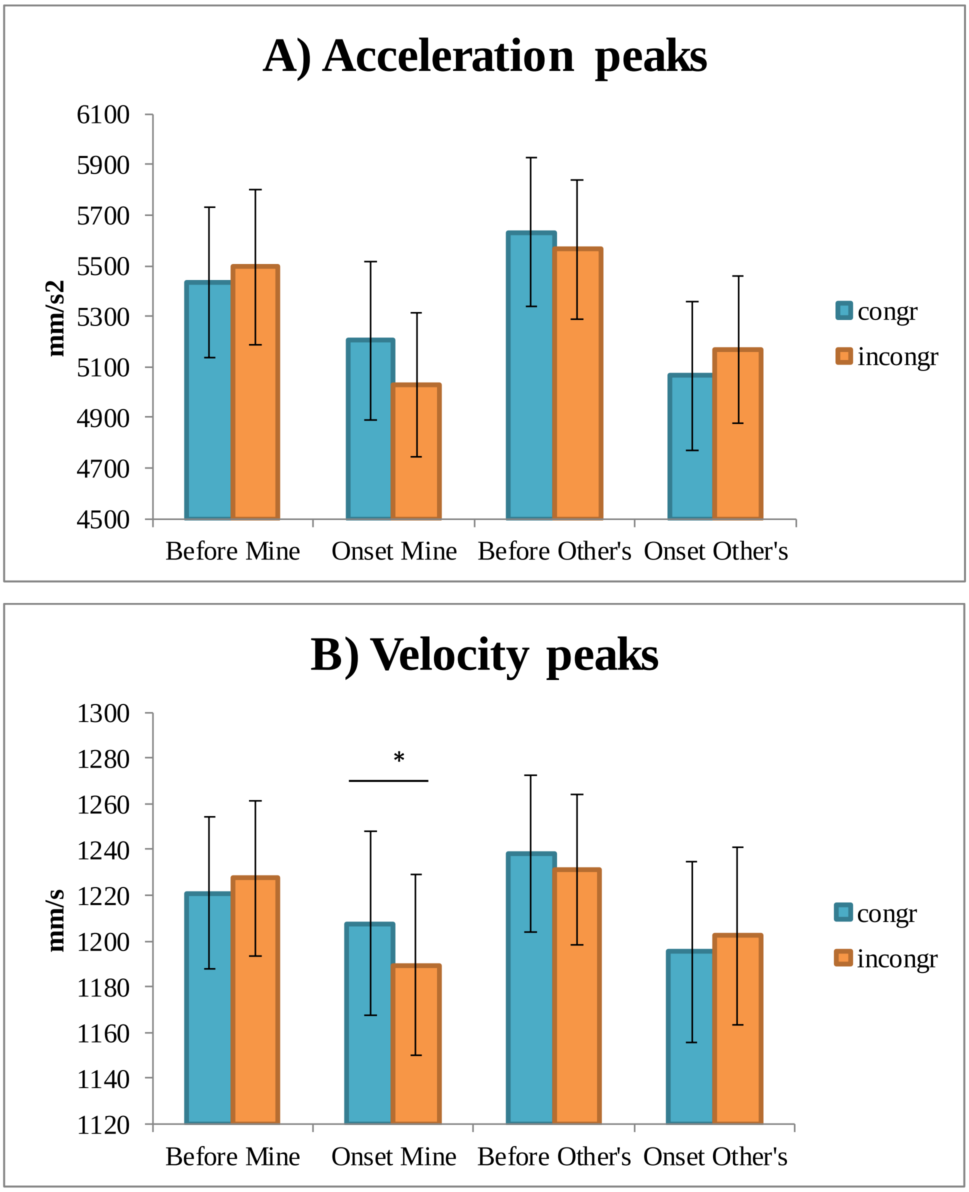
Figure 7.2 Bar plots (with SEM) show the modulation of VTI (incongruent minus congruent RTs difference) as a function of Phase (before vs. onset movement), Ownership (Mine vs. Other's) and Action (execution vs. observation). Asterisks indicate significant differences between VTI before and at the onset of the grasping movement when the participant executes the action toward one's own object (Execution Mine) and when the participant observes the peer's action toward the peer's object (Observation Other's).

Motor performance

Transport component

Kinematic analyses showed a consistent effect of phase for both latency and amplitude of peaks of all the transport component parameters (*acceleration latency*, F(1,30)=39.27, p<.001, η^2_p=.57; acceleration peak, F(1,30)=29.10, p<.001, η^2_p=.49; *velocity latency*, F(1,30)=27.98, p<.001, η^2_p=.48; *velocity peak*, F(1,30)=4.97, p=.033, η^2_p=.14; *deceleration latency*, F(1,30)=17.23, p<.001, η^2_p=.36), with the only expectation of amplitude of the *delectation peak* (F(1,30)=1.68, p=.20, η^2_p=.05). When VT stimulation was delivered at the onset of the movement, rather than before, movements displayed delayed and lower acceleration (*acceleration latency:* onset 224±10 ms vs before 194±8 ms; *acceleration peak*: onset 5117±290 mm/s2 vs before 5531±283 mm/s2), velocity (*velocity latency*: onset 399±14 ms vs. before 366±11 ms; *velocity peak*: onset 1199±39 mm/s vs before 1229±32 mm/s), and deceleration wrist peaks (*deceleration latency*: onset 555±18 ms vs. before 515±13 ms).

More interestingly, the effect of phase on the maximal amplitude of transport component parameters was modulated as a function of object ownership and spatial congruency of VT stimulation (*acceleration peak*, F(1,30)=8.56, p=.007, η^2_p=.22; *velocity peak*, F(1,30)=11.11, p=.002, η^2_p=.27; *deceleration peak*, F(1,30)=11.89, p=.002, η^2_p=.28). The Phase by Spatial congruency by Ownership significant interactions were explained by the fact that the movements in the incongruent trials, as compared to the congruent trials, were characterized by decreased *acceleration* (incongruent =5030±285 mm/s2 vs. congruent = 5203±313 mm/s2, marginally significant p=.082), *velocity* (incongruent =1190±40 mm/s vs. congruent = 1208±40 mm/s, p=.020), and *deceleration peaks* (incongruent =-4708±299 mm/s vs. congruent =-4908±312 mm/s2, p=.019) when the actions started toward the owned (belonged or whatever we decide for the paper) object. On the contrary, the remaining comparisons for the transport component parameters did not differ (all ps > .14, see Figure 7.3). No other significant main effect or interaction was observed.



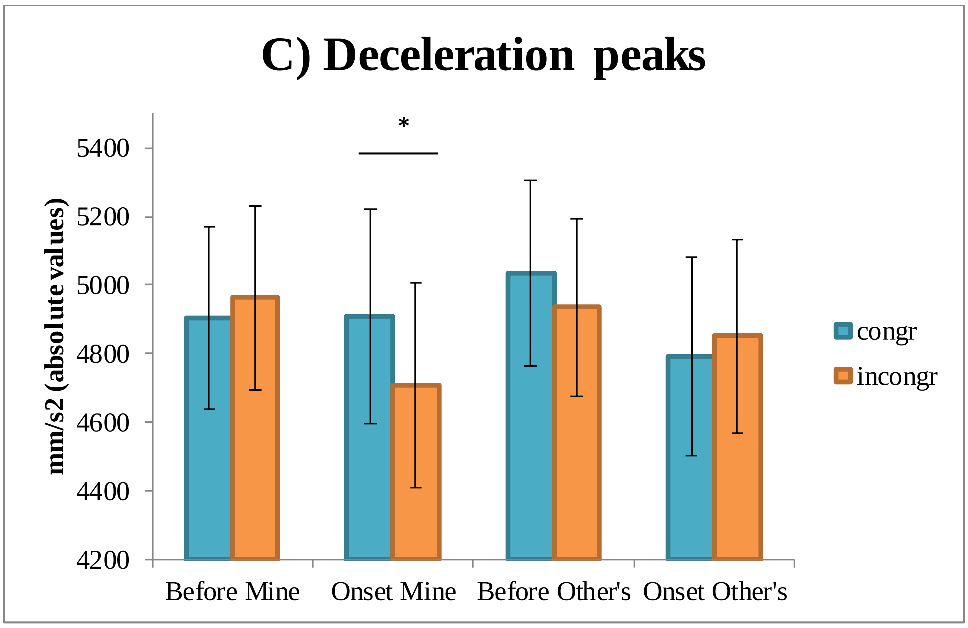


Figure 7.3. *Bar plots (with SEM) display the Acceleration (A panel), Velocity (B panel), Deceleration (C panel) peaks of the transport component of the grasping action, as a function of Spatial congruency (congruent or incongruent), Phase (before vs. onset movement), and Ownership (Mine vs. Other's). Asterisks indicate significant differences between maximal amplitude of velocity (B) and deceleration (C) peaks reached when congruent or incongruent VT stimuli were administered at the onset of the movement toward one's own object (Onset Mine). The same tendency was found in acceleration peaks (A, congruent vs. incongruent Onset Mine p=.08)*

Grip component

The phase of VT stimulation also affected distancing the thumb and the index finger during the grasping movements (latency MGA, F(1,30)=18.57, p<.001, η^2_p=.38; MGA, F(1,30)=6.21, p=.019, η^2_p=.17). Participants displayed a longer latency and wider maximum aperture of their finger when multisensory stimuli were delivered at the onset of the movement rather than before (latency: onset 673±27 ms vs before 623±18 ms; MGA: onset 93±1 mm vs before 91±1 mm). This main effect of Phase on MGA latency interacted with Spatial congruency of stimuli (F(1,30)=4.27, p=.048, η^2_p=.12) and, more relevant, the two factors significantly interacted with Ownership (F(1,30)=5.11, p=.031, η^2_p=.15). Post-hoc tests showed the maximum aperture of the fingers occurred later when incongruent, rather than congruent, VT stimulation was delivered when the participant's hand started moving towards one's own object (incongruent= 675±27 mm, p=.010 vs. congruent= 662±26 mm), whereas no difference emerged between congruent and incongruent VT trials in all the remaining comparisons (all ps>.25; see Figure 7.4) No other statistically significant effect was found.

Movement reaction time and duration of the grasping movement

The main effect of Phase significantly affected movement RTs from the Go signal (F(1,30)=104.08, p<.001, $\eta^2{}_p$=.78) . Motor RTs were slower when stimulation occurred at the onset of the movement (480± 13 ms) rather than before (373±11 ms). No other factor statically modulated the movement RTs. Duration of the moment was similarly affected by the phase (F(1,30)=7.58, p=.010, $\eta^2{}_p$=.20). The effect of Phase was modulated by Spatial congruency of multisensory stimuli (F(1,30)=6.36, p=.017, $\eta^2{}_p$=.18) and, once again, the three factors significantly interacted (F(1,30)=4.89, p=.035, $\eta^2{}_p$=.14). Indeed, the duration of the movement toward one's one object was longer in incongruent, as compared to congruent, trials only when VT stimulation occurred at the movement onset (incongruent 863±31vs. congruent= 834±30 p=.010, p>.75 for the other comparisons, see Figure 7.4).

