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FEELING THE EMOTIONS AROUND US: HOW AFFECTIVE STIMULI IMPACT VISUO-TACTILE INTERACTIONS IN SPACE

Ph.D. Candidate:

CHIARA SPACCASASSI

802630

Tutor: ANGELO MARAVITA

Coordinator: MARIA TERESA GUASTI

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I dedicate this manuscript to Gianfry,
who always lovingly believed in me.

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Abstract

The constant understanding of the external world is such a natural process that all of us takes it for granted. However, exploring the world around us implies complex neural processes, which require the integration of signals coming from different sensory modalities. Peripersonal Space (PPS) is a privileged region of space, immediately surrounding our body, in which visual and bodily signals are promptly integrated in order to form a coherent neural map of the surrounding space (Hunley & Lourenco, 2018). Since the discovery of such a visuo-tactile integrated system in the monkey brain (Rizzolatti et al., 1981, Graziano et al., 1997), it has been shown that PPS amplitude is not fixed, but it can be dynamically shaped by specific experimental manipulations (Fogassi et al., 1996). Recently, different authors indicated how this portion of space is sensitive to interoceptive influences (Ardizzi & Ferri, 2018) as well as to individual differences (Hunley et al., 2017) in healthy human population. However, some important questions remain unsolved.

The present thesis aims to investigate, through behavioural and electrophysiological studies in healthy humans, how visuo-tactile integration in space can be shaped by intrinsic and learned valence of objects as well as by anxiety emotional states. Indeed, in the literature ambiguous results have been so far collected concerning the role of intrinsic value of nearby stimuli in triggering multisensory processing in PPS (Ferri et al., 2015). Furthermore, there is no study exploring how visuo-tactile interactions could be modulated by learned stimulus valence. In Study 1 and 3, these questions have been addressed by using a visuo-tactile interaction paradigm in which participants were requested to respond as fast as possible to a tactile stimulus while an approaching visual one (with intrinsic valence in Study 1 and learned valence in Study 3) was located at specific distances from their body (Canzoneri et al., 2012). The results of Study 1 and 3 seem aligned to each other: positive and negative stimuli entail larger visuo-tactile interactions in space than neutral ones. Indeed, at longer distances from the body, visuo-tactile interactions are

dynamically modulated by valence-connoted looming visual stimuli. At shorter distances, instead, all stimuli acquire saliency regardless of their intrinsic or acquired valence, due to their proximity, and then relevance, to the body. Overall, a view of PPS as a gradient modulating visuo-tactile integration is discussed.

Study 2 was carried out in order to exclude that the above-mentioned results might be due to tactile expectancy (Kandula et al., 2017). Indeed, the more the visual stimulus approaches the body without tactile input, the more the bodily stimulus expectancy increases, thus entailing a stronger preparation to respond to it (Umbach et al. 2012). By using the same visual stimuli – that now recede away from participants' body - and spatial distances as in Study 1, it was shown that the different valence of the stimuli is not able to produce any kind of effect in space. This result stresses the validity of the findings reported in Studies 1 and 3, highlighting the more ecological suitability of looming rather than receding stimuli to assess PPS.

Study 4 investigates the neuronal oscillations related to visuo-tactile coupling in near and far space for both positive and negative visual stimuli. In particular, we would like to replicate Wamain et al. (2016) results, which state that objects in near space are coded in motor terms, but only when the goal of the perceiver is to interact with them. Indeed, they showed motor cortex activation gradient from peripersonal to extrapersonal space when participants were asked to estimate their reaching capabilities in relation to visual stimuli located at different distances from their body. Instead, replicating the same experimental paradigm with a different task – i.e to indicate if the visual object is prototypical or not – authors failed to find such an activation of the motor area. By using a tactile discrimination task while valence-connoted visual stimuli were presented in near or far space, we found beta power desynchronization after 300 ms from visual stimulus presentation in near space over sensorimotor cortex, thus revealing a motor activation for valence-connoted visual stimuli close to the body but not when they were located far from it. This result stresses that visuo-tactile interactions genuinely assess PPS representation, thus corroborating the presence of such a multisensory system in the human brain (Maravita et al., 2003, Làdavas & Farnè, 2004). However, no effect of valence was found in the present EEG task, thus confirming Study 1 and 3 results, indicating a similar modulation of visuo-tactile integration exerted by positive and negative stimuli in space.

Study 5 explores how state and trait anxiety (Spielberger, 1983) can alter the prioritizing effect of congruent visuo-tactile stimulation in space. Indeed, it is known that high level of trait anxiety enlarges the defensive PPS (Lourenco et al., 2011, Sambo & Iannetti, 2013) while there are few and weak clues in literature about the relation between the state anxiety and PPS (Iachini et al., 2015). By adopting a revised version of the Temporal Order Judgment (TOJ) task as in Filbrich et al. (2017), participants were asked to report the presentation order of near or far visual stimuli while ignoring tactile cues, before and after doing an anxiety provoking task. Despite we were unable to report an overall prioritizing effect of congruent visuo-tactile interaction in near space, it has been found that participants who experienced a higher temporary state of anxiety showed a marked inhibitory effect of the congruent tactile cue on the near visual stimulus processing compared to participants who experienced less state anxiety. This finding seems to be compatible with previous results showing that high levels of state anxiety entail an overfunctioning of the alerting and orienting attentional networks as well as an increased amygdala response over threat-related stimuli (Pacheco-Unguetti et al., 2010, Bishop et al., 2004). On the other side, high trait anxiety participants' response to the congruent multisensory stimulation seems to be more facilitated in near than in far space, compatibly with previous studies indicating a reduced executive control in trait anxious subjects (Pacheco-Unguetti et al., 2010).

Taken together, the five studies illustrated in the present thesis stress the privileged integration of visual and tactile stimuli inside PPS and its permeability to emotional related states. On one side, it has been shown that the intrinsic and learned positive and negative valence of visual stimuli forge visuo-tactile interactions in space in a similar way, entailing an extending multisensory integration in space (Studies 1 and 3) as well as a motor cortex activation when located close to the body (Study 4). On the other side, we showed that the visuo-tactile congruency in near space is particularly susceptible to different kinds of anxiety: its facilitation effect is disrupted when experiencing a temporary state of high anxiety while it is enhanced when suffering from high trait anxiety condition (Study 5).

General Introduction

1. Visuo-tactile integration in space

In everyday life, we experience the space around us as unitary and harmonious. However, this spatial construct is the product of information that comes from different portions of space. Indeed, a growing neuroscientific evidence in literature seems to indicate that our brain contains a modular representation of space, illustrating how the space around us is fragmented and heterogeneous. Despite the variety of theories that have tried to classify different partitions, conventionally space is divided in two main sectors: peripersonal and extrapersonal space (Brain, 1941, Grüsser, 1983, Cutting & Vishton, 1995, Previc, 1998) (Figure 1).

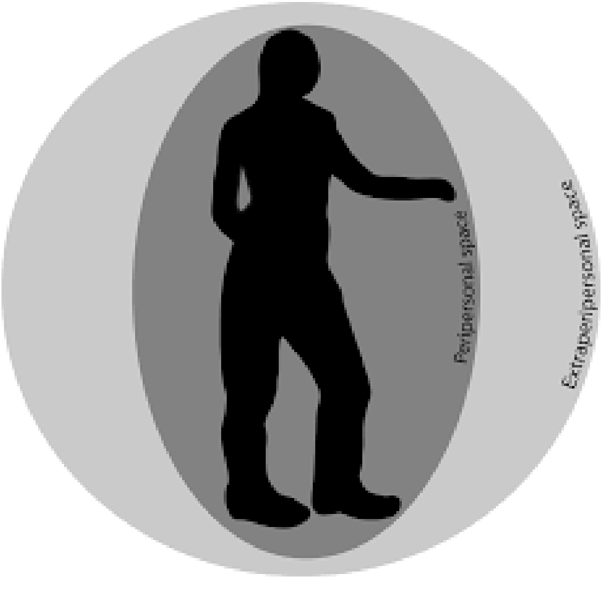

Figure 1. Spatial division taken from Clèry et al., 2015. *Peripersonal space* is the space in which we can act through reaching actions, *extrapersonal space* includes the far space, which is possible to explore by oculomotor inspection.

Peripersonal space is commonly described as the space immediately surrounding our body, in which it is possible to interact with an object for approaching or avoidance purposes, characterized by the close link between bodily and visual processing (Rizzolatti et al., 1981, a,b, Graziano & Cooke, 2006); extrapersonal space is instead the portion of space beyond the range of short-term actions which is mainly explored by oculomotor inspection (Grüsser, 1983, Clèry et al., 2015).

From the very beginning of space representation research, neurophysiological studies in monkeys have revealed brain areas specialized for the coding of the space surrounding the body, namely the Peripersonal Space (PPS). Specific neurons have been reported in the putamen as well as in parietal and frontal lobes that effectively respond only when visual stimuli are located in close spatial proximity to a particular body part (e.g. face or hand). These neurons respond to both tactile and visual stimuli when the latter are presented within the visual receptive field (RF) of the cells (Fogassi et al., 1996, Graziano et al., 1997, Duhamel et al., 1997). These receptive fields are restricted to the space around the animal’s hand or face, and their response typically decreases with increased distance between the stimuli and the macaque body. This implies that that bimodal neurons seem ideally suited to locate a stimulus with respect to the hand (i.e., in hand-centered coordinates) rather than in retinal or head-centered coordinates (Fogassi et al., 1996; Gentilucci et al., 1988; Graziano & Gross, 1993; Graziano et al., 1994; Rizzolatti et al., 1981).

In particular, these multisensory cells seem to share the following functional properties (Làdavas, 2002):

1) visual and tactile RFs are in spatial register
2) visual RFs have a limited extension in depth
3) their visual activity shows a response gradient
4) visual RFs work in coordinate systems centred on body parts

Indeed, these cells have a visual RF that matches the location of tactile RF on body surface and it remains anchored to the tactile RF when the latter moves (Rizzolatti et al., 1981 a, b, Fogassi et al., 1996, Graziano et al., 1999).

Importantly, its spatial location does not change when the eyes move. Moreover, this multisensory integration appears restricted to the space immediately surrounding the monkey's hand, face or body. Indeed, the visual response of these bimodal cells is stronger at shorter distances: when visual stimuli are presented very close to their tactile RF, the discharge frequency of these cells is not distinguishable from those evoked by delivering touch within the tactile RF (MacKay & Crammond, 1987). However, under specific circumstances, the visual properties of these neurons can encode for portions of space not strictly limited to the surrounding area of their tactile RF. As shown by Fogassi et al. (1996), an increase in stimulus velocity produced an expansion in depth of visual RFs of somato-centered neurons in F4. Therefore, beside to the more general rule by which the discharge of these neurons tends to decrease as the distance between visual stimulus and cutaneous RF increases, this finding demonstrates that the extension of the space they encoded is not fixed, but it can be modulated by contingent factors. Importantly, it has been showed in literature that the visuo-tactile properties of these multisensory cells are sensitive to different kinds of experimental manipulation. Indeed, in a seminal study, Iriki et al. (1996) demonstrated that the visual RF of bimodal cells can be extended in space in order to incorporate non-corporeal objects. After the monkeys were trained to actively use a tool to retrieve a distant food pellet, authors reported a dynamic extension of the visual RF of bimodal cells to incorporate tool. This means that these bimodal neurons discharge not only in near space but also in far space reachable by tool, only after the tool training manipulation. Far space is then capable of being remapped as near or, rather, PPS can dynamically extend its boundary to new reachable locations. Taken together, these findings indicate that the ventral premotor cortex, parietal areas and putamen in monkey's brain form an interconnected system that integrates visual and tactile signals in order to encode PPS, which properties can be shaped by specific factors (Farnè & Làdavas, 2000).

By close analogy with monkey studies, neuropsychological findings have provided evidence that also the human brain forms integrated visual–tactile representations of the PPS surrounding specific body parts. A wealth of neuropsychological data comes from neglect patients through which it has been possible to confirm many PPS features reported in non-human primate literature, thus establishing the high degree of functional similarity between the humans and monkeys' visuo-tactile system (Làdavas, 2002). Unilateral spatial neglect is a neuropsychological condition commonly following a damage to the right hemisphere of the brain, in which a deficit in attention to and awareness of the contralateral side of space is observed (for a review see Halligan, Fink, Marshall, & Vallar, 2003). This kind of patients exhibits the phenomenon of cross-modal extinction, that is, the inability to report the contralesional stimulus when presented simultaneously with the ipsilesional one, delivered in a different sensory modality (Critchley, 1949, De Renzi, 1982). In a study conducted by Làdavas et al. (1998) on neglect patients suffering from tactile extinction, it has been showed that a visual stimulus presented near the patient's ipsilesional hand had an inhibitory effect on the processing of a tactile stimulus delivered on the contralesional hand to the same extent as an ipsilesional tactile stimulation did. This strong link between vision and touch in human PPS representation was also stressed by another interesting result found by the authors: a visual stimulus presented near the contralesional hand was able to improve the detection of a tactile stimulus applied to the same hand. However, when visual events occurred far away from patient's hand, they do not compete with the left tactile event processing. The aforementioned study provides unequivocal evidence of the existence of an integrated system that controls both visual and tactile inputs within the PPS centered on the hand in humans. Furthermore, it suggests that this system is functionally separated from the one responsible of visual information control in the extrapersonal space. In addition to this, a very interesting study conducted by Maravita et al. (2001), showed that after an active use of a tool, neglect patient who originally showed a cross-modal (visuo-tactile) extinction only in near space, seem to exhibit neglect also in the far space (reachable by the tool). This study reported that right-hand visual stimuli extinguished 94% of simultaneous left tactile stimuli in PPS, while right visual stimulation extinguished only 34% of simultaneous left touches in extrapersonal space. However, when the far visual stimulus was reachable by the right hand through the stick, 69% of left tactile stimuli were subjected to extinction. The most interesting part of this research is that only when the sticks were firmly and actively held, connecting the far visual stimulus to patient's hand, the crossmodal extinction of left tactile stimuli significantly increased. This finding clearly demonstrates that humans can incorporate a non-corporeal object in their body schema representation only after an active use of it, thus enlarging visuo-tactile interactions in space.

Another interesting neuropsychological evidence that corroborates these findings – separate coding for PPS and extrapersonal space as well as PPS plasticity – comes from studies using line bisection task in neglect patients. It is well known that when performing a line bisection task, neglect patients misplace the midpoint of a line towards the ipsilesional side due to their failure to detect all stimuli presented in the contralesional side of space (Schenkenberg et al., 1980). In this single-case study by Halligan & Marshall (1991), the neglect patient exhibited a typical poor performance when performing the task in peripersonal space, but not in extrapersonal space. This demonstrates that human brain has two different neural representations for near and far space. In another similar study, Berti and Frassinetti (2000) replicated the near-far space dissociation by asking the neglect patient – suffering from neglect in near space - to bisect line using a laser pointer. By contrast, when performing the task with a stick, the patient showed neglect also in extrapersonal space. These findings suggest that tool use can extend neglect from the peripersonal to the extrapersonal space, thus highlighting the plasticity of PPS representation (see also Neppi-Mòdona et al., 2007).

Lastly, another interesting result in this domain, was obtained by Cowey et al. (1999), who demonstrated that the transition between peripersonal to extrapersonal space is gradual, rather than abrupt. Using a line bisection task on thirteen neglect patients, they demonstrated that the errors in drawing the midpoint did not arise abruptly at the reaching distance. Therefore, it could be truly assumed that the boundary between near and far space is not rigid in humans. On the contrary, it seems that a sort of gradient progressively rules the transition from near to far space.

In summary, the impaired performance showed by neuropsychological patients in line bisection task seems to reflect the same principles of multisensory integration revealed by single-units studies in monkey brain.

In addition to these studies, there is a mole of research on healthy population demonstrating that PPS and extrapersonal space representations differ from each other, thus enriching the previous literature with interesting new results. A large amount of evidence comes from behavioural studies adopting the aforementioned line bisection task (Varnava et al., 2002, Longo & Lourenco, 2006, Gamberini et al., 2008). Longo & Lourenco (2006) asked healthy adults to bisect line in its midpoint at different distances controlled for both veridical and angular size. The task was done by using both a laser pointer and a stick. When the laser pointer was used, there was a shift from left to right in bias as stimuli moved from peripersonal to extrapersonal space – this effect of the left side preference at short distances showed by neurologically normal individuals is also known as *pseudoneglect* (Jewell & McCourt, 2000). On the contrary, when the stick was used, a leftward bias was observed at all distances tested. This result clearly indicates that the tool extends the range of near space. Moreover, the authors highlighted the gradual transition from near to far space as revealed by the general continuous shift found with stimuli moving further away from the body. This result does not conceive PPS as the space within arm's reach, but rather as a more general space surrounding the body, thus not placing any kind of categorical limit on our ability to act.

Furthermore, the size of PPS could change in relation to the specific body part that is stimulated. Indeed, Serino et al. (2015) demonstrated that PPS extension is bigger for the trunk than for the face or the hand (Figure 2). These results suggest that at least three body-part specific PPS representations exist in human, differing in amplitude and directional tuning.

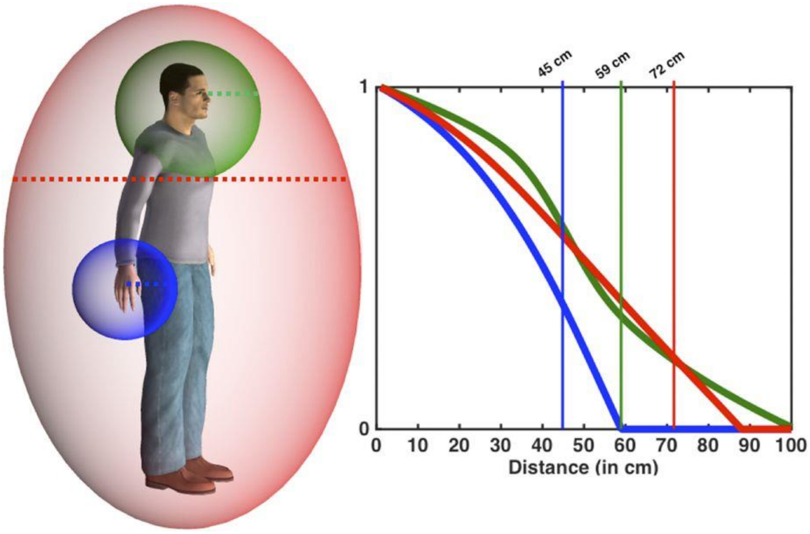

Figure 2. PPS amplitude for hand, head and trunk. Figure taken from Serino et al. 2015

A very recent and elegant study conducted by Noel et al. (2018), reported that the peri-face and peri-trunk spaces of healthy individuals enlarge as the velocity of an approaching auditory stimulus increases. For the first time, the extension in depth of PPS neuron's RFs has been now documented in humans to change dynamically as a function of the velocity of incoming stimuli, thus corroborating previous non-human primate results (Fogassi et al., 1996). However, several higher-order variables have been described to dynamically influence the representation of PPS in humans. For example, Teneggi et al. (2013) demonstrated that PPS representation is sensitive to social modulation, showing a link between low-level sensorimotor processing and high-level social cognition. Indeed, they found that PPS boundaries shrink when subjects face another individual, as compared to a mannequin, placed in far space. Furthermore, these authors found that the PPS boundary changes as a function of the social experience we have facing another individual. Indeed, following an economic game, PPS boundaries between our self and another individual seem to merge, but only when the confederate behaved cooperatively with us. Furthermore, Lourenco et al. (2011) showed that trait feelings of claustrophobic fear predicted the size of near space. Specifically, people with larger PPS reported higher rates of claustrophobic fear than individuals with smaller PPS. These results demonstrate that PPS size is adaptively modulated by anxiety and personality-traits (see also Taffou & Viaud-Delmon, 2014, Haan et al., 2016, Hunley et al., 2017).

Overall, all the experiments discussed above, clearly demonstrate that PPS is characterized by a strong visuo-tactile interaction that can be extended in space depending upon specific experimental manipulation. Therefore, PPS representation seems to be plastic also for healthy humans, given its capacity of shrinking and extending its amplitude in response to the ongoing low-level factors (sensory and motor) and higher order context (emotional and social).

2. Visuo-tactile experimental paradigms to assess PPS

Recently, different authors have proposed two interesting experimental paradigms to study visuo-tactile interactions in the peripersonal space: the visuo-tactile interaction paradigm (Serino et al., 2015, Haan et al., 2016, De Paepe et al., 2016) and the temporal order judgment task (Filbrich et al., 2017).