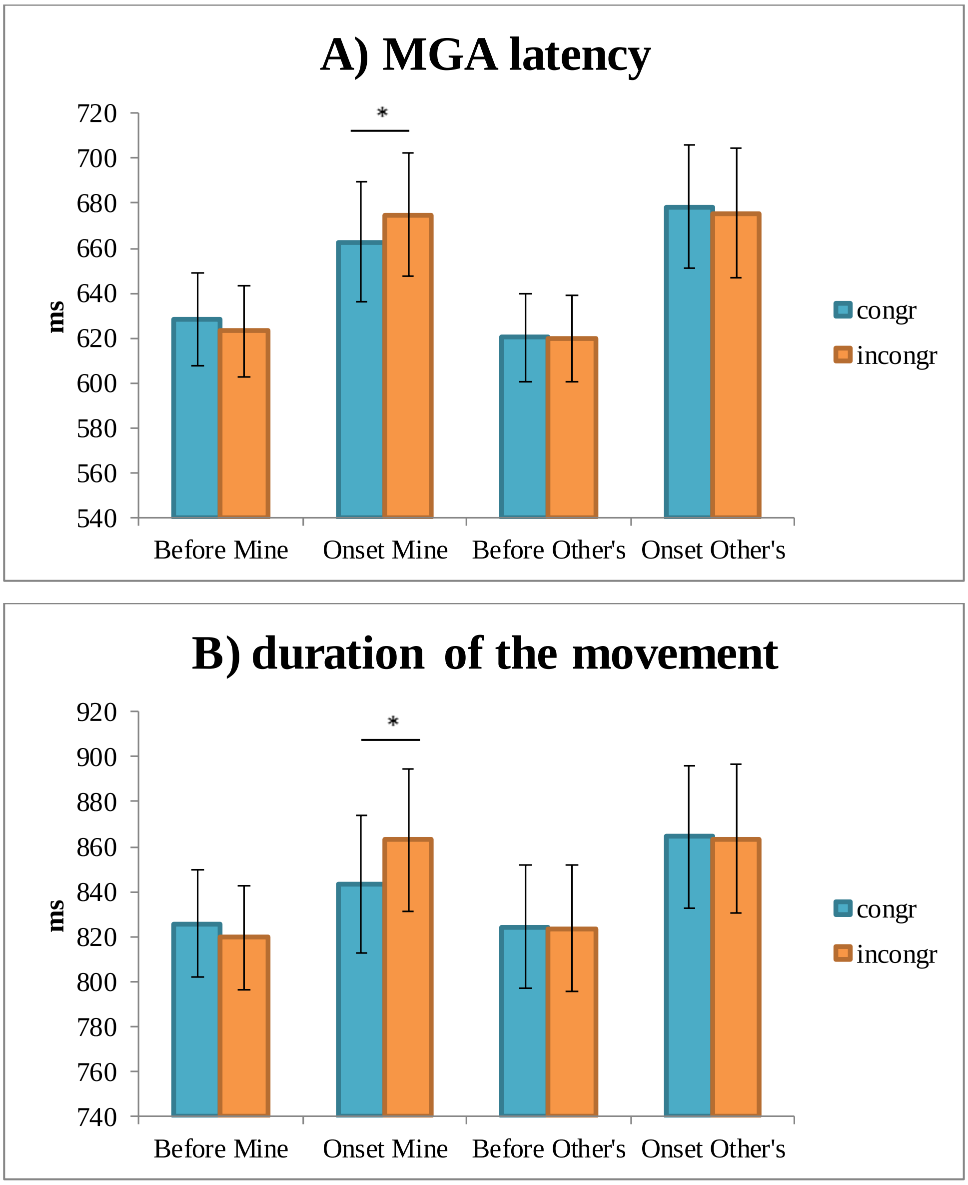


Figure 7.4. *Bar plots (with SEM) show latency of MGA (A panel) and duration of the whole grasping action (B panel) as a function of Spatial congruency of stimuli (congruent or incongruent), Phase (before vs. onset movement), and Ownership (Mine vs. Other's). Asterisks indicate significant differences between congruent or incongruent trials when VT stimuli were administered at the onset of the movement toward one's own object (Onset Mine).*

Correlations between Interpersonal Reactivity Index (IRI) and visuo-tactile interaction (VTI)

Correlation analysis revealed a selective association between Interpersonal Reactivity Index (IRI) and visuo-tactile interaction (VTI) during observation conditions. In particular, there was a positive correlation between PD and VT performance only when stimulation was delivered at the beginning of the peer's action toward his/her object (r=.40, p=.026, see Figure 7.5), but not before (r=.33, p=.07). VTI did not correlate with any other IRI scale (all |r|s<.31, all ps>.08).

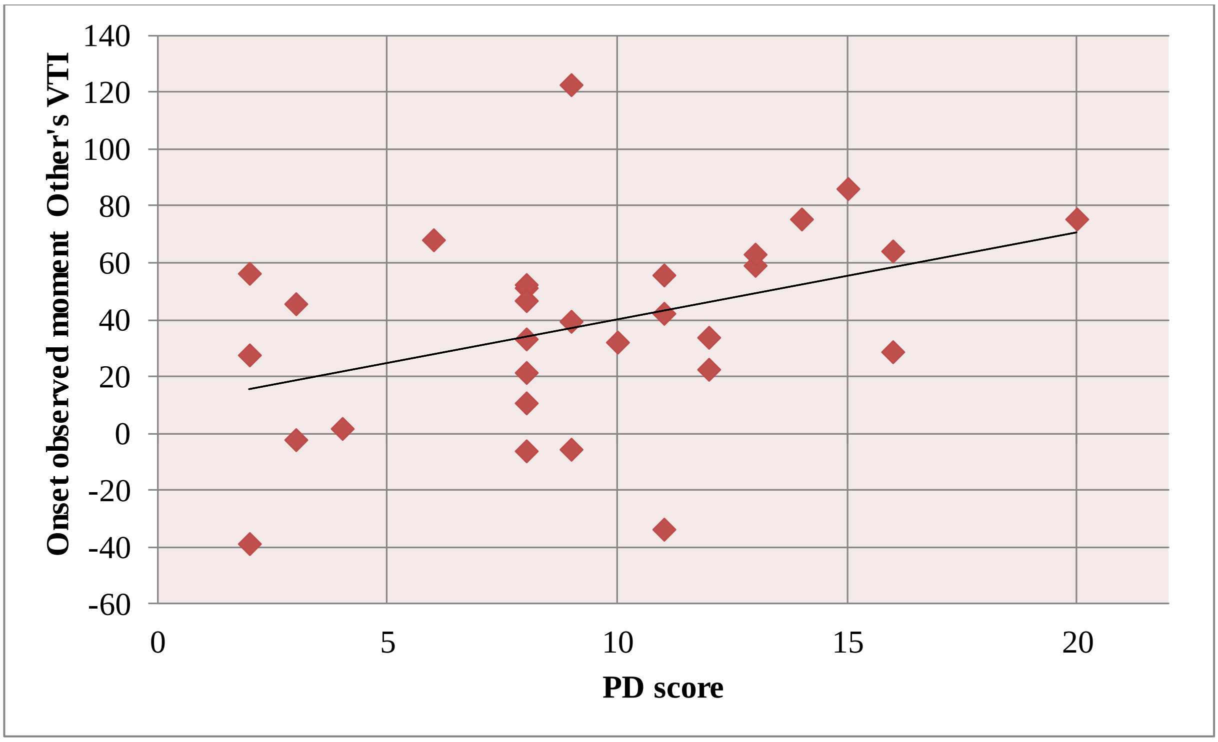


Figure 7.5 *Scatter plots (with best-fitting regression line) showing VTI displayed when observing the peer initiating movements toward his/her object (Onset Observed movement Other's) as a function of Personal Distress (PD) scores.*

7.1.4 Discussion

This study explores for the first time the impact of object ownership on multisensory-motor processing underlying the PPS representation. To test the effects of acquired arbitrary ownership on PPS remapping, we examined the dynamic relationship between visual signals from “owned” objects and tactile signals on the hand during action. Consistent with previous evidence (Brozzoli et al. 2009, 2010, see also the second charter), visual signals from the target object affects perception of touches more strongly at the beginning than before grasping action unfolding. However, here we revealed that this action-dependent VTI changes arose only when the participants performed movements toward the object that had been previously (and arbitrarily) assigned to themselves, resulting thus as “their object” (mine condition). In fact, this difference in terms of VTI before and during action disappeared when the participants reached for and grasped the target object that had been assigned to the peer in front of them (other’s condition). To note that two objects were given (and not chosen by the participants) at the same time and were identical aside from a colour band denoting the ownership. Nonetheless, arbitrary assignment of objects to ownership category, namely “mine” or “other’s”, was found to subsequently modulate the increase in real time of VTI during initial phase of action. Such increased VTI when the hand moved, compared to when it was immobile, indicates a modulation of PPS boundaries: when the target of the action was an object “owned” by the participant, it was remapped within PPS as soon as the hand moved to grasp it. On the contrary, attributing the ownership of an identical object to the peer was sufficient to abolish PPS remapping, as indicated by the lack of VT changes when acting on the peer’s object.

This is in line with a previous study demonstrating that ownership influences visuomotor interactions with other’s propriety by suppressing the affordances evoked by other’s object (Constable et al. 2011). Specifically, participants made judgments about stimuli that were presented on the handles of mugs that had previously been assigned ownership to either themselves or the experimenter. Standard stimulus–response compatibility effects were normal when the mugs belonged to themselves but were abolished when they belonged to the experimenter. However in that case, the “other” contrasting the “mine” condition was the experimenter, who remained in the room but did not actively participate in the task. In our experiment participants were instead tested in pairs and they each owned one of the two target objects. This dyadic setting allowed us to extent previous findings by documenting a potent influence of ownership status in a more ecological situation when the owner is not a detached (or imagined) “other”, but the peer standing in front of us.

Interestingly, the power of such a modulation emerged during observation conditions, i.e., when participant were not required to grasp the action target. Even though the participant’s hand was not moving, an increased VTI occurred when the peer was executing a grasping movement toward his/her own object (other’s condition): visual events from the peer’s object interacted with touch perception on the participant’s immobile hand. In particular, we detected a stronger VTI when observing the peer starting the movement, as compared to before. Crucially, if the target of the acting peer’s action was the observer’s object (mine condition), no difference in terms of visuo-tactile strengthening arose when contrasting VT performance before vs. at the onset of the observed movement. That is, the same self-owned object that was remapped within PPS during active execution of grasping actions did not affect one’s PPS when observing another agent interacting with one’s own propriety. Nevertheless, action-dependent modulation of one’s PPS was instead triggered when observing the other acting on his/her own propriety: the same observation condition with the only exception of a different ownership status.