Visuo-tactile interaction paradigm. This experimental paradigm is adapted from the original audio-tactile interaction task developed by Canzoneri et al. (2012), investigating the influence of dynamical auditory stimuli on tactile processing. In the visuo-tactile interaction paradigm, a visual stimulus approaches to or recedes from a specific body part (e.g. the hand) while a tactile input is delivered to the same body area (Figure 3). The tactile stimulus may 'hit' participant's body while the visual one is located at different distances from the stimulated body part (e.g. 15, 30, 45, 60, 75, 90 cm). The task is to respond as fast as possible to the tactile stimulus through a foot pedal. The basic assumption of this paradigm is that the visual stimulus speeds up tactile reaction time only when it is located inside participant's PPS (i.e. faster reaction times when the visual stimulus is located inside than outside PPS). This effect is due to the strong and preferential visuo-tactile link in peripersonal space, underlying the bimodal cells activation in putamen, premotor cortex and parietal regions (Fogassi et al., 1996). The visuo-tactile interaction paradigm appears to be very suitable to assess PPS because of the high ecological validity of moving objects closely resembling those in real life.

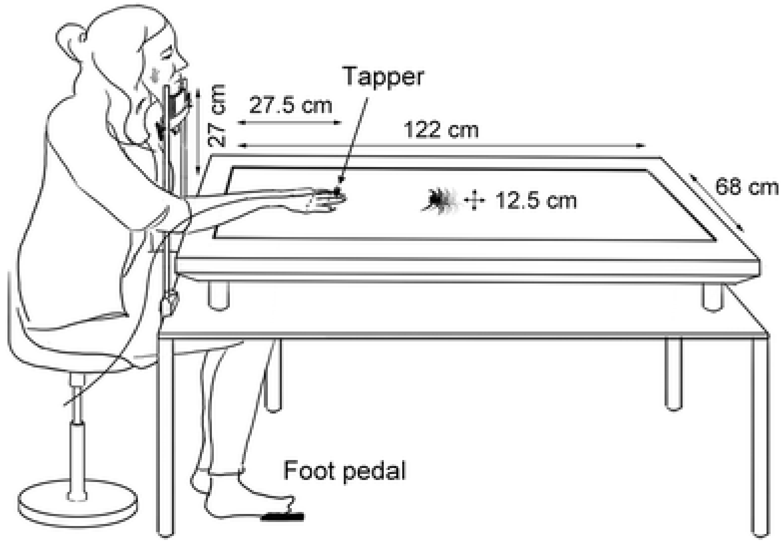

Figure 3. Visuo-tactile interaction paradigm illustration taken from Haan et al. (2015)

Based on this paradigm, Canzoneri et al. (2012) developed a mathematical method to assess PPS boundary, by applying a function adequately describing the relationship between tactile RTs and the timing at which the different tactile stimuli were delivered (i.e. the spatial distances tested). In this innovative study, they compared two possible functions, a sigmoidal function and a linear function. As can be read from Canzoneri et al. (2012) study, the sigmoidal function is described by the following equation: $y(x) = ymin + ymax * e(x-xc/b)/1+ e(x-xc/b)$, where x represents the independent variable (i.e., the distances), y the dependent variable (i.e., the reaction time), ymin and ymax the lower and upper saturation levels of the sigmoid, xc the value of the abscissa at the central point of the sigmoid (i.e., the value of x at which $y=(ymin+ ymax)/2$) and, finally, b establishes the slope of the sigmoid at the central point. The linear function, instead, is described by this equation: $y(x)=y0+ k \cdot x$. The x and y values have the same meaning as above, y0 represents the intercept at $x=0$ and k denotes the slope of the linear function. For each subject, the two functions are fitted to the averaged tactile RTs at all the spatial distances tested, separately for the approaching and receding visual stimulus condition. The reason behind this differentiation is that multisensory effect in space is generally significantly stronger for approaching visual stimuli than for receding ones (Serino et al., 2015, Kandula et al., 2017). As can be seen from Figure 4, the fitting of the RTs in the approaching condition has a sigmoidal shape while the RTs in the receding condition are better explained by a standard linear fit. Therefore, this finding stresses the more ecological impact of an approaching stimulus on bodily related processing compared to receding ones.

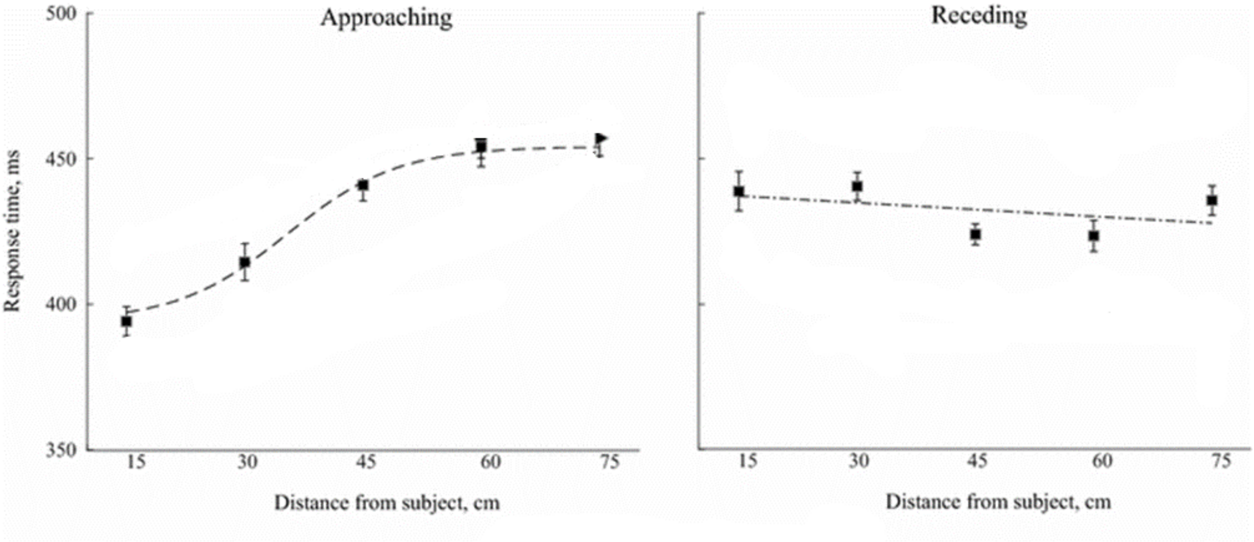

Figure 4. Sigmoidal fit of the approaching condition (left side) and linear fit of the receding condition (right side). This figure is adapted from Kandula et al., 2017

Temporal order judgment paradigm. A recent and promising experimental paradigm designed to assess visuo-tactile interactions in space, is a variant of the Temporal Order Judgment (TOJ) task. In the classical TOJ task, two tactile stimuli are delivered in a very rapid temporal sequence, one to the right and the other to the left hand of participants, whose task is to indicate which stimulus they perceived first (Yamamoto & Kitazawa, 2001). This brand-new method was described for the first time by Filbrich et al. (2017) in their seminal work about the nociceptive stimulus influence on PPS extension. In this task, participants have to look at the fixation LED located in front of them during the whole duration of the experiment. After a little delay from the offset of the fixation LED, a tactile stimulus is delivered in one of the two participant's hands. Just after the tactile stimulation, two target LEDs, positioned near (40 cm) or far (90 cm) from participant's trunk, turn on in a rapid temporal sequence. Participants are instructed to ignore tactile stimulation while responding to the visual stimuli, indicating as accurate as possible which one of the two LEDs turned on first (Figure 5).

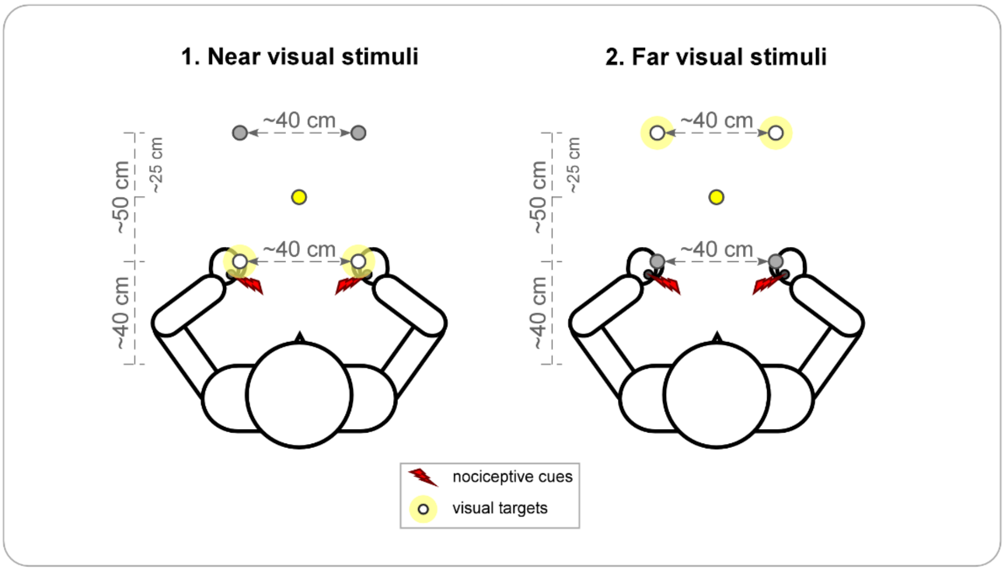

Figure 5. Temporal order judgment task to assess PPS. Two couples of target LEDs were placed near (40 cm) or far (90 cm) from participant's trunk. Before their onset, a brief nociceptive stimulus could be delivered to one participant's hand (unilateral condition) or to both hands (bilateral condition). Picture is taken from Filbrich et al. (2017)

The difficulty in performing the task mostly depends on two main factors: first, in half of the trials the lateralization of the tactile input is not congruent in respect of the order of the LEDs appearance, thus generating a conflict effect; second, the temporal interval between the two visual stimuli (Stimulus Onset Asynchrony, SOA) is variable (e.g. ±10, ±30, ±55, ±90, ±200 ms) and in some trials it may be so short to make the task very hard to accomplish.

Based on this task, it is possible to measure two different parameters, that are 1) the Point of Subjective Simultaneity (PSS, top part of the Figure 6) and 2) the Slope (bottom part of the Figure 6). These measures correspond respectively to the α and β parameters of the following logistic function *f(x) = 1/1+ exp (-β (x-α))*. The α defines the threshold of the function, which corresponds to the SOA at which the two visual stimuli are perceived as occurring first equally often (i.e. it matches the 0.5 criterion on the ordinate). Consequently, this measure corresponds to the PSS - the amount of time one stimulus needs to precede or follow the other in order for the two stimuli to be perceived as occurring simultaneously (Spence et al., 2001). The β parameter defines the slope of the logistic function and it describes the noisiness of the results. Indeed, its steepness depends on the accuracy of participant's responses recorded during the experiment.