Here it is worth noticing that these findings cannot be interpreted in terms of different deployment of attention resources across conditions (for reviews see Plasher, 1994, Carmela et al., 2017). One could indeed argue that the VTI changes during actions could be a mere epiphenomenon of the fact the brain is currently performing a dual task: participants execute the action and at the same time discriminate touches on the acting hand. Another could also argue that the more participants were close to begin the action, the more they were paying attention to the target object location (Mason et al., 2015; for a review see Baldauf and Deubel 2010). However, we consider unlikely an interpretation of our results in terms of attentional resources for two main reasons. First, no change in VTI emerged when the target was owned by the peer, despite the participant was simultaneously performing both the perceptual VTI task and the motor task. Second, and more striking, an increased VTI was found during observation, namely when the participant was not required to move their hands.

In addition, the effects of our simple yet critical ownership manipulation were not limited to perceptual VTI: kinematic patterns of movements were indeed critically influenced by ownership status of the to-be-grasped object. Just as the strength of the VTI, quantified as the difference between RTs for incongruent and congruent VT trials, was enhanced at the instant of movement initiation, the kinematic profile differed between congruent o incongruent VT trials when stimulation occurred at the movement onset. Again in parallel with the VTI, this modification in movement kinematics was found only when grasping the object possessed by the acting participant. Namely, kinematic analyses consistently showed decreased maximum amplitude of the acceleration, deceleration and velocity peaks for incongruent as compared to congruent trials at the onset movement toward one’s target. Likewise, when contrasting the same experimental conditions, maximum grip aperture of the fingers displayed later latency in incongruent rather than congruent trials. Finally, despite having similar motor reaction times from the go signal, the participants performed grasping movements that lasted longer if incongruent rather than congruent VT stimuli were presented at the initial phase of the action directed toward one's own object.

Notably, these selective changes in kinematic parameters could not be interpreted in terms of joint action - that is, when individuals interact together to achieve a joint goal, by coordinating their actions (e.g., Sebanz et al., 2006). In our study, participants either performed their own grasping actions or passively observed the other person's actions, in randomly interleaved trials. That is, participants took turns and never acted at the same time upon the same object within a trial, not for a common aim. Individuals' actions were here undertaken at different times, not coordinated in any way, and the observed action was not relevant to a participant's own subsequent action. Worth noticing, only one out of the two objects was presented in each block and the attributed ownership was mutually exclusive, i.e. the same target was categorized as self-owned object for one member of the experimental pair (mine condition) and, at the same time, as other-owned object for the other member (other condition). Moreover, the finding that the kinematic profile diverged only when movements were performed towards one's own object clearly rules out the joint action account.

In sum, attributing ownership did affect specifically visuo-tactile processing as well as kinematic pattern of the movement itself. As soon as VT perception of congruent or incongruent stimulation started to diverge at the onset of a movement to act upon the self-owned object, the profile movements differed also. Such a modulation was disclosed for the transport as well as for grip component parameters, albeit to different extents: in the former case ownership status selectivity affected amplitude peaks, whereas in the latter case only latency of the maximum index-thumb distancing. This finding can be considered, to the best of our knowledge, as the first striking and remarkable link multisensory perception of PPS and kinematic pattern of the action.

In addition, multisensory perception during action observation was selectivity associated with a specific facet of empathy. The increased of VTI while watching the peer starting the action toward his/her object correlated with self-reported tendency to experience discomfort in distress situations: the more VTI, the higher Personal distress score. This result would therefore suggest the "social" effects induced by the potentially simulated action on PPS could be linked to dispositional emotional empathy.

7.2 Experiment 2

In the first study PPS remapping was found only when acting upon own propriety (mine condition) and a similar remapping on one's PPS was also revealed when observing a peer acting on his/her own propriety (other's condition). In the second study we aimed at further exploring such a interesting modulation due to the ownership status. The question motivating our second inquiry is quite straightforward: what happens to multisensory-motor processing of PPS when the target object belongs to the two agents involved? If the target is attributed to both participants of the experimental pairs, the "owned" object should be simultaneously experienced as "mine" and as "other's". We should accordingly expect a PPS remapping, as index by VTI, not only when grasping but also when observing the other grasping the shared object. As in the previous study, kinematic movements should again mirror the VTI performance with selective changes when VT stimulation occurred at the onset of the movement. Also, the VTI during observed condition could be associated to dispositional empathy. Lastly, to corroborate effectiveness of our manipulation and, at the same time, to assess the dual (i.e., mine and someone else's) nature of shared ownership (i.e., ours), we asked participants to explicitly report their feelings of ownership by the means of an ad hoc questionnaire.

7.2.1 Methods

Participants

A statistical power analysis based on data from the previous study was performed for sample size estimation. On the basis of power analysis, we set a target of 14 same-sex pairs. Twenty-eight healthy participants (12 women men, 16 men, mean age= 22.93 years, SD=3.53 years) with normal or corrected-to-normal vision took part in the study. All participants were right-handed but one ambidextrous as assessed by the Edinburgh Handedness Inventory (mean score: 72. 42, SD=22.90) and had no history of neurological or psychiatric disorders. They were naive as to the experimental hypotheses being tested and provided written informed consent to participate. The study was approved by the Inserm ethics board and complied with the ethical standards outlined in the Declaration of Helsinki (World Medical Association, 2013).

Design

The procedure was similar to Experiment 1 with the following exceptions. Before starting the experimental session, each participant in a pair received three glass-shaped objects. The three objects were physically identical, aside from the (blue or yellow or green) colour band placed on the upper part that served to mark the grasp landing positions. Participants were told they each owned one of the two (yellow or blue) glasses (the mapping of colour to attribute individual ownership of the two objects was counterbalanced between participants). The third (always the green) glass was assigned to both participants by saying that they both owned the green glass. After explicitly assigning the three objects (i.e., mine, other's, ours), the experimenter asked participants to bear object in mind for the whole duration of the experiment. Before starting the experimental VTI task all participants had a practice session of 25 trials for each object (the order was counterbalanced across participants). After a break, participants performed the experimental VTI task with the green object only (128 trials). At the end of the VTI task they were asked to complete a questionnaire to assess their perceived feeling of ownership over the shared green object. At the end, Interpersonal Reactivity Index (Davis, 1983) was administrated.

Ownership questionnaire

An ad hoc questionnaire was administered to measure self-report feelings of ownership over the shared object thought self-anchoring scaling. Items were 9 sentences in which possession of the objet and agent (i.e. the subject of the verb) describe different relations of participant-object propriety. Specifically, sentences were instances of three predicative possessive constructions in which ownership of the shared object was ascribed to either one or the other agent or to both agents (i.e., the possessive adjective was my/his-her/our own). For each possessive construction the action was ascribed to either one or the other agent or to both agents (i.e., the subject was I /the person in front of me/ the person in front of me and I), thus resulting in a 9 possible combinations. Participant was therefore asked if "I had the feeling that the object that I/the person in front of me/ the person in front of me and I were grasping during the experiment was of my/his-her/our own". Participant had to indicate how well each sentence described his/her feelings by marking a 20 cm-long horizontal line in which the extreme left represents "strong disagreement" and the extreme right represents "strong agreement". The items were randomly administered. Experimenter remarked that all the sentences were referred to the share object.

7.2.2. Statistics

Similar to the previous study, to examine the effects of shared object ownership on the PPS changes, a two-way ANOVA was conducted with within-subject factors of Phase (before vs. onset movement), Action (execution vs observation) on VTI. If shared object ownership triggers a similar PPS remapping while executing or merely obverting actions directed to the target, we should expect an increased VTI at the action start, as compared to before, in execution as well as in observation action conditions.

For the motor task, a series of two-way ANOVAs was conducted with Spatial Congruency (congruent vs. incongruent) and Phase (before vs. onset movement) as within-subject factors on the kinematic parameters: latency and amplitude of acceleration, deceleration and velocity peaks (transport component) as well as for MGA (grip component). Two additional ANOVAs were run for movement reaction time and duration of the grasping movement. All together, these analyses were aimed to test whether spatial congruency of multisensory stimulation could congruently affect not only VTI but also the kinematic profile of grasping movements toward the shared target.

As complementary evidence for the efficacy of our manipulation, an ANOVA was computed on the average score of the ownership questionnaire taking Agent (I vs. the peer vs. we) and Possession (mine vs. peer’s vs. ours) as with-in subject factors.

Lastly, we performed a series of separate Pearson product moment correlations between each IRI scales and VTI in the two action observation conditions (i.e. before and onset observed movement).

7.2.3 Results

Visuo-Tactile Interaction

Analysis revealed an overall significant action-dependent modulation of VTI, as indicated by the main effect of phase, F(1,27)=13.11, p=.001, η^2_p=.33. Regardless of whether the participant was moving or observing the peer moving, greater VTI were found at the onset (37±7 ms) than before movement execution (14±5 ms). Indeed, since the two-way interaction was not significant, F(1,27)=0.39, p=.54, η^2_p=.01, the increased VTI at the beginning of movement was present during both action execution (before 15 ±6 ms vs. onset 41±11) and action observation (before 15 ±7 ms vs. onset 32±6 ms, see Figure 7.6).

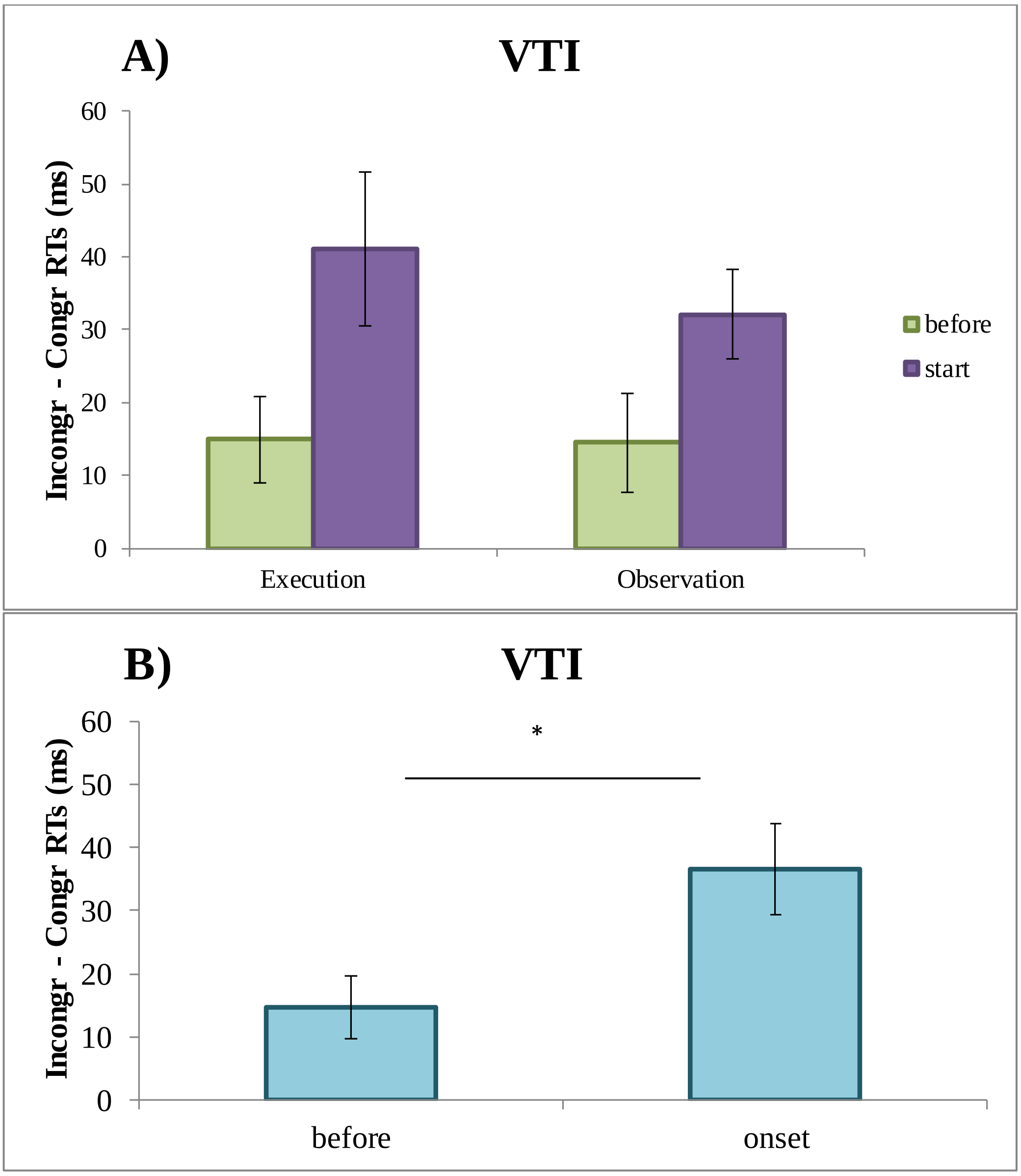


Figure7.6 Bar plots (with SEM) show the modulation of VTI (incongruent minus congruent RTs difference) as a function of Phase (before vs. onset movement), and Action (execution vs. observation). A) The upper graph displays the not significant interaction of Phase (before vs. onset movement) by Action (execution vs observation). B) The lower graph displays the significant main effect of Phase (before vs. onset movement). Asterisk indicates significant differences between VTI before and at the onset of the grasping movement.

Motor performance

Transport component

The effect of Phase emerged in the peak latencies of all the transport component parameters (*acceleration latency*, F(1,27)=20.07, p<.001, η^2_p=.43; *velocity latency*, F(1,27)=22.22, p<.001, η^2_p=.45; *deceleration latency*, F(1,27)=13.50, p=.001, η^2_p=.33), as participants reached the relative peaks later when VT stimulation was delivered at the beginning of the movement, rather than before (*acceleration latency*: onset 216±11 ms vs before 186±9 ms; v*elocity latency*: onset 357±11 ms vs before 326±10 ms; *deceleration latency*: onset 501±14 ms vs before 5469±12 ms). The same significant effect was accordingly found for the *peak* amplitudes of the *wrist acceleration*, F(1,27)=7.90, p=.009, η^2_p=.23, with decreased maximum peaks at the onset (6470±274 mm/s2) with respect to the before movement conditions (6999±338 mm/s2). The Spatial congruency impacts on the *deceleration peak* amplitude only (F(1,27)=5.66, p=.025, η^2_p=.17), resulting in decreased peaks in incongruent trials (incongruent=-5984 ±275 mm/s2; congruent = -6097±286 mm/s2).

Interestingly, the Phase by Spatial congruency interaction affected amplitude of the peaks of the transport component parameters of the movements (marginally significant trend in *acceleration peaks*: F(1,27)=3.36, p=.078, η^2_p=.11, *velocity peaks*: F(1,27)=7.14, p=.013, η^2_p=.21, *deceleration peaks*: F(1,27)=4.57, p=.04, η^2_p=.15). Post hoc analyses revealed that spatial incongruent VT stimulation, as compared to congruent one, delivered at the moment onset produced lower *acceleration* (incongruent =6362±261 mm/s2 vs. congruent = 6577±3293 mm/s2, p=.011), *velocity* (incongruent =1351±33 mm/s vs. congruent = 1374±32 mm/s, p=.001), and *deceleration wrist peaks* (incongruent =-5864±281 mm/s2 vs. congruent = -6115±274 mm/s, p=.034, see Figure 7.7). Finally, the Phase by Spatial congruency interaction was found to be significant for the latency of the *acceleration peaks*, F(1,27)=4.63, p=.04, η^2_p=.14, as there was tendency to increased latency in incongruent, (219±12 ms) compared to congruent, trials (212±10 ms, p=.07) if VT stimuli were administrated at the onset of the grasping movement . No other statistically significant effect was found.

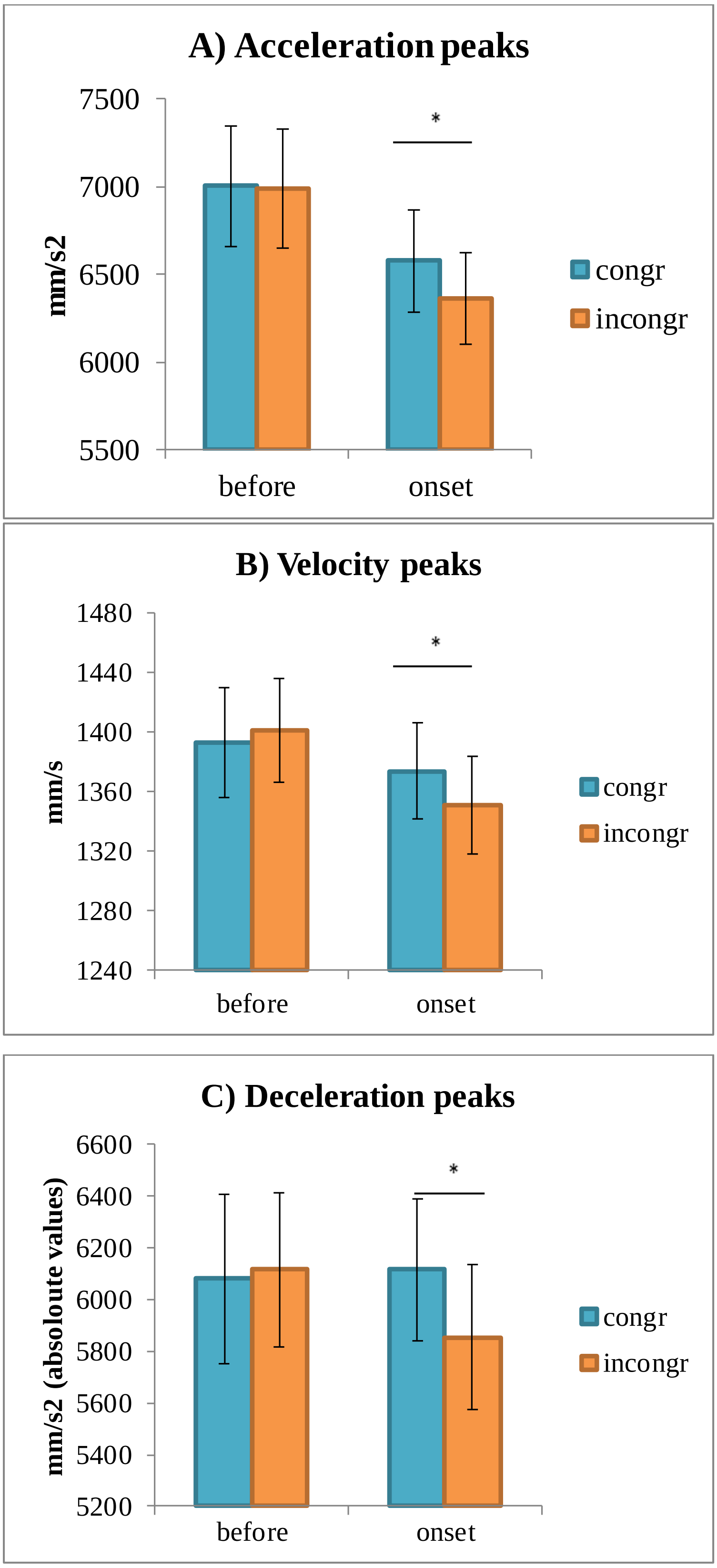
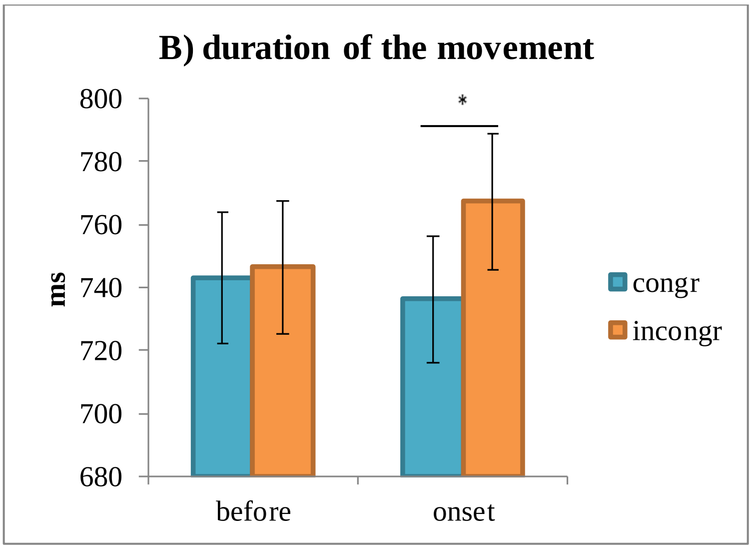


Figure 7.7 Bar plots (with SEM) show the Acceleration (A panel), Velocity (B panel), Deceleration (C panel) peaks of the transport component of the grasping action as a function of Spatial congruency of stimuli (congruent or incongruent) and Phase (before vs. onset movement. Asterisks indicate significant differences when congruent or incongruent VT stimuli were administered at the onset of the movement.

Grip component

The Phase and the Spatial Congruency of VT stimuli affected latency of the maximum thumb -index finger distance during the grasping movements (main effect of Phase: F(1,27)=7.10, p=.012, η^2_p=.21; main effect of Spatial congruency, F(1,27)=4.55, p=.042, η^2_p=.14). Participants displayed longer latency when stimulation was administered at the beginning of the movement (571±17 ms) rather than before (before 545±16) and when a spatially incongruent (560±16 ms), rather than a congruent (555±16 ms), VT stimulation was presented (560±16 ms). Interestingly, the two factors significantly interacted (F(1,27)=4.64, p=.04, η^2_p=.15). Post-hoc testes showed the maximum aperture of the fingers occurred later when incongruent (577±17 ms), rather than congruent (566±17 ms), VT stimulation was delivered as soon as participants' hand started moving (p=.006), while no difference emerged between congruent and incongruent VT trials before movement onset (p=.97, see Figure 7.8). No one of the factors being exanimated affected MGA peaks during grasping movements.