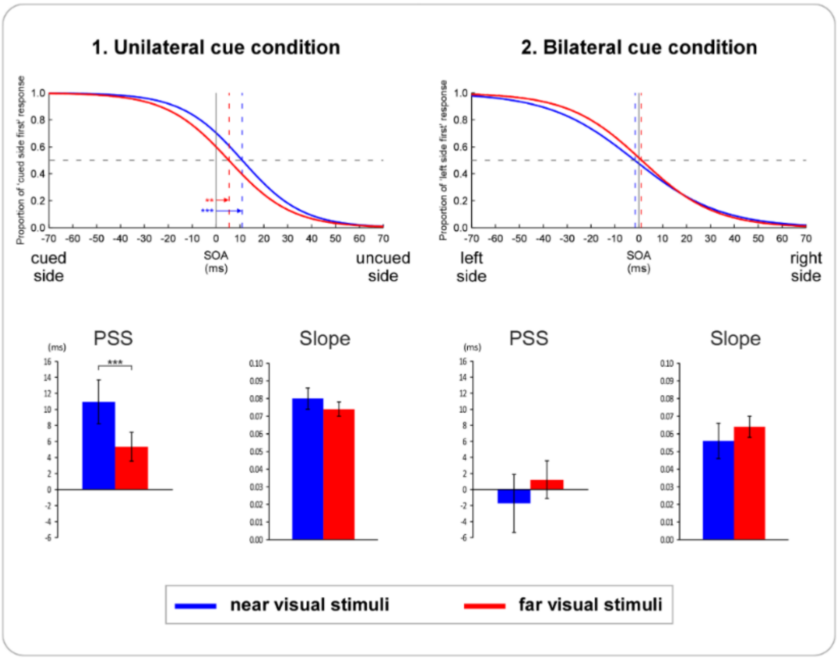

Figure 6. Sigmoidal curves representing how nociceptive stimulus interacts with visual one in near (blue line) and far (red line) spaces for the unilateral cue condition (Panel 1) and bilateral cue condition (Panel 2). Figure taken from Filbrich et al., 2017

In the study mentioned above (Filbrich et al., 2017), the authors discovered that the presence of unilateral nociceptive stimuli prioritized the perception of visual stimuli presented in the same side of space as the stimulated hand, with a significantly larger effect when visual stimuli were presented near the body than when they were presented farther away (Figure 6).

Importantly, these visuo-spatial biases were related to the spatial congruency between the hand on which nociceptive stimuli were applied and the visual targets. Indeed, when the nociceptive stimuli were congruent with the visual ones, they increased the performance accuracy of visual processing especially in near space. The facilitation effect in PPS due to the visuo-tactile congruence is clearly evident from the curves shown in Figure 6 (left side). As can be seen from the plot, when comparing the proportion of "cued side first" response with near visual stimuli to that found for far visual stimuli, there is a significant shift of the curves toward the uncued side (i.e., positive SOA values). This indicates that uncued near visual stimuli (LEDs that turn on first in the uncued side of space) have to be presented several milliseconds in advance compared to cued near visual stimuli (LEDs that turn on first in the cued side of space), in order to have an equal chance of being perceived as occurring first. By contrast, when the visual target is preceded by a bilateral nociceptive stimulation (i.e. tactile stimulus simultaneously delivered in both hands), no facilitation effect is present, thus entailing no differences between near and far space processing as indicated by the absence of shift in the curve (Figure 6, right side).

3. The two ways to conceive PPS: reaching vs defensive space

Since the discovery of bimodal neurons in monkeys and their responsiveness to the vision of objects located in proximity of the body, PPS has been viewed as the reachable and graspable space (Rizzolatti et al., 1981). Indeed, every object identified as inside the PPS can actually be grasped and manipulated, while those located outside this space cannot be reached without, for instance, moving toward them. The view of the PPS as a space that serves the control of object-oriented actions has been corroborated by a large number of human studies showing a functional link between voluntary object-oriented actions and the multisensory coding of the surrounding space. An example comes from Brozzoli et al. (2009) who investigated whether different actions performed on the same object imply different PPS modulations. To this end, participants were asked to either grasp or point to a target object. During the execution of these actions, they had to discriminate whether a tactile stimulus was delivered on their right index (up) or thumb (down), while ignoring a visual distractor. The results demonstrated that during the actual approaching phase of the grasping and pointing movements, voluntary grasping actions triggered a stronger functional link with the multisensory coding of PPS than that evoked by pointing actions. These findings suggest that the performance of an action induces a continuous remapping of the multisensory PPS as a function of online sensory and motor transformation complexity, in line with the hypothesis of PPS representation functional role in the motor control of voluntary actions. Furthermore, as highlighted in the previous paragraph, a vast amount of studies in both healthy and neurological population suggests that the active use of a stick that allows reaching the objects located beyond the near space, is capable to extend the edges of the PPS in order to include far reachable objects (Maravita et al., 2001, Làdavas et al., 2000). Altogether, this evidence seems to indicate that visual-tactile neurons coding for the space near the body can also discharge for the far space reachable by a tool, thus supporting the view of the PPS as the space in which objects can be grasped and manipulated. However, two seminal neurophysiological studies in monkeys showed that this portion of space may underlie a different function (Cooke et al., 2003, Graziano & Cooke, 2006). Indeed, they found that the electrical stimulation of PPS-related brain areas led the monkey to produce defensive-like movements such as withdrawing, blocking or ducking the head, which are really similar to those movements evoked by an air-puff directed to monkey head.

The idea that there is a safety zone surrounding the body can already be found in the pioneering work of the Swiss biologist Heini Hediger (1955). During his period as director of the Zurich zoo, Hediger observed that the animals displayed different behaviours when in proximity of other animals. Usually, when a potential predator invades its flight distance - the area surrounding an animal that if intruded by a potential predator or threat will lead to alarm and escape behaviour - the animal flees or withdraws from it. Even when the other animal belongs to its own species, there is a “personal” distance at which the proximity of conspecifics becomes no longer tolerable. This alternative way of seeing the surrounding space as a defensive area around the body has been proven by different experimental researches. The first evidence about the existence of a “defensive” PPS in humans was provided by Sambo and colleagues (2011, 2012). They showed that the hand blink reflex (HBR), a typical defensive reflex consisting of the eye blink due to the electrical stimulation of the wrist, increased when the hand was located near the face compared when it was located far from the face. This finding demonstrates that the brain stem circuits mediate the tonic and selective top-down modulation from higher order cortical areas responsible for encoding the somatosensory stimulus location in external space coordinates. Moreover, several behavioural studies using the visuo-tactile paradigms described in paragraph 2, found interesting results about the presence of this safety margin in healthy individuals after specific experimental manipulations. For example, an even more growing line of research investigates the relation between peripersonal space and personality traits, such as anxiety and fear. Haan et al. (2015) showed that the visuo-tactile integration in peri-hand space is stronger when the approaching visual stimulus is a threat (e.g. spider) rather than a non-threatening stimulus (e.g. butterfly) but only for participants who were afraid of spiders. In a very similar experiment by Taffou and Viaud-Delmon (2014), participants had to detect tactile stimuli to the hand while a threatening (e.g. dogs barking) or non-threatening sound (e.g. sheep bleating) was presented from behind the participant. Responses were faster when threatening sounds appeared closer to participant hand and this effect depended on the reported fear of dogs. Indeed, dog-fearful participants exhibited a larger peri-hand space compared to non-fearful participants, given that the sound of barking dogs started influencing tactile detection earlier in the trial for the former than for the latter. All these findings demonstrate that visuo-tactile predictions are important for maintaining bodily integrity, thus providing evidence for the existence of a safety zone surrounding our body that is advantageous for survival. Furthermore, in the experiment conducted by De Paepe et al. (2014), participants were requested to indicate the temporal order of two nociceptive stimuli presented in a rapid succession on participant's hands – one stimulus on each hand - while ignoring a previous visual stimulation. Visual cue stimuli were presented at four different locations in each trial: either unilaterally or bilaterally, and either on the participant's hands (in near space) or in front of the participant's hands (in far space). They found that the perception of nociceptive stimuli was biased in favour of the stimulus delivered on the hand adjacent to the unilateral visual cue, especially when the cue was presented in near space. These crossmodal interactions can be explained by a peripersonal space frame of reference, which is used to map the position of nociceptive stimuli, thus confirming the existence of such a kind of safety margin around the body to alert an organism to possible external threats.

Based on the existing literature, de Vignemont & Iannetti (2015) wondered how many peripersonal spaces could exist. In their review, the authors proposed the distinction between two models of PPS: the Swiss Army Knife Model and the Specialist Model (Figure 7). The first model assumes that there is only one neural representation of PPS. Therefore, different visual stimuli (e.g., a tempting object like an apple or a threatening one like a spider) are always mapped in the same brain PPS regions, but depending on the nature of the stimulus itself, the observer can activate different actions towards the object (e.g., the apple produces an approaching movement while the spider an avoiding action). Therefore, in this Swiss army-knife model, the context differs and determines the final motor outcome, but the sensory stimulus is always mapped on the same PPS cortical map (Figure 7, left panel). By contrast, the Specialist model, postulates that there are at least two different neural representations of PPS, the defensive map and the working map. When a sensory stimulus is presented in the environment, it activates one of the two PPS neural maps (e.g., the apple is then represented in the working map, while the spider in the defensive map), which in turn triggers the appropriate action towards the object (working action like approaching the apple vs defensive action like avoiding the spider, respectively). Therefore, in the Specialist model, the meaning of the stimulus defines the PPS representation in which the stimulus is mapped (Figure 7, right panel).

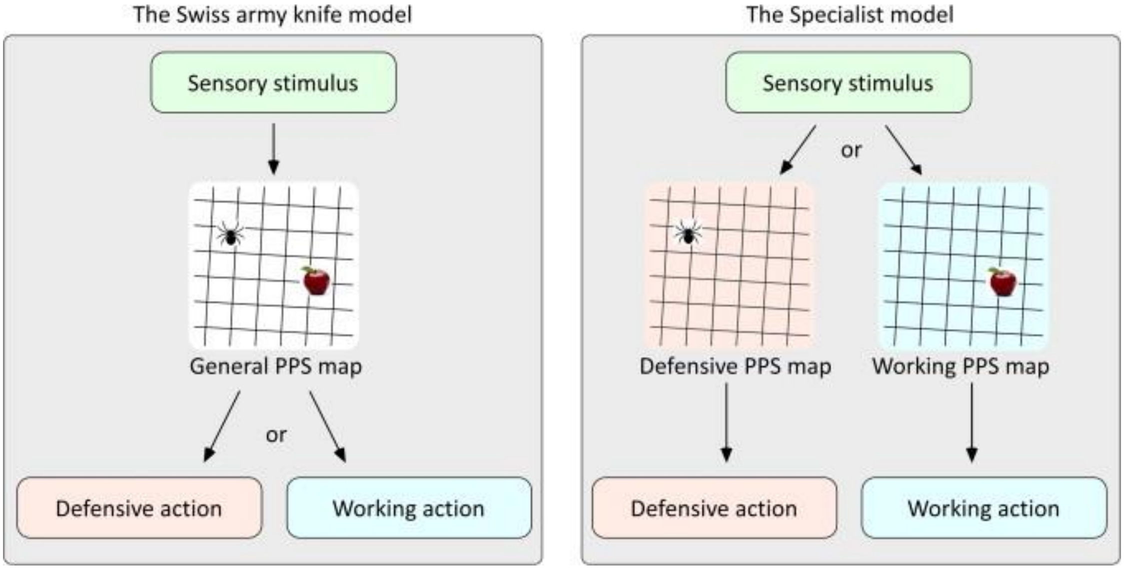

Figure 7. The two models of PPS representation, taken from de Vignemont & Iannetti, 2015

From the motor perspective, the distinction between the working and defensive PPS is reasonable, given that each function corresponds to a specific action, which could be goal-oriented and approaching for the former or protective for the latter PPS representation. Generally, as stressed by the authors of the review, the working PPS requires more voluntary actions, such as approaching something positive or tempting, while the defensive PPS is more related to automatic actions, such as avoiding something negative or threatening. However, it could be pointed out that the dichotomy between goal-oriented actions for the working PPS and automatic actions for the defensive PPS, is not always true. For example, sometimes, to avoid a possible threat (e.g., a spider approaching our body), we can perform a voluntary action (i.e., we can grasp it in order to capture it) in a defensive situation. Moreover, as the authors of the review stressed, defensive behaviour does not require always actions. For instance, in a dangerous situation, we can implement the freezing strategy or playing dead (Avenanti et al., 2012). Finally, it is worth noting that it is not always true that a goal-oriented action is voluntary. For instance, in humans, automatic motor activations can be found during the observation of manipulable objects (Chao and Martin, 2000, Grafton et al., 1997). What therefore really matters is the purpose of the action, that could be working or defensive. Despite it is not possible to unequivocally support one of the two models, as things stand at the moment, the authors of this review have tracked down some hints in literature that seem to give more credit to the Specialist model, to the detriment of the Swiss army-knife model. Indeed, they argued that anxiety seems to have opposing effects on the two PPS: specifically, it decreases the extension of the working space while it increases the amplitude of the defensive space. For example, Graydon et al. (2012) asked participants if they were able to reach and grasp a target positioned at various distances from their body. When anxiety was experimentally induced, participants underestimated their perceived reaching abilities as well as their ability to grasp the objects compared to non-anxious participants. Therefore, anxiety seems to reduce our movements and consequently the amplitude of the working space. On the other side, instead, Sambo & Iannetti (2013) demonstrated that individuals with high levels of trait anxiety – a stable personality characteristic of unpleasant feelings in response to the anticipation of a perceived threat - assessed by the STAI questionnaire (Spielberger, 1983), have a larger defensive PPS amplitude (measured by HBR) than people with low anxiety scores. Another study that the authors of the review took as evidence of their Specialist model assumption, was conducted by Lourenco et al. (2011) who used a line-bisection task to assess PPS in relation to anxiety. In this research, authors found that participants with higher levels of anxiety of enclosed spaces and physically restrictive situations (assessed by CLQ – claustrophobia questionnaire) have a larger PPS compared to participants with lower CLQ scores. This means that for the anxious subjects, the rightward transition of the line bisection occurred at longer distances than that displayed by non-anxious participants. This result was interpreted in a defensive framework, given that an over-projection of the protective near space may play an important role in the aetiology of claustrophobia. In summary, it seems that anxiety reduces the reaching space while increases the protective space because it could make us feel less able and prompt to respond to potential environmental stimuli, thus leading to a drop of reaching and grasping capabilities on one side, and to the necessity to have more space and time to react to potential threats on the other. However, despite the presence of these hints in the existing literature in favour of the Specialist model, no studies that clearly compare these two kinds of spaces have been conducted so far. Therefore, empirical evidence is necessary to validate one of the two models in order to establish if it is possible to refer to PPS as a unique neural map (the Swiss army-knife model) or as a dual representation (the Specialist model).

4. The close relationship between body and space

As pointed out in the previous paragraphs, the space immediately surrounding our body can be defined as follows: "*Peripersonal space contains the objects with which one can interact in the here and now, specifies our private area during social interactions and encompasses the obstacles or dangers to which the organism must pay attention in order to preserve its integrity*" (Coello et al., 2012, p. S131). What immediately stands out from this definition, is the strict relation between this privileged sector of space and our body. Indeed, as stressed in the previous paragraphs, the bodily and spatial information must be strongly linked given that the space around our body is represented with reference to the body. Therefore, it is not surprising that PPS is mainly viewed as a privileged interface between our body and the external world (Cardinali et al., 2009). Pierre Bonnier's (1905) was the first to have the insight about the existence of a sense of bodily space, by introducing the term "*aschématie*", indicating the class of symptoms showed by patients who occupied the space in an inappropriate manner with some body parts. Subsequently, Head and Holmes (1911–1912) coined the notion of "body schema", which can be defined as a representation of body-parts' dimensions and their positions in the external space. The main proprieties of this representation are:

1. to be finalized to action
2. to be dynamically updated
3. to be strictly internally coherent

The first property of the body schema can be fully understood when we are going to make a movement. In these occasions, our brain needs to compute the position, shape and dimension of both the target and our own body. For instance, when we are going to reach something, we have to pay attention not only to the target position in space, but also to the body-part we are planning to use in order to execute that specific action (i.e. the arm for the reaching purpose). The spatial positions and dimensions of the different body parts are computed by integrating information coming from different somatosensory modalities, such as proprioception, kinesthesia and touch. Thus, the body schema represents both position and configuration of our body as a 3-dimensional object in space through a complex combination of sensory information, especially tactile and visual ones. This integration allows both to localize stimuli in external space with respect to the body and to act towards them. Regarding the second property of the body schema, it is well known that movements and positions of body parts in space must be online tracked in our body representation in order to make it realistic in every single moment of our life. Head and Holmes (1911–1912) were the pioneers in thinking that body schema could be plastic. Indeed, in their seminal work, they wrote: "*By means of perpetual alterations in position we are always building up a postural model of ourselves which constantly changes. Every new posture or movement is recorded on this plastic schema, and the activity of the cortex brings every fresh group of sensations evoked by altered posture into relation with it. Immediate postural recognition follows as soon as the relation is complete*". Furthermore, related to the third property, the body schema does not accept any kind of incoherence. This means that when a conflict occurs between two sensory inputs, the brain aims to solve it in favour of one of them. Resolving these inter-sensory inconsistencies can result in interesting sensations, responsible for many perceptual illusions as, for example, the rubber hand illusion (Botvinick & Cohen, 1998). Given its peculiarities, as Cardinali et al. (2009) highlighted in their review, the body schema appears difficult to be distinguished from the notion of multisensory peripersonal space (Rizzolatti et al., 1981, di Pellegrino et al., 1997) (Table 1). Indeed, the plastic features of spatial and bodily representations, together with their involvement in action performing, have raised the question whether sufficient evidence exists for them to be considered as two opposite sides of the same coin.

	Peripersonal Space	***Body Schema***
Sensory Input	Vision Audition Touch	Proprioception Kinesthesis Touch
Functional Properties	Defensive movements Voluntary actions	Body knowledge for action
Neural Mechanism	Parietal–frontal bimodal neurons	Pre-frontal and parietal cortex

Table 1. Table of the different sensory modalities, functional properties and neural mechanisms contribution for the peripersonal space and the body schema (adapted from Cardinali et al., 2009)

In literature, there are several studies highlighting the strict analogy between PPS and the body schema that in most cases have been demonstrated by tool-use paradigms. As mentioned in the above paragraphs, tool use can enlarge PPS both in monkey's brain (Iriki et al., 1996) and in humans (Farnè & Ladavas, 2000, Maravita et al., 2001). One explanation given to this phenomenon offered by Iriki et al. (1996) as well as by Maravita et al. (2003), is that the tool could be incorporated in the body representation as an extension of the hand that wields it, so that the displacing on the far end of the hand would have the same effects of the tool itself, thus entailing an enlargement of PPS. More specifically, Canzoneri et al. (2013) tested the hypothesis that tool use simultaneously affects PPS and body representation, by administering to healthy participants body tasks (i.e. tactile distance perception task and body landmarks localisation task) and PPS task (i.e. audio-tactile interaction task), before and after a brief training with tool. They found that tool use extended PPS representation and the perceived length of the arm, thus supporting the view in favour of a unified body and space representation. Moreover, in a similar methodological study, Canzoneri et al. (2013) tested a group of amputee patients by administering the same tactile distance task and audio-tactile interaction task on the stump of the amputated limb, while wearing or not wearing their prosthesis. They found that when performing the tasks on the amputated limb without the prosthesis, PPS boundaries as well as the perception of the arm length become smaller compared to results obtained while wearing the prosthesis. In addition to clearly indicate that both body and PPS incorporate the prosthesis into their representations, these findings show that the prosthesis acts like a tool thanks to its capability to restore the action potentialities of the body in space. Indeed, prosthetic arms are able to extend multisensory integration in space as well as to elongate the perceived length of the stump, thus stressing the strong overlap between PPS and body representation.

Another line of experimental studies investigating body/space interaction took advantage of methods reflecting body parts on a mirror (Maravita et al., 2000, Maravita et al., 2002, Pavani et al., 2000) as well as immersive virtual reality, that typically creates the strong perceptual illusion of being in the displayed scene (Sanchez-Vives & Slater, 2005) and may elicit the illusion that the events occurring in the virtual scenario are real (Slater, 2009). For instance, de Borst et al. (2018) investigated with fMRI how priming with whole-body first or third person perspective virtual reality training modulates the PPS network during perception of approaching social threat. The virtual scenario displayed a female avatar in the hallway of a house reached by a male aggressor who approached the viewers and entered their peripersonal space, verbally abusing the female avatar. The scenario could be viewed from a first or third person perspective. The results indicated a significant effect of first versus third person perspective priming on the neural activity in the PPS network. After first person perspective priming, all the neural regions of the PPS network, including premotor cortex, intraparietal sulcus and the superior parietal lobe, were more synchronized across participants during PPS intrusion. On the contrary, when participants were primed with a third person perspective, there was not such activation. This suggests that when participants experience more the virtual bodily illusion, the PPS is aligned with the virtual body as demonstrated by the synchronized activity in the fronto-parietal network following PPS threat intrusion.