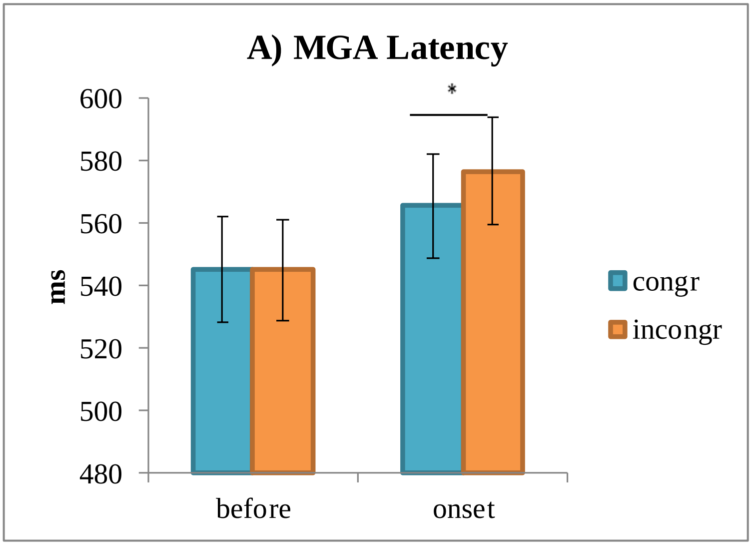


Fig 7.8. Bar plots (with SEM) show latency of MGA (A panel) and duration of the whole grasping action (B panel) as a function of Spatial congruency of stimuli (congruent or incongruent) and Phase (before vs. onset movement). Asterisks indicate significant differences between congruent or incongruent trials when VT stimuli were administered at the onset of the movement.

Movement reaction time and duration of the grasping movement

The main effect of Phase significantly modulated movement RTs from the Go signal (F(1,27)=54.48, p<.001, η^2_p=.68) , since they were slower in trials where VT stimulation was administrated at the onset of the movement (458± 13 ms) rather than before (358±16 ms). Duration of the whole moment was marginally affected by the phase (F(1,27)=3.74, p=.063, η^2_p=.12). Additionally, The effect of Phase interacted with the Spatial congruency (F(1,27)=12.02, p=.002, η^2_p=.31), since the duration of the grasping action was longer in incongruent (767±21 ms), as compared to congruent (736±20 ms), trials only when VT stimulation occurred at the beginning of the movement (p<.001, see Figure). No other significant main effect or interaction was detected.

Ownership questionnaire

Analysis on the questionnaires revealed a main of effect of Possession, F(2,54)=17.68, p<.001, η^2_p=.39, as the object was overall perceived as belonging to both members of the experimental pair (ours= 13.41±1.13) rather than belonging to one of the two members (mine=8.02±1.03, peer's =5.536±0.77, ours vs. mine or peer's ps<.001; mine vs. peer's=.072). More interestingly, the feeling of possession was moderated by the Agent (F(4,108)=9.95, p<.001, η^2_p=.27). First, whomever the action of grasping was referred to, the object was perceived as belonging to both members of the pair: whether the subject of the action was the participant (13.23 ±1.2), the peer (13.23±1.21), or both the agents (13.78±1.17), the feeling of "our" shared ownership did not differed (ps>.58). Second, participants reported higher scores of perceived "our" shared ownership as compared to perceived individual ownership (i.e. mine and peer's), regardless of whom was the referred agent of the action (all ps<.005). Even more remarkably, participants felt the target as being more of their own when the action was attributed to themselves (the object I was grasping was of my own= 10.05±1.36), rather than to the peer (the object the person in front of me was grasping of my own =6.83±1.20) or to both (the object the person in front of me and I were grasping was of my own=7.18±1.23, ps<.013). Conversely, participants tended to attribute object ownership more strongly to the peer when the action of grasping was referred to the peer (the object the person in front of me was grasping was of his/her own= 8.76±1.14), than to participants themselves (the object I was grasping was the of his/her own = 3.98±0.90) or to both the agents (the object the other person and I were grasping was of his/her own = 3.86±0.71, p<.001, see Figure 7.9).

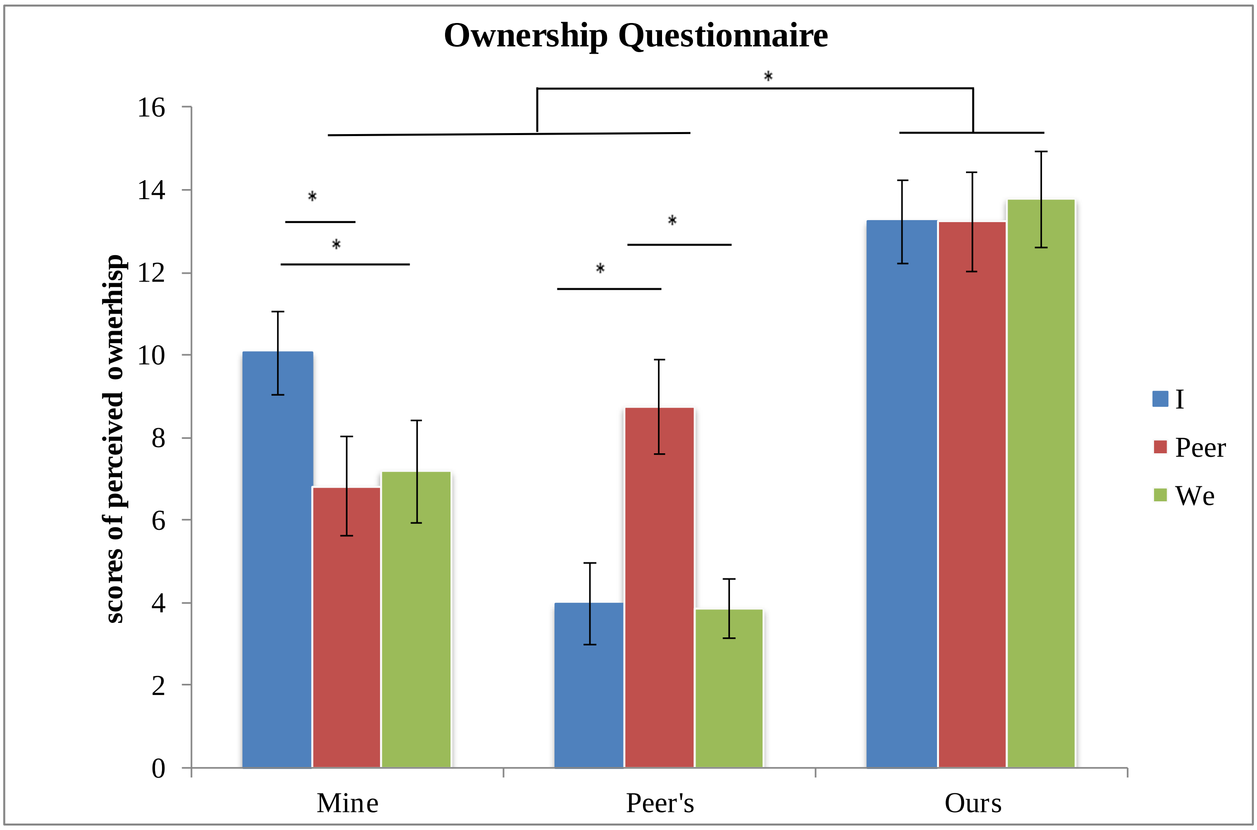


Figure 7.9 Bar plots (with SEM) display scores of the self-reported feelings of possession (Mine vs. Peer’s vs. Ours) over the object as a function of the Agent (I vs, the Peer vs. We). Asterisks indicate significant differences among conditions. Overall, participants perceived the object as “ours”. However, participants perceived it as more their own object (Mine) when they were the agents (I), and more of other person (Peer’s) when the peer was the agent of the action (Peer).

Correlations between Interpersonal Reactivity Index (IRI) and visuo-tactile interaction (VTI)

Correlation analysis found a positive association between Personal Distress (PD) scale of IRI and VTI when multisensory stimulation was delivered only at the onset of the peer's movement (r=.42, p=.027, see Figure 7.10), but not before (r=.04, p=.85). No other correlation was observed between VTI and the remaining scales (all |r|s<.31, all ps>.11).

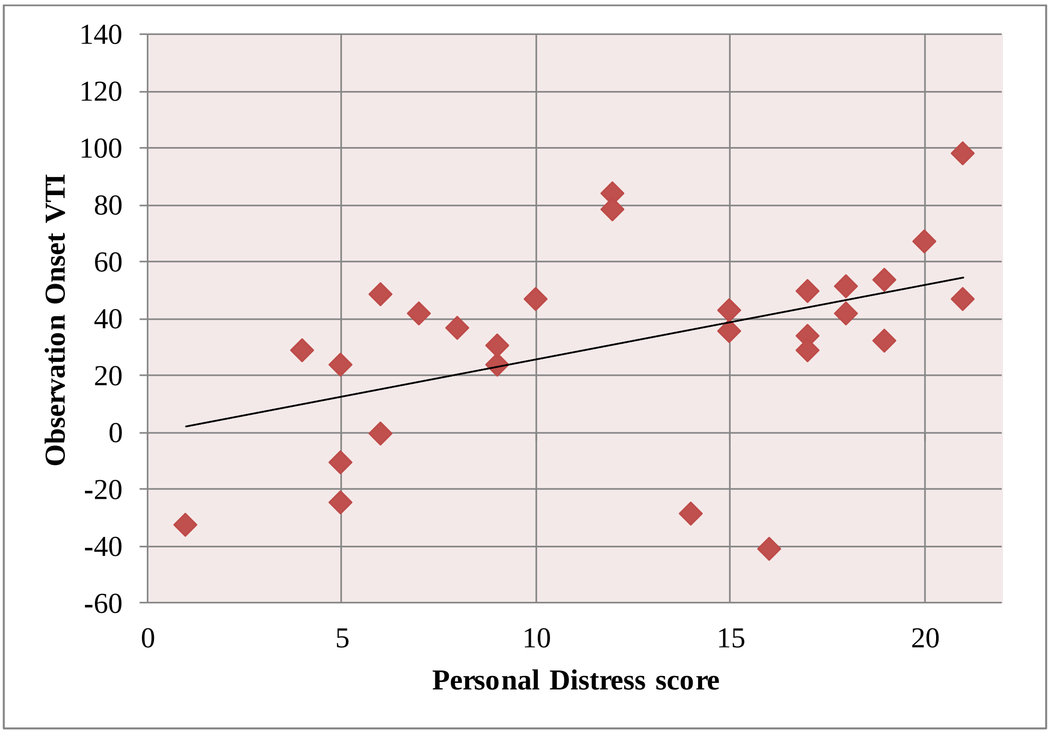


Fig 7.10. Scatter plots (with best-fitting regression line) showing VTI when observing the peer starting the movement (Onset Observed movement) as a function of Personal Distress (PD) scores.