Even if the evidence presented in literature are not so strong to disentangle the question raised by Cardinali et al. (2009), it is possible to conclude that it may be very difficult to separate the neural systems involved in body representation from those underlying PPS representation. Further research is therefore needed in order to add even more knowledge to this complicate issue. Concluding this chapter, I would like to cite the French phenomenological philosopher Merleau-Ponty (1963), who firmly asserted that the experience of the body is a source of expression of the space because the body inhabits space, it is not in space. Therefore, living the body means living the space and body’s relationship with space is necessarily intentional, as he wrote: “*Now the body is essentially an expressive space. If I want to take hold of an object, already, at a point of space about which I have been quite unmindful, this power of grasping constituted by my hand moves upwards towards the thing. I move my legs not as things in space two and a half feet from my head, but as a power of locomotion which extends my motor intention downwards*”.

General aims

The general aim of this thesis is to provide a more detailed investigation on the plastic changes of the space surrounding our body. In the present work, I am going to describe five different studies conducted on heathy population showing how emotional factors are crucial in modulating the visuo-tactile interactions underlying PPS. Although changing body properties (i.e., tool-use studies) as well as social context (i.e., fair vs unfair cooperation with a confederate) have been shown to alter PPS representation, little is known about how changing the value of an object (Study 1, 2, 3, 4) as well as the transient anxiety state (Study 5) influences PPS properties.

More specifically, in Study 1, I focused my attention on the role played by the intrinsic valence (positive, negative and neutral) of looming visual stimuli as well as their arousal level (high and low) in shaping PPS. This research arises from the ambiguous results obtained by Ferri et al. (2015), in which they found that negative stimuli are encoded faster than positive and neutral ones, thus entailing a larger PPS for the former than for the latter. However, in a pre-experimental study, these authors found that the arousal level of the negative visual stimulus was significantly higher than that of positive and neutral stimuli, thus leading to a dubious interpretation of the results found in terms of valence. In Study 1, 15 visual stimuli (5 positive-high arousal, 5 negative-high arousal, 5 positive-low arousal, 5 negative-low arousal, 5 neutral-low arousal) were prior validated in a pre-experimental session. Then, 36 healthy participants performed the visuo-tactile interaction task (previously explained in paragraph 2), by responding as fast as possible to the tactile input delivered on their right hand by pressing a foot pedal, while the approaching visual stimuli were located at specific spatial distances from their body (15, 30, 45, 60, 75, 90 cm). Considering the double function of PPS as a reaching and defensive space (see paragraph 3), I hypothesize that both negative and positive stimuli can enlarge visuo-tactile interactions in space, compatible with an extension of reaching PPS boundaries for positive stimuli (reaching space) and an enlargement of defensive PPS limits due to negative stimuli (defensive space).

In order to exclude that confounding factors could explain data found in Study 1, 36 healthy participants performed a revised version of the visuo-tactile interaction task of Study 1. These two studies are identical except for the direction of visual stimuli: in Study 2 they receded from rather than moved toward participant's body. This allowed to exclude a possible role of tactile expectation in modulating PPS. Indeed, the more the visual stimulus travels toward participant's body without being accompanied by the tactile input, the higher is the expectation of the perceiver to receive the bodily stimulus (Kandula et al., 2017, van Ede et al., 2011). This high expectancy implies a major motor readiness in responding to the tactile stimulus (Umbach et al., 2012) and could cover for the effect of visual stimulus proximity to the body in speeding up RTs to the bodily inputs (Maravita et al., 2003).

In Study 3, the relation between visuo-tactile integration in space and learned valence of visual looming stimuli was investigated. Despite it is known in literature that secondary valence (i.e. monetary reward) is very feasible in shaping our behaviour (Tzschentke, 1998, Childs et al., 2017), there is not any study investigating how the visuo-tactile interactions in space could be affected by the learned valence of stimuli. 36 healthy participants first underwent a value-learning task - its effectiveness was previously assessed in a pre-experimental session by using the IAT procedure (Greenwald et al., 2003) - in which they learned to associate a specific monetary outcome (reward, loss or neutral event) to three visual stimuli. After that, they performed a visuo-tactile interaction task, in which a tactile input was delivered to their right hand while the three conditioned approaching visual stimuli (positive, negative and neutral) were located at specific spatial distances from it. Considering that the conditioned value of objects can be as effective in guiding our behaviour as the intrinsic value (Delgado et al., 2006), I expect to find the same expected results as in Study 1, namely an enlargement of visuo-tactile interactions in space due to positive (reaching space) and negative stimuli (defensive space).

Study 4 aims to investigate the neuronal oscillations of the visuo-tactile interactions and their modulation by the intrinsic stimulus valence. A new set of visual stimuli was previously validated in a pre-experimental session that allowed to select 20 couples of visual stimuli (20 negative, 20 positive with the same arousal level and grasping difficulty) paired by semantic, colour or shape association. Afterwards, the same static visual stimuli were used in a visuo-tactile interaction task while EEG was recorded. By presenting them in two main sectors of space (near space and far space), participants concurrently received in the half of trials a tactile input on their right hand (thumb or little finger), thus taking under control the ratio of true vs catch trials (Kandula et al., 2017). Their task was to discriminate where they perceived the vibration by pressing one of the two buttons (right, left) with their left hand. In the remaining half of the trials, participants had to simply look at the visual stimuli without giving any response. Moreover, behavioural data was also recorded in the same experimental group by administering a staircase procedure (Cornsweet, 1962) in order to extensively measure PPS amplitude in relation to stimulus valence. Despite the explorative nature of the study, we could expect that the motor cortex activation – revealed by the desynchronization of mu and beta rhythm - could be equally sensitive to the positive and negative valence of the visual stimuli inside PPS (in line with the activation of reaching vs defensive PPS, respectively) and that it could progressively diminish from peripersonal to extrapersonal space (as in Wamain et al., 2016).

In Study 5, the object of investigation concerns how visuo-tactile interactions can be spatially modulated by a temporary state of anxiety. Whilst it is well known in literature that stable traits of anxiety are effective in shaping PPS (Lourenco et al., 2011, Sambo & Iannetti, 2013), little is known about how transient states of anxiety influences PPS representation. To pursue this aim, we administered to 20 healthy participants a revised version of the Temporal Order Judgment task (TOJ, previously explained in paragraph 2) in order to measure PPS, before and after the experimental breathing condition (to breathe with a straw and the nose plugged for 2 minutes) as well as before and after the control breathing condition (to breathe normally for 2 minutes).

Considering the high sensitivity of PPS for the interoceptive states (Ardizzi & Ferri, 2018) as well as the effectiveness of this anxiety manipulation in shaping behaviour, emotions and cognitive states (Graydon et al., 2012), it is possible to expect an enlargement of the defensive PPS after the experimental breathing condition but not after the control breathing condition. This expected result should be revealed by the different prioritizing effect of congruent visuo-tactile stimulation following the two anxiety manipulation conditions: we should expect an equal multisensory facilitation in near and far space after breathing with the straw as opposed to a greater visuo-tactile facilitation effect in near than in far space after normally breathing.

Overall, the present set of studies provides novel experimental evidence showing the critical influence of emotional related states on visuo-tactile integration process in space.

Studies 1, 2, 3

Everything is worth when it is close to my body: how spatial proximity and stimulus valence affect visuo-tactile integration[1]

Introduction

A number of studies in humans and animals suggests that the space near the body holds a special status as a space for integrating visual and bodily signals for perception and action (Rizzolatti et al., 1997, Farnè et al., 2005, Macaluso & Maravita, 2010). Neurophysiological studies in monkeys revealed a large fronto-parietal network coding the space near our body, termed peripersonal space (PPS). Many neurons coding for the PPS have the peculiarity of being multisensory, predominantly responding to both visual and tactile stimulations. Such visuo-tactile neurons typically show a tactile receptive field (RF) centred on a specific body part and a visual RF that overlaps with the tactile one, thus forming a single responsive region mapping the bodily surface and the space immediately adjacent to it (Rizzolatti et al., 1981 a, b, Fogassi et al., 1996, Graziano et al., 1999). Research work in healthy people and brain damaged patients supports the existence of an analogous PPS system in humans, suggesting functional similarities with non-human primates (Làdavas et al., 1998, Spence et al., 2004).

The PPS holds specific properties, as characterized by the response to visual stimuli at different distances from the body or by their integration with somatic stimuli.

First, the multisensory properties of PPS are anchored to the position of single body parts and are not necessarily modulated by gaze position. Such a body-

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[1] The experiments reported in the present section are published in Acta Psychologica: Spaccasassi, C., Romano, D., & Maravita, A. (2019) “Everything is worth when it is close to my body: how spatial proximity and stimulus valence affect visuo-tactile integration” *Acta Psychologica*

centered representation of the space around us allows an extremely accurate evaluation of the distance between our body and nearby objects, thus leading to the creation of an appropriate motor program towards them. Indeed, the first described function of the PPS is to reach and grasp objects located near the body, serving as an interface between perception and actions (Rizzolatti et al., 1997). Moreover, it has been shown that a lesion to the neural areas subtending the processing of PPS in the monkey brain, leads to various types of motor response impairments, mainly impacting visually-guided reaching actions (Battaglini et al., 2002, Rizzolatti et al., 1983). Interestingly, a more recent perspective seems to highlight the defensive aim of this portion of space. In particular, it has been shown that the electrical microstimulation of the monkey PPS neural areas evoked defensive movements, like withdrawing or blocking actions (Cooke & Graziano, 2003, Graziano & Cooke, 2006). Considering the proximity between this portion of space and our body, it seems an adaptive strategy to be equipped with such a safety area for the early detection of potential approaching threats. Whether PPS for action and defence are controlled by the same or different system, is still a matter of debate (de Vignemont & Iannetti, 2015).