This follow-up experiment was designed to address a relevant issue: how ownership over an object belonging to two actors can "shape" the multisensory-motor interactions between the body and the object itself. By assessing the interaction between visual information coming from the to-be-grasped object and tactile processing on the acting hand, we demonstrated that PPS remapping takes place as soon as one of the two agents initiated the movement to interact with the shared object. In other terms, either executed or observed by participant or the peer, the action directed toward the object previously assigned to the pair triggers a PPS modulation. A relative increase in VTI was detected not only when the participant but also the peer was about to grasp the shared target. Such an increased VTI at the onset of movement indicates that the shared object, located far from the initial hand position, was remapped within one's PPS as soon as one's own or the peer's hand moved to grasp it.

Such modulations of PPS boundaries during execution as well as observation were present in the previous experiment but with two different object ownerships. The action-dependent changes of VTI during action unfolding were indeed found to occur if the target object was assigned to the participant (mine condition), but not if an identical object was assigned to the peer (other's condition). Also, participations displayed a similar enhanced VTI when merely observing the peer initiating the action toward the object assigned to peer (other's condition), but not to the participants themselves (mine condition). In the current experiment we revealed that such effects during execution and observation could jointly occur if the target is at the same time "my" and the "other's" object, that is, if the target is "ours".

Corroborating our hypothesis, results from questionnaires importantly add to these behavioral findings, in that they support the effectiveness of "our" manipulation and shed insight into the nature of such a shared ownership. Indeed, participants perceived the object as truly belonging to both members of the pair: they reported similar feeling of shared ownership either when one or the other or when both members were interacting manually with the target object. Intriguingly, this feeling of shared possession seems to depend on a joint contribution of the two individual (mine and other's) ownership categories. Albeit the shared "our" ownership is still predominant, individual "one's own ownerships" is emphasized when the action is ascribed to one of the two social actors involved. If the participant is the agent of the grasping action, the target is more attributed the mine ownership category, if the peer is the agent the target is more attributed to other's ownership category. This could explain why we unveiled a PPS remapping when the participant was to actively grasp the shared object: from the first experiment we can infer that such action-dependent PPS modulation can emerge as long as the object is actually perceived as being "mine". The same reasoning can explain why we also disclosed a similar PPS remapping when the participant observed the peer grasping the shared object: we can infer that PPS boundary changes during observed action can emerge as long as the shared object is perceived as being "other's own".

Kinematics data further confirm the hypothesis that object ownership is more attributed to the participants when they physically interact with it. Just like for the movements toward one's own object recorded in the first experiment, the kinematic parameters were similarly modulated by both the phase and the spatial congruency of VT stimulation. The phase of stimulation constantly modulated all the kinematic parameters, especially their latencies. Most interesting, the movements differed mainly when a congruent or incongruent VT stimulation was presented at the beginning of the action: the spatial arrangement of multisensory stimuli resulted in different pattern kinematics only when VT stimuli were administrated during, but not before, movement onset. Specifically, results from the transport component of the grasping action reveled decreased maximum amplitude of the acceleration, deceleration and velocity peaks for incongruent as compared to congruent trials delivered at the onset movement. Likewise, maximum grip aperture of the fingers displayed later latency and, more generally, the whole grasping movements lasted longer if incongruent rather than congruent VT stimulation was presented as soon as the hand moved. As a whole, such differences in movement profile across conditions mirror those observed in the first experiment when participants were grasping the object they "owned", suggesting that object that is shared between the two actors (ours) is, at least partially, experienced as one's own (mine).

Finally, another internally replicated result appears to point to complex and mutual relationships between multisensory perception-action and social interactions: conceptual ownership and emotional responses seem to be entangled in this intricate loop. We consistently found that the increased VTI while observing the peer during the initial phase of his/her grasping action correlated with self-reported tendency to experience discomfort in distress situations: the more VTI, the higher Personal distress score.

7.3 Discussion

Ownership is an important component of social interactions. Accordingly, scholars have recently explored the possibility that knowledge of possessions could have an impact upon our sensorimotor system and on the relationship between action and perception. Since ownership influences how individuals physically interact in a given environment, it is important to understand how ownership status affects the arena of our daily body(ies)-object interaction: the PPS. In this regard, it is indeed surprising that, so far, there has been no attempt to examine the impact of object ownership on the multisensory-motor processing underling the coding of the space around us. The last experimental contribution of this dissertation is aimed at filling this gap.

In the first experiment we showed that minimally attributed object ownership selectivity shape PPS boundary. In particular, if the target of the action, located beyond PPS, "belongs" to the participant, the owned object is remapped within PPS as soon as the hand moved to grasp it. Under the very same conditions, no PPS remapping occurred if the hand was moving to grasp the peer's objects. Fascinatingly, action-dependent PPS modulation emerged again when simply observing the peer acting on his/her own object. Hence, these findings pose two main questions: 1) why (and how) may attributed ownership affect relatively low-level perception-action processes? 2) how may observation of another person unfolding an action produce perceptual changes similar to those induced by a self-produced action? In the following session I offer some tentative of answer to these relevant questions.

There are a variety of factors that may influence the individual's bias for self-owned compared to other-owned objects, including the *mere exposure effect* (which refers to the concept that familiarity of an object increases an individual's preference for that object, see Zajonc, 1968), visual cues of physical control like spatial proximity to an object or temporal priority in seeing it, (Scorolli et al., 2014), amount of touch (Peck and Shu 2009; Wolf et al., 2008) and physical action (Truong et al., 2016). Aware of these possible additional factors, our design was aimed at controlling for potentially confounding variables that could account for different VT and motor modulations. First at all, we gave and assigned objects' ownership at the same time to both participants of the experimental pairs. No particular emphasis was given to ownership: the experimenter just explicitly assigned the two objects by explaining that the participants would own and use the two assigned items for the whole duration of the experiment. Second, we kept the duration of time during which the participants were exposed to the two stimuli equal across all conditions. Third, the objects were placed at equal distance from the starting positions of each participants' hand (and from the whole body). Last, the participants had to follow external instruction as to when taking their turn (unpredictable random order) to grasp the object, again ensuring an equal amount of action and possession manipulation.

Despite minimalist and equal possession attribution, ownership affected profoundly both sensory and motor processes of the dyad, constituently across two experiments. Here I suggest that this is possible simply because acquiring possession over an object establishes a special association with the body self. Ownership is generally experienced as involving self–object relations and, in keeping with James's original insight, there seems to be a continuum between the core self, which depends on body ownership, and the extended self, which encompasses extracorporeal possessions. Thus, self-owned item can be considered as symbolic expressions of the body self. One could even be tempted to speculate that owning an object might eventually prove to be somewhat similar to body-ownership (e.g. Blakemore and Frith, 2003; Gallagher, 2000), given the inextricable link between the self and property (James, 1890). On that note, Porteous (1976) claimed that there are three satisfactions that derive from ownership: (a) control over space per se, (b) personalization of space as an assertion of identity, and (c) stimulation (achieved, for example, by thinking about, using, improving, or defending one's possessions–territory). It is tempting to speculate that the abstract social construct of ownership is therefore grounded in the representation underlying the action space between the body and the object. Consequently, our naturalistic and indirect interactions with property can be massively influenced so that, for instance, the action target, despite being far from the hand, is remapped within PPS only if it belongs to the agent. Instead, this modulation does not arise if PPS is "informed" that the action target belongs to another social actor. Noteworthy, observing another actor acting on his/her property generates a remapping similar to what was found during execution of own action toward own property. Here I will suggest that such an interesting finding can be interpreted in the light of the putative "mirror-like" properties of PPS.

Mirroring refers to the apparently similar neural processing of observed actions as for self-made actions, particularly within regions of the brain previously thought of as selectively coding motor control, i.e. self-made actions (di Pellegrino et al. 1992, Fabbri-Destro and Rizzolatti 2008; Heyser 2010). Thus, observing an action performed by another individual evokes a motor and somatosensory-related activation in the observer's brain that is akin to that which occurs during the planning and effective execution of that action (I refer to this as 'simulation'). Indeed, when we observe an action for instance, we simulate the observed behavior within our own motor system (Rizzolatti and Craighero, 2004, Rizzolatti and Sinigaglia, 2010). However, we do not only simulate observed motor behavior, we also simulate observed somatosensory events within our own somatosensory systems, for instance when seeing someone in pain (Bufalari et al., 2007; Lamm et al, 2011; Riĕcanský et al., 2014) or observing someone being touched (Keysers et al., 2004, 2010;

Blakemore et al., 2005; Schaefer et al., 2012; Ebisch et al., 2008). Importantly, motor and somatosensory events usually do not occur in isolation in a social environment. When we observe somebody grasping an object, for example, this also involves the observation of somatosensory events (i.e. the person touching the object). Therefore, it is not surprising that functional magnetic imaging studies have yielded evidence for the involvement of somatosensory brain areas in action observation (action-based somatosensory simulation). While these findings suggest that the somatosensory consequences of observed actions are simulated jointly to the motor component thereof (Keysers et al., 2010; Gazzola and Keysers, 2009; Avenanti et al., 2007), direct evidence for this comes from a recent study investigating the specificity of action-based somatosensory simulation (Deschrijver, et al, 2016). The authors presented index or middle finger tapping movements of a human or a wooden hand, while simultaneously presenting 'tap-like' tactile sensations to either the corresponding or non-corresponding fingertip of the participant. By comparing processes of action-based somatosensory simulation with felt touch, the authors showed that an interaction between the two was present at an early stage of somatosensory processing [P50, N100 and N140 sensory evoked potentials (SEPs)] and at a late stage of higher-order social processing [P3-complex]. While the former process may reflect simulative/mirror mechanism, the latter one may reflect higher-order self-other distinction by signaling simulated action-based touch that does not match own tactile information (in this case when watching tapping movements of a wooden hand).

The same processes could potentially be employed also when touch perception interact with visual processing. That is to say, VTI involved in the PPS representation could be established even simulating the other's action. This is in accordance with recent findings supporting the existence of neurons that code PPS with mirror-like proprieties, which are active for sensory stimuli both in one's own PPS and in the PPS of others. In non-human primates, it has indeed been revealed the existence of bimodal parietal neurons which encode sensory events occurring in the space around the monkey's own hand, as well as the space around another individual's hand (Ishida et al., 2010), and similar findings have recently been reported in human premotor cortex (Brozzoli et al., 2013). Specifically, a single cell recording study by Ishida and colleagues (2010) showed bimodal neurons located in the VIP that responded not only to tactile or visual stimuli delivered within the PPS of the monkey, but also to visual stimuli presented within the PPS of the experimenter facing the monkey- in this case the mapping was occurring in the visuo-tactile domain. This provides first evidence for the existence in the macaque's brain of a mirror mechanism that allows the animal to map stimuli delivered within the PPS of another individual onto its own PPS. In humans, Brozzoli et al. (2013) identified a region within the left ventral premotor cortex likely containing peripersonal neurons with mirror proprieties: these neurons encode a physical visual stimulus in hand-centered coordinates regardless of whether the visual physical stimulus is near the participant's own hand or someone else's hand. This finding indicates that the human ventral premotor cortex contains a low-level common representation of the space around one's own hand and another person's hand- in this case, however, the mapping was tested in the visual domain only.

Yet, no study has documented a behavioral modulation of PPS with mirror-like properties. Here we demonstrated for the first time that action-dependent VTI changes could similarly arise when overtly performing the movements as well as when observing the same movement performed by someone else. Such remapping may possibly incur the benefits of the putative mirror proprieties of PPS. Once again, this distinctive multisensory-motor processing is modulated by object ownership status so that it occurs when observing the other person interacting with his/her propriety. Just like the self-owned object is remapped within one's own PPS, the other-owned object is similarly remapped if the other person acts upon it, probably through simulation processes trigged by observation of the other' s action. These mechanisms can contribute to social cognition, being, at least partly, based on co-representing other people's actions and sensations in brain areas dedicated to experiencing these ourselves (Gallese et al.; 2004; Jaeger et al., 201; Uddin et al., 2007; Gallese 2009). PPS could thus be just one of the multiple systems our brain is endowed with to interact in our environment with socially relevant stimuli, be it a socially connoted object or another individual. Indeed, whether considered to be a shared or individual property, possession over an item is critical for the PPS dynamic properties to emerge, both when acting in first person and when merely observing a peer acting on her own belonging.

Related to this, one last issue needs to be addressed, namely the correlation between VTI during observation of the peer's action and the scores of one scale of IRI. Previous research has already demonstrated an intruding link between the ability to empathize with others and perception of the action (Gallese and Goldman, 1998, Kaplan and Iacoboni 2006; Gazzola et al., 2006; Pfeifer et al., 2008; Lamm and Majdandzic 2015; Biard et al., 2011). Here we disclosed a positive association of VTI during observation only with the Personal Distress scale, which measures the emotional response one experiences when watching someone else experience strong emotion. This scale is considered as being an emotional component of empathy (David, 1983). In this regard, recent evidence suggests that there are two possible systems for empathy: a basic emotional contagion system and a more advanced cognitive perspective-taking system (Preston and de Waal, 2002; Decety and Jackson, 2004; Leiberg and Anders, 2006; Lamm et al., 2007; Shamay-Tsooty et al 2009). These two systems are partially independent and, more interestingly, the emotional empathic sub-processes are involved in simulation and mirroring (Gallese, 2003, 2005; Kaplan and

Iacoboni, 2006), whereas the cognitive sub-component plays a critical role in 'mentalizing' or 'Theory of Mind' (Gallagher and Frith, 2003). While neuroimaging studies have been increasingly capable of characterizing the neural networks involved in emotionally and cognitively based empathy (Hynes et al., 2006; Vollm et al., 2006; Schulte-Ruther et al., 2007), a recent lesion study tested directly the neuroanatomical and behavioural double dissociation existing between these two components (Shamay-Tsooty et al., 2009). The study showed that a necessary area, critically involved in the emotional component of empathy, is area 44, which is roughly considered as the homolog to the F5 region in the monkey brain (where the first population of neuron mirror population was identified). This would thus corroborate the hypothesis that the internal simulation of others' action is thought to support the ability to empathize with others (Gallese 2003).

Within this enriched framework, the relation between VTI and PD may suggest that emotional component of empathy could be an additional variable that links spatial perception, action observation and execution in social interactions. Further studies are, however, needed to confirm and better qualify this relationship.

Overall, the findings from the first experiment were replicated in the second investigation where we pushed forward our social manipulation. By assigning ownership of the target object to both the participants of the experiment pair, we disclosed that multisensory interactions are dynamically enhanced during action, no matter if the action is really executed or simply observed. Because of the shared (i.e., my + your) nature of this belonging/property, in the second experiment we demonstrated the joint action of both individual ownerships upon the same object. Such a dual heart of the shared property is captured not only by the PPS sensory-motor changes, but also by the reported feelings of ownership over the target. Indeed, perception of "our-ness" seems to be constituted by two components: one that I refer to as "mine-ness" and second one that I refer to as "your-ness". Specifically, feeling of mine-ness would appear to emerge if the grasping action upon the target is attributed to the self. In other terms, although the mutual target is overall perceived as being "our own", there would seem to be a tendency to attribute the object to the self when the social actor is performing a voluntary action upon the joint object. On the other hand, the tendency to attribute the object to other people, i.e., feeling of your-ness, would emerge when the other individual is physically interacting with target. In this particular case, both the observer and the agent would congruently assign object ownership to the person that is about to manipulate the object: the observer would perceive feeling of yourness over the shared target, while the agent feeling of mineness. In this context, ownership would therefore evoke a sensorimotor-based simulation or mirroring of the interaction with the object in the observer's brain, by reenacting the visuo-motor, affective and social experiences one has when interacting oneself with the object. In light of these speculations, it is reasonable to suggest that ownership, as a social construct, may be embodied in the sensorimotor system, and through this embodied process, the target of ownership becomes a part of the individuals' 'extended sense of 'us'.

It should be noted that these findings could be considered as an empirical demonstration of what Pierce and Huver (2010) advanced: the emergence of shared possession. The development of a shared sense of ownership is seen by the authors as dependent upon person-object, other-object, and person-to-person interactions. Such emergence of collective feelings hinges on a collective recognition of shared action and control over the potential target of ownership. This could occur through a shift in the personal reference from the self (i.e., a personal feeling that the target is MINE) to "us" by including others (i.e., the personal sense that the target is OURS).

Before concluding I would like to cite again Pierce et al.'s work (2009), where the authors suggested that there may be a reciprocal relationship between psychological ownership and some territorial behaviors. The personalization of space, for example, might be seen as a way of simultaneously claiming and exercising control over a target (i.e., the act of claiming may be seen as a means of exercising control over an object); thereby, contributing to the eventual emergence of experienced control over the target and subsequent experiences of ownership for that target. This sense of ownership may then result in subsequent marking (control- and identity-oriented) and/or defensive (anticipatory and reactionary) territorial behaviors as suggested by Brown et al. (2005). At this point for the reader it should be quite clear the parallel with PPS. Although the shared (interpersonal) or collective (in-group) ownership are yet unexplored field, in this final session I put forward several hypothesis and speculated about the possible mechanisms though which these social constructs could emerge. All these hypotheses will need to be tested empirically in future research.

Chapter VIII: Conclusions and perspectives

> "Dicebat Bernardus Carnotensis nos esse quasi nanos, gigantium humeris insidentes, ut possimus plura eis et remotiora videre, non utique proprii visus acumine, aut eminentia corporis, sed quia in altum subvenimur et extollimur magnitudine gigantea"
>
> "Bernard of Chartres used to say that we were like dwarfs seated on the shoulders of giants. If we see more and further than they, it is not due to our own clear eyes or tall bodies, but because we are raised on high and upborne by their gigantic bigness"
>
> Joannes Saresberiensis

The idea that distinct regions of space relative to the body are represented differently by the brain might at first sound odd, given that we generally perceive the space around us as continuous. Yet, in a continuum from fundamental to applied research, many significant scientific contributions in interdisciplinary research fields such as cognitive neuroscience and social psychology support the view that we construct functionally distinct representations of space. Among these, the zone that surrounds the body is of paramount importance, not only for humans but also for any living organism. We closely monitor the objects (both animate and inanimate) that enter into this arena, as we monitor our own limbs as they extend beyond the boundaries of the immediate body space to interact with objects in the outer world.

In the neurocognitive field, such a space is captured by the concept of PPS. Thirty years after neuroscientific research has established the peculiar status of closeness for multisensory-motor interactions, definition of this portion of space has remained quite vague, allowing for many variations. Moreover, its functions are still a matter of current discussion. Only recently, in fact, this issue has been addressed in the literature, in the lights of the confusion that *surrounds* this notion, especially when comparing results reported in social psychology and in cognitive neuroscience.

Thus, on account of this on-going debate, we first provided clear support to the hypothesized function of PPS, that is, to inform the motor system for accurately guiding actions towards objects in the nearby space. This idea was actually posited formally 20 years ago (Rizzolatti et al., 1997) and, in fact, evidence described above (Chapter I) seems to support the involvement of some PPS areas in reaching and grasping. Yet, a clear demonstration of a prominent role of PPS in the control of actions is still lacking. Critical support for this hypothesis would derive from evidence that PPS plastic changes occur before rather than after movement onset. Hence, in the first study (Chapter II) we critically tested for this hypothesis and its prediction and we report behavioural evidence for an updating of PPS visuo-tactile interaction that anticipates overt movements, occurring as early as during the action planning. Specifically, our results showed that enhancement of multisensory interaction between visual signals from the action target and tactile signals from the acting hand started in the planning phase. This result is in line with the hypothesis that planning to grasp an object induces a modulation of PPS boundaries such that the action target, despite being far from the hand, is coded was it was within PPS. These findings thus support the notion that multisensory processing of PPS serves a functional role by contributing to the control of voluntary appetitive actions. Despite the novelty of the result, it remains a behavioural investigation. Any direct evidence would come from electrophysiological studies in the monkey, recording from bimodal cells in a grasping set. Nevertheless, the results from this study allow putting forward several hypotheses that need to be tested in more detail in future studies building on the present findings. For example, we suggested that modulation of multisensory perception occurring in the planning phase of a grasping action might arise from activity within the premotor-parietal network involved in the multisensory hand-centred representation of PPS. Given this intriguing overlap, a fMRI investigation could critically test the new experimental hypothesis we posit: multisensory changes originating during action planning may be coded at the level of the PPS representation. Following the same line of reasoning, a combined approach employing TMS and kinematic techniques could investigate whether perturbing the planning phase of the action (following interference of the aIPS-vPM, for instance) could result not only in alterned kinematics patterns but, more crucial, in a reduced remapping of PPS. Moreover, I believe that these combined approaches should place an emphasis on an important criterion for determining the underlying neural mechanisms: the precise timing of visuomotor transformations as well as of multisensory interactions during action.

In line with this, we also suggested that multisensory PPS remapping might reflect a continuous process that not only starts developing during action planning, but also evolves on-line during action execution to monitor and possibly adjust movements until their completion. From this perspective, we anticipate that multisensory interaction could undergo a decrease during later stages of action execution, despite the hand moving closer to the object from which visually interfering information originates. This is to say, remapping of PPS will be dynamically updated with respect to the motor command until such remapping is functional for the action unfolding If sudden or unexpected changes occur in the environment, PPS representation could be used to abort or inhibit preplanned movements that became useless, or to facilitate newly emerging movements. Such a mechanism might thus allow for the rapid selection of appropriate actions, for example when the position of a target object unexpectedly changes, or when we are unexpectedly required to avoid an approaching object (Makin et al., 2012). Finally, this mechanism could therefore account for both appetitive and defensive proposed function that space around the body.

More recently, it has been suggested a possible involvement of the multisensory PPS representation in the guidance of motor interactions **between** individuals. Needless to underline that our most meaningful interactions in the world take place with objects that are of emotional and motivational significance to us, e.g., other human beings. In the social psychology literature, the space around the body is termed IPS and has been defined as the ‘area individuals maintain around themselves into which others cannot intrude without arousing discomfort or even withdrawal’ (Hayduk, 1978, 1983; Sommer, 1969).