Second, the discharge of these multisensory neurons shows a gradual modulation depending on the position of the visual stimulus in space, increasing progressively as the stimulus comes closer to the monkey’s body without any sudden change of response pattern with distance (Fogassi et al., 1996, Graziano et al., 1997). Indeed, when visual stimuli are presented very close to their tactile RF, the discharge frequency of these cells is not distinguishable from those evoked by delivering touch within the tactile RF (MacKay & Crammond, 1987). However, under specific circumstances, the visual properties of these neurons can encode for portions of space not strictly limited to the surrounding area of their tactile RF. For example, the visual RF of the afore-mentioned visuo-tactile neurons expands when the velocity of approaching visual stimuli increases, such that fast-moving stimuli are signalled earlier than slower ones (Fogassi et al., 1996). This assumption has been recently confirmed also in humans, as shown by the enlargement of perifacial and peri-trunk space size related to the increasing velocity of the approaching stimulus (Noel et al., 2018). Furthermore, it has been found that the use of tools that extend reaching space, determines an elongation of visual responses from near to far space, compatibly with a plastic expansion of PPS. In monkeys, Iriki et al. (1996), found that following tool-use training, the neuronal activity of bimodal cells encoding PPS was present also in far space, thus including the entire length of the rake. In humans, bisecting lines in far space using a tool instead of a laser pointer has shown to expand visual neglect from near to far space (Berti & Frassinetti, 2000, see Farnè & Ladavas, 2000, Maravita et al., 2001 for related data in patients with crossmodal extinction). In a similar vein, in the healthy population, the alert responses to noxious stimuli dynamically increased after the active use of a tool, leading to an extension of the defensive space near the body (Rossetti et al., 2015).

In addition, and crucial to the present work, it has been found that the extension of the PPS is also sensitive to the affective valence of visual stimuli. This is not surprising if one considers the role of PPS as multisensory interface for body/object interaction for action and self-protection. In particular, a reaching-estimation study conducted by Valdés-Conroy et al. (2012), showed that objects with positive affective valence tend to be perceived reachable at locations at which neutral and negative ones are perceived as non-reachable. Although this study clarifies that stimulus valence may affect body-space interactions, it does not address the question whether PPS is affected by stimulus valence, given that PPS may not be limited to the space within arm's reach (Longo & Lourenco, 2006)[2]. The authors suggested that their results concern the higher desirability soaked in positive objects, compared to negative ones – also considering that positive and negative stimuli had the same arousal levels. Indeed, it seems that stimuli associated to a positive value tend to be perceived as physically closer than negative ones, with the final aim

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[2] As the reviewer suggested, it is right to clarify this sentence: Valdés-Conroy et al. (2012) results cannot be taken to implicate that PPS boundary is larger for positive objects than for negative ones. Indeed, reachability relies upon metric knowledge of the body, not the space around it. Therefore, body representation rather than PPS is more likely to be at stake, thus remaining the question of whether PPS is affected by stimulus valence unsolved.

to stimulate the perceiver to approach them (Balcetis et al., 2010). These results seem to be in line with those reported by Teneggi et al. (2013), showing that fair cooperative interaction with another person leads to an expansion of PPS, measured by an audio-tactile interaction paradigm. By using the same experimental paradigm, Ferri et al. (2015) showed that sounds associated with negative emotional valence lead to an extension of peripersonal space as compared to both neutral or positive ones. This means that the reaction times to the tactile stimulus were significantly faster at far distances for the negative looming sound than for a more pleasant or neutral one. However, this study didn't finely control for the arousal level of the used stimuli, so that conclusions about valence might be confounded by the different arousal level of the stimuli. Indeed, it is worth noting that in the pre-validation session of the study conducted by Ferri et al. (2015), emerged that negative stimuli were judged as more arousing than the other two. The effect of stimulus-driven arousal is likely to play a relevant role in these results, given that seeing or hearing alerting approaching stimuli induces an untimely preparation to respond to them, as demonstrated by the time-to-collision underestimation of threatening looming stimulus reported by Vagnoni et al. (2012). Such a subjective perception of reduced distance would have the adaptive effect of inducing faster reactions to threatening objects on a collision course with the observer.

More research is therefore needed in order to understand how the intrinsic valence, as well as the arousal level of stimuli, can shape visuo-tactile interactions in space. Additionally, no study investigated the role of learned valence in modulating PPS yet. It is well known that a negatively or positively conditioned stimulus can exert a strong effect in human motivational behaviour. For example, it has been shown that monetary loss can be as effective in driving aversive conditioning as an electric shock (Delgado et al., 2006). In the same vein, P3 amplitude – classically associated with high motivation and arousal – increases with increasing monetary reward (Goldstein et al., 2006). Moreover, it has been recently confirmed the short-term feasibility to use secondary reward in choosing preferences between two visual stimuli associated with different monetary reward levels (Childs et al., 2017). Indeed, people seem to exhibit a propensity for the high conditioned choice than for the low conditioned one, in strict analogy to results already present in rodents' literature (Tzschentke, 1998).

In the present paper, we aimed at clarifying how intrinsic and learned valence of visual stimuli approaching to or receding from our body can shape the extension of multisensory integration in space. In the first two experiments, we used a visuo-tactile interaction task to measure the spatial multisensory integration, manipulating both the intrinsic valence and the arousal level induced by the stimuli - i.e. the level of psychophysiological activation induced in the perceiver by a given stimulus (Fowles, 1980) - of visual looming (Experiment 1) and receding (Experiment 2) stimuli. In the third experiment, participants first underwent a conventional instrumental conditioning paradigm (Raymond & O'Brien, 2009) in order to associate different affective values to different visual stimuli. Such conditioned stimuli – rewarded, punished and neutral – were then used as approaching stimuli in a visuo-tactile interaction paradigm. Based on the existing literature, we can hypothesize that positive stimuli – both intrinsic and conditioned ones – entail faster responses at far spatial distances than negative and neutral ones, leading to stronger multisensory integration in space, because of their desirability (Valdés-Conroy et al., 2012, Teneggi et al., 2013). Or, on the contrary, we could obtain that negative stimuli – both intrinsic and conditioned ones - trigger stronger visuo-tactile interactions in space than positive and neutral ones, given the aversion and repulsion feelings related to them (Ferri et al., 2015). However, considering the double nature of PPS as a reaching/working space and safety zone around our body (de Vignemont & Iannetti, 2015), we can also imagine that both positive and negative stimuli lead to an increase of visuo-tactile interactions in space, functional to an activation of reaching/working PPS for desirable stimuli or of defensive PPS for negative ones.

1. Experiments 1 & 2 - Intrinsic valence modulates PPS

The purpose of these experiments was to better define how visuo-tactile interactions can be spatially modulated by stimuli featuring an intrinsic valence (Experiment 1), while controlling for the role of tactile expectation (Experiment 2).

1.1 Methods

1.1.1 Participants

Experiment 1. 36 healthy subjects (13 males, mean age 24,11 years, standard deviation 4,15, range: 19-42, all right-handed except one by self-reported) participated in the experiment. All participants had normal or corrected-to-normal vision. All subjects (students of University of Milano-Bicocca) received credits for their participation to the study. This research was performed in accordance with the Declaration of Helsinki and was approved by the local committee of the Department of Psychology, University of Milano-Bicocca.

Experiment 2. 36 new, naïve healthy subjects (14 males, mean age 24,39 years, standard deviation 2,98 range: 19-30, all right-handed except one by self-report) participated in the experiment. All participants had normal or corrected-to-normal vision. All subjects (students of University of Milano-Bicocca) received credits for their participation to the study. This research was performed in accordance with the Declaration of Helsinki and was approved by the local committee of the Department of Psychology, University of Milano-Bicocca.

1.1.2 Visual stimuli selection and validation

In a pre-experimental session, a first group of subjects (N = 40, 21 females, mean age 24,05 years, range =19-41) was invited to rate 40 visual stimuli using a 9-points Likert scale. They had to rate both the pleasantness and the arousal level generated by each stimulus, by choosing one out of the nine alternatives (ranging from -4 “completely negative/relaxing” to +4 “completely positive/exciting”, where 0 was the neutral point). The experimental visual stimuli included 16 positive stimuli (8 more arousing and 8 more relaxing), 16 negative stimuli (8 more arousing and 8 more relaxing) and 8 neutral stimuli. This procedure allowed us to select the 15 stimuli used in the successive experimental step (Figure 1), according to the arousal and valence scores in order to create 5 different groups of stimuli classified by valence (positive, negative, neutral) and arousal (high, low). The experiment was run by OpenSesame software 3.1 (Mathôt et al., 2012).

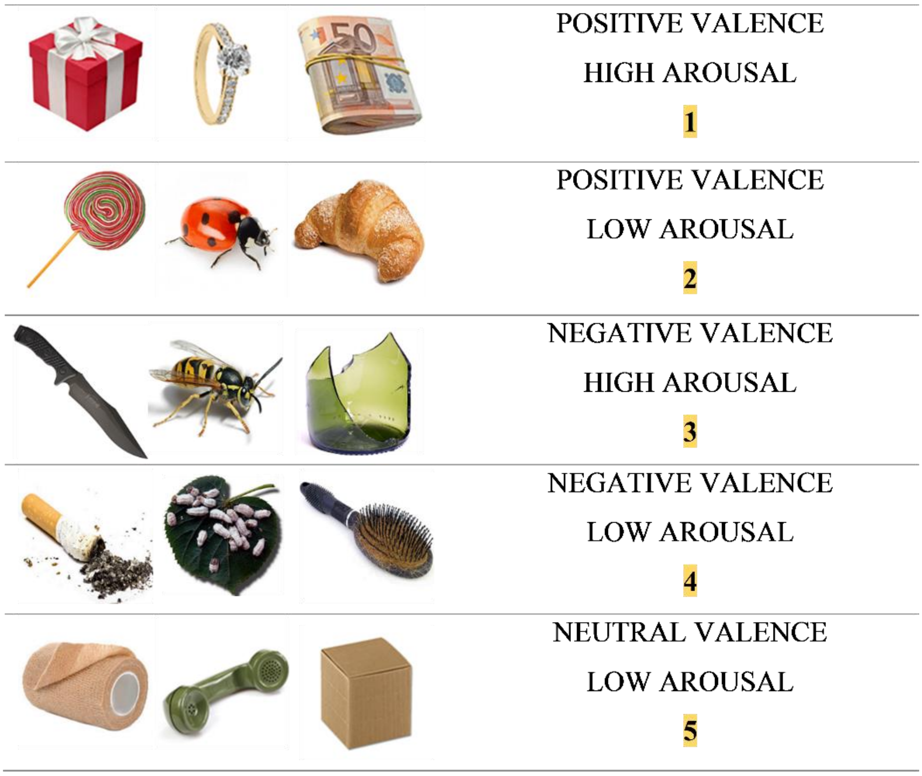

Figure 1. Experimental visual stimuli selected from the validation session and classified by valence and arousal: GROUP 1-Positive Valence & High Arousal; GROUP 2-Positive Valence & Low Arousal; GROUP 3-Negative Valence & High Arousal; GROUP 4-Negative Valence & Low Arousal; GROUP 5-Neutral Valence & Low Arousal