Because of some similarities between the two constructs and the their functions ascribed, scholars have recently looked with great interest at the possibility that the same underlying processes mediate interactions with both inanimate and animate objects within the space surrounding our body. Since some authors have therefore raised the question of whether PPS and IPS share some functional features, here we tested this hypothesis by taking advantage of another remapping of PPS, particularly that one induced by “typical” tool-use (Chapter IV). To this purpose, Reaching- and Comfort-distance tasks between two individuals, designed to respectively measure the PPS and the IPS, were carried out before and after a single tool-use session. The results show that tool-use ‘extends’ the PPS, as measured by the Reaching-distance task, but does not affect the social IPS, as measured by the Comfort-distance task. Contrary to most of the previous studies, which have suggested a communality between the action-related PPS and the social-related IPS, we thus disclose a dissociation in the plastic proprieties of PPS and IPS, suggesting that there may actually be no functional overlap between these sectors of space.

In a second study (Chapter V), we introduced a novel form of “social” tool-use setting in which a tool becomes an instrument for cooperating, to further test the hypothesized identity between PPS and IPS. This was done to overcome a potential limitation of the previous study. Indeed, one may have argued that IPS modulation was not observable because the classical tool-use manipulation was not ‘‘social” enough: Stressing the sensorimotor body-objects interaction might have thus endorsed only PPS plasticity, whereas IPS plasticity may require a more social context to emerge. In fact, in the second investigation both space were affected by the social manipulation, but they were actually directionally dissociated. The finding that social tool–use enlarge PPS BUT reduces IPS, inducing differential and opposite changes on each representation, clearly disconfirms the identity option. In accordance with the hypothesis that the functional properties of PPS and IPS may differ, we also demonstrated that perception of the space between conspecifics is selectivity influenced by different factors (namely, the arm length and the familiarity with the other) according to the spatial representation examined (namely PPS and IPS, respectably). If the arm length role in modulating the perceived reachable distance fits with previous findings and confirms a close relationship between body-action capabilities and PPS (e.g., Longo and Lourenco, 2007), one may have expected this factor to be involved also when regulating interpersonal social distances. On the contrary, here we disclose that only the perceived familiarity with the confederate correlated with IPS, another important piece of evidence indicating that the two spatial representations are not completely overlapping dimensions. Again, this is particularly interesting given that PPS was measured from a social perspective by asking to estimate the reachable to estimate the reachable distance with respect to a person, instead of an object.

In this regard, one could argue that the reachable space could be just one operationalization of PPS representation and that, related to this, the reachability is just one of the various tasks used to measure PPS. If one constrains the label ‘PPS’ to its physiologically inspired definition, i.e., the multisensory, body- part-centred representation of the space immediately, the reaching-distance task employed in our studies might actually test only the visual-motor aspects of the action space, rather that multisensory interaction between visual and tactile processing. Likewise, many other investigations conceive PPS as homologue of reaching space (see Ocelli et al., 2011 for a review, but also Cardinali et al, 2009b for a distinction between PPS and reachable space) and have therefore employed paradigms assessing visually the reachability of objects to assess PPS and its neural correlates (e.g., Gabbard et al., 2005; Bourgeois et al., 2014; Gallivan et al., 2009, 2011). Notwithstanding there is overlap in brain processing of PPS and reaching functions (Rizzolatti et al., 1997), reachability judgments might not necessary involve the multisensory network underlying PPS coding. Related to this issue, a recent fMRI study, aimed at investigating the neural correlates of reachability judgements, revealed fronto-parietal and cerebellum activity (Bartolo et al., 2014). This cluster also included the superior parietal occipital cortex (SPOC), an area that is recruited both in PPS coding (Gallivan et al., 2009) and in visual guidance of arm movements in humans (Cavina-Pratesi et al., 2010; Filimon, 2010; Filimon et al., 2009). Despite there being many challenges in establishing interspecies homologies, current evidence suggests that SPOC may be the human homologue of macaque V6A (Bosco et al., 2010; Cavina-Pratesi et al., 2010; Filimon et al., 2009). Hence, one could argue that reachability judgments could potentially rely more on the reach-related F2-MIP/V6a network than the F4-VIP and F5-7b circuits. Although we are aware of this potential limitation, we did choose such the reachability task to sensibly compare the effects of the same manipulation on both reachable and comfortable space, as a proxy of PPS and IPS respectably. It could be encouraging for further research to jointly assess the two constructs with several tasks. For instance, PPS has been investigated by multisensory interaction paradigms as well as by line bisection tasks, whereas IPS has been investigated also with simulation measures. Using multiple tasks to assess several aspects of each construct would provide stronger basis to ascertain whether that the two spaces are dissociated.

Furthermore, there are several ways in which future work can build upon these insights. In this regard, fMRI could also add crucially to this hypothesis. Integrating behavioural as well physiological measures along with fMRI can bolster our understanding of how humans experience peri- or inter-personal space perception. In this context, future studies could adapt Holt et al.'s (2014) and Perry et al.'s (2015) methods by modifying the fMRI task such that participants are required to indicate the point at which they are still comfortable during virtual approach and withdrawal. This would determine how the results from neuroimaging studies actually correspond to the results of the "real" comfort-distance paradigm. Comparing IPS preferences in a fMRI-friendly IPS task with preferences in the comfort-distance paradigm would allow one to substantiate that virtual and behavioral interpretations of IPS intrusion are indeed measuring similar constructs and to support the claim that the observed differences in neural activity are actually a result of monitoring IPS as opposed to just getting bigger and smaller or approaching and withdrawing (like in the original work by Holt et 2014). Physiological measures could critically corroborate the parallel between the simulated task in the scanner and the canonical comfort-distance paradigm. Such an approach integrating several measures would truly allow comparing the brain activation elicited by such an "ecological" fMRI-friendly IPS task with the brain action previously reported for PPS representation in humans. Adding on this, by using Brozzoli and colleagues' fMRI adaptation paradigm (Brozzoli et al., 2011, 2012), further investigations could disentangle whether the same neural populations actually code both social stimuli (such as faces or whole human bodies) and non-social stimuli (such a ball or car). Only these approaches could critically test for any overlap/dissociation at the neural level between the brain areas implicated PPS and IPS and support the functional dissociation between the two sectors of the space that we reported here at the behavioural level.

When considering the theoretical implications of the findings reported in this dissertation, I propose that, to devise appropriate models of PPS and IPS, one should bear in mind that, at least in the present experimental conditions, there is no complete functional overlap between these sectors of space. Indeed, theoretical model dealing with the problem of how humans regulate action and social space may potentially suffer from misconceptions. Conflating the PPS and IPS concepts - without proof of identity- may come at risk of biasing our knowledge, whereas falsifying the identity hypothesis will critically inform current theoretical models about space perception. Although is not supported by neuroimaging studies yet, I believe that even a single example of functional (double) dissociation is indeed sufficient to warn scholars to refrain from this risky conflations between the two concepts, and to critically inform current theoretical models about space perception. After all, even if we could use one single space representation as frame-of-reference for interacting with other objects and people, it would make sense that the spatial representations that we use flexibly conform to the task at hand. While it is certainly possible that new associations and mutual influences between PPS and IPS will be reported in the future, they do not imply that PPS and IPS share a common representation, nor that they are the same nosological entity.

Notably, if the assumption of functional identity with IPS does not appear to be legitimate, the possibility that PPS is involved in the guidance of interpersonal motor interactions still exists (e.g., Brozzoli et al., 2014). In humans, the data available are sparse and limited to indirect behavioral evidence of the influence of social variables on multisensory perception (Teneggi and others 2013) or of the existence of a shared representation of PPS for oneself and another person (Brozzoli and others 2013). Within this emerging new perspective, the last study (Chapter VII) was aimed at demonstrating that not only social significance of the other person, but also social value attributed to the target of our action could be an eminent variable to be tested for proving the role of PPS in social interactions. Among the nonphysical cultural and social features that can bias the perception of target objects as well as execution of motor acts toward them, we investigated the ownership status. The results from the first study in Chapter VI indicate a fascinating modulation of PPS boundaries due to object ownership. Specifically, on condition that it is “owned” by the participant (i.e., if it is “my” property), the target of the action is remapped as if it were within PPS as soon as the hand moved to grasp it. On the contrary, attributing the ownership of an identical object to the peer sitting in front (i.e., if it is “other’s” property) is sufficient to abolish PPS remapping. Interestingly, such a similar modulation emerged during observation conditions: even though the observer’s hand was immobile, a remapping of the observer’s PPS occurred when the peer was unfolding a grasping movement toward his/her own object. In the second study we further explored these selective PPS modulations: if the ownership of the target object is shared, PPS remapping emerged not only when grasping but also when observing the other person grasping the shared object. The findings that such effects during action execution and observation could jointly occur when the target is “ours” are likely due to the fact the shared object is perceived at the same time as “my” and the “other’s” object. Taken together, such findings offer exciting new opportunities for future research and the implications offered several prospective.

First, this study documented the first behavioural modulation of PPS during observed action. Hence, I suggested that PPS remapping may also display mirror properties. Though few attempts have been made, this mirror-like PPS system has been rarely investigated and the exact nature as well as the link with the putative human mirror system remains unclear. From a neurophysiological point of view, future studies should quantify the relationship of the PPS neurons not only with mirror, but also with canonical mirror neurons in the monkey brain. Indeed, these neurons are of particular interest because they appear to code object as target for both one's own and other's action, suggesting that they could play a major role in predictive representation of others' impending actions (Bonini et al., 2014). On the other hand, human studies could additionally elucidate the determinants as well as the specificity of such PPS remapping during action observation. One may question, for instance, which visual cue coming from the other’s movement is critical to trigger the simulation of the one’s own movement: is just the onset of the movement itself or one of the early kinematic patterns (e.g. peaks of acceleration or velocity) enough to determine a (simulated) action-dependent modulation of PPS? More speculatively, based on the data of the first investigation, one might even think that the internal simulation may actually occur prior to overt onset of the movement performed by the other individual. That is to say, visual information about other’s movement might not be that critical, inasmuch the simulated action in the brain’s observer could occur before the other’s hand start to move to grasp the action target.

Second and even more interesting, the mirror-like effects revealed here were modulated by the status of ownership in such a fascinating way that it should prompt research to include ownership as a variable of interest in PPS studies. However, how could the mere knowledge of object status specifically boost or eliminate this apparently low-level multisensory-motor changes in PPS representations? As owned objects are considered as an extended self, is property a form of self-other distinction that can be found in the human sensorimotor system? I will conclude with a final question for the future. Is the socially based construct of ownership itself grounded in simulative processes, such that in the observer’s brain it can induce a mirroring of the interaction with the object, by re-enacting the visuo-motor, affective and social experiences one has when interacting oneself with the object? The results from this research can only be taken as a preliminary step and further studies are needed to address these questions. Providing experimental answers to the previous questions presents a challenge for the future and opens new avenues of research for social and neurocognitive investigations.

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