Preliminary visual stimulus validation. We conducted a preliminary analysis in order to explore Valence and Arousal mean scores relative to each visual stimulus. Then, for each category (Figure 1) the 3 visual stimuli characterized by the most relevant scores were chosen and a repeated measure ANOVA comparing Valence and Arousal scores was performed. A main effect of Valence ($F_{(4.61)}$=53.55; p<.001) was found, indicating that not all the visual stimuli were not rated equally pleasant. Post-hoc analyses (Tukey) revealed that group 1 did not differ from group 2 (p=0.999), which were both different from, respectively, group 3 (all p<.001), 4 (all p<.001) and 5 (p=.003, p<.004). Furthermore, group 3 and 4 did not differ (p=0.994), but they were both significantly different from group 5 (p<.012, p<.007). A main effect of Arousal was also reported ($F_{(4.6)}$=49.47; p<.001), suggesting that not all the stimuli induced the same level of activation. Post-hoc analyses (Tukey) revealed that group 1 did not differ from group 3 (p=.09) but they were both significantly different from group 2 (p<.001, p=.003), 4 (p=.003, p<.001) and 5 (p<.001, p<.001). Furthermore, group 2, 4 and 5 were not significantly different from each other (2 vs 4 p=.327, 2 vs 5 p=.954, 4 vs 5 p=.134).

1.1.3 *Procedure*

Experiment 1. Subjects sat in a barely illuminated room with their right hand palm down on the table just adjacent to a wall placed on their right side, where they watched the visual stimulus approaching their hand during the experiment. The visual stimuli were displayed by means of a projector (Acer P7200i) connected to a computer (HP 6555b) and consisted of looming images lasting 1500 ms and covering a distance of 1 meter, travelling at a constant speed of 66 cm/sec. All the visual stimuli were included inside a 180 by 180 pixels square and were projected in a 100x75 cm working space on the wall. Participants were asked to put their stimulated hand on a support adjacent proximal limit to the projection area, so that at the end of each animation, the visual stimulus contacted the participant's hand as if pretending to touch it (Figure 2). All the animations were presented on a white background. In agreement with the previous validation phase, looming stimuli were 3 positive stimuli with high arousal (group 1 – gift, ring and money), 3 positive stimuli with low arousal (group 2 – lollipop, ladybug and brioche), 3 negative stimuli with high arousal (group 3 – knife, wasp and broken bottle), 3 negative stimuli with low arousal (group 4 – infested leaf, dirty comb and cigarette butt) and 3 neutral stimuli with low arousal (group 5 – bandage, phone receiver and little box) (Figure 1). Along with the visual stimulus, in 85% of the trials, subjects also received a tactile stimulus delivered on the fingertip of middle finger of their right hand through a solenoid (Heijo electronics, www.heijo.com) with a diameter surface of 1.5 cm. The tactile pulse was a single pulse of 40ms duration and consisted of a clearly perceivable tap delivered through a 4mm diameter magnetic rod placed inside the solenoid. The stimulator was controlled by a computer through an ad-hoc built control relais-box (Tattile Box, s/n Touch15001, EMS, Bologna, Italy). The remaining trials were catch trials (15%) in which no tactile stimulation was delivered and no response was expected. Participants were asked to press a pedal when they perceive the tactile stimulus on their hand. Tactile stimuli were delivered at different temporal delays from the visual stimulus onset, corresponding to 6 different spatial positions of the approaching stimulus to the hand, namely 15, 30, 45, 60, 75 and 90 cm. The total experiment consisted of a random combination of 12 stimulus repetitions of each stimulus type for each spatial distance, randomly intermingled with 64 catch trials for a total of 424 trials. The inter trial interval was 800 ms. During the entire experiment, participants wore headphones with white noise in order to cover the tactile stimulation noise. Stimulus presentation and response collection were controlled by OpenSesame software 3.1 (Mathôt et al., 2012).

Experiment 2. The experimental task and set up were identical to Experiment 1 (see paragraph above), except for the movement of the visual stimuli (Figure 1) whose direction was receding, and not approaching, from the participant's hand (Figure 2).

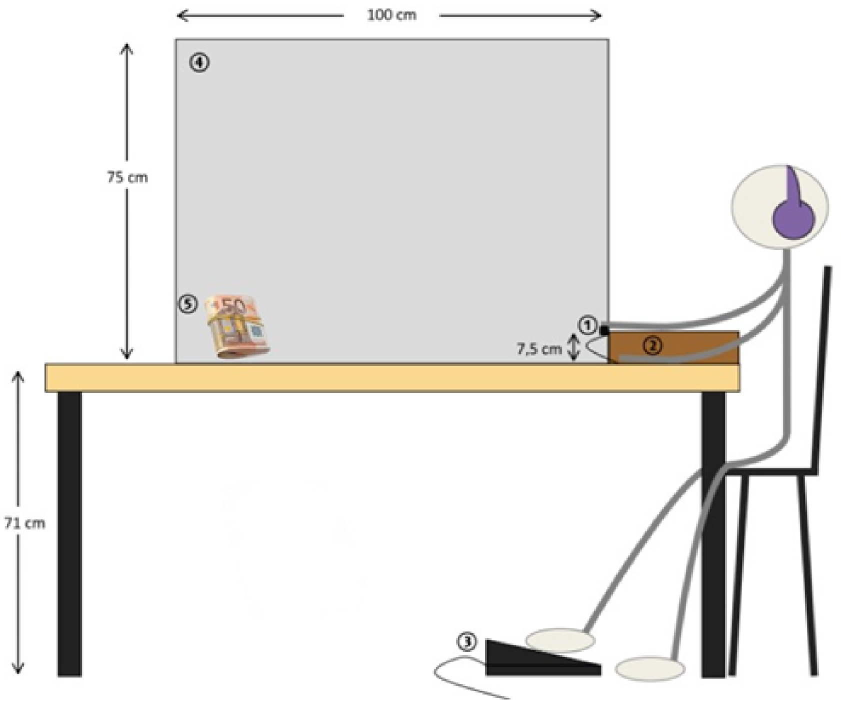

Figure 2. Overview of the experimental set-up.
1.Solenoid 2. Support for the hand 3. Pedal 4. Projected working area 5. Starting position of the approaching visual stimulus (Experiment 1) or final position of the receding visual stimulus (Experiment 2)

1.2 Results

Visuo-tactile interaction task (Experiment 1). One subject was removed from data analysis due to high rate of response anticipation, exceeding 3 SD from the overall sample mean (M ± 3 SD =35 ± 42.3 trials). Mean accuracy of the remaining 35 participants was 98.55% (± 2.59%) correct responses. Since accuracy was at ceiling, it was not further analysed.

Analysis was instead focused on RTs that were explored with a linear mixed effect model (LMM) as implemented in the package "lme4" in R software (Kuznetsova et al., 2016, for a similar approach see De Paepe et al., 2016). Initially we transformed RTs in their Log values to reduce the impact of eventual extreme values, improving data distribution (Ratcliff, 1993). Then LMM analysis required four steps. First, we searched for the random intercept between the variables Id (represented by subjects) and Trial, that significantly increased the fit of the model compared to a null model. In the second step, we established fixed factors adding exponential models of Distance, in order to understand the best fitting curve of the data. In the third step, we looked for the most parsimonious model that fitted the data through a systematic restriction of the full model, comparing fit increment using χ^2 test and taking under control the measure of fit goodness using likelihood ratio. Finally, in the fourth step, we inspected the ANOVA table of the final model describing main effects and interactions. P-values were calculated based on Satterthwaite's approximations.

We started running the first linear mixed model including, as fixed factors, Distance (from 15 to 90 cm) as continuous variable and Valence as nominal variable (positive, negative and neutral) in order to keep under control the effect of any stimulus valence on RTs, independently from their arousal level[3]. First, we estimated the random structure. We found that the variable Id significantly increased the fit of the model ($\chi^2_{(1)}$=6637.5, p<.001), at odds with the variable Trial ($\chi^2_{(1)}$=2.2678, p=.13); therefore only Id was used as random effect in the next steps. After establishing the fixed factors of Distance and Valence, we found that a quadratic function of Distance improved the fit of the model in respect to a linear relationship ($\chi^2_{(1)}$=551.13; p<.001), by contrast, a cubic ($\chi^2_{(1)}$=1.3539; p=0.24) or quartic ones ($\chi^2_{(2)}$= 2.46; p=0.29) did not improve the model fit significantly. The most parsimonious linear mixed model included all fixed and random factors together with their two-way interaction. In this final model, we found a main effect of Distance ($F_{(1,11706)}$=53.42; p<.001) (Figure 3), followed by a significant main effect of Distance^2 ($F_{(1,11706)}$=565.01; p<.001). No main effect of Valence was recorded ($F_{(2,11706)}$=1.14; p=.32). A significant two-way interaction between Distance and Valence ($F_{(2,11706)}$=3.02; p=.048) was also found (Figure 3).

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[3] Note that the neutral condition has only one Arousal level (low), while positive and negative conditions have two Arousal levels (low and high). Therefore, they are not comparable in the same linear mixed model.

In order to discover the effect of Arousal, we ran another linear mixed model, including Distance (from 15 to 90 cm), Valence with two levels (removing the neutral condition), Arousal (high, low) and Block (from 1 to 4). These were manipulated within subjects. We found that the most parsimonious linear mixed model included all fixed factors without any interactions. A main effect of Distance ($F_{(1,9346.0)}$=116.54; p<.001) was found (Figure 3), followed by a significant exponential main effect of Distance^2 ($F_{(1,9346.0)}$=431.56; p<.001) and a main effect of Block ($F_{(3,9346.1)}$=17.96; p<.001). Arousal ($F_{(1,19346.0)}$=0.43; p=.51) or Valence ($F_{(1,9346.0)}$=0.01; p=.91) were not significant.

Overall, these findings suggest that there is a similar modulation exerted by all the three valence categories of stimuli at near distances, while further away from the body, the neutral one seems to be encoded in a different way from the others (Figure 3).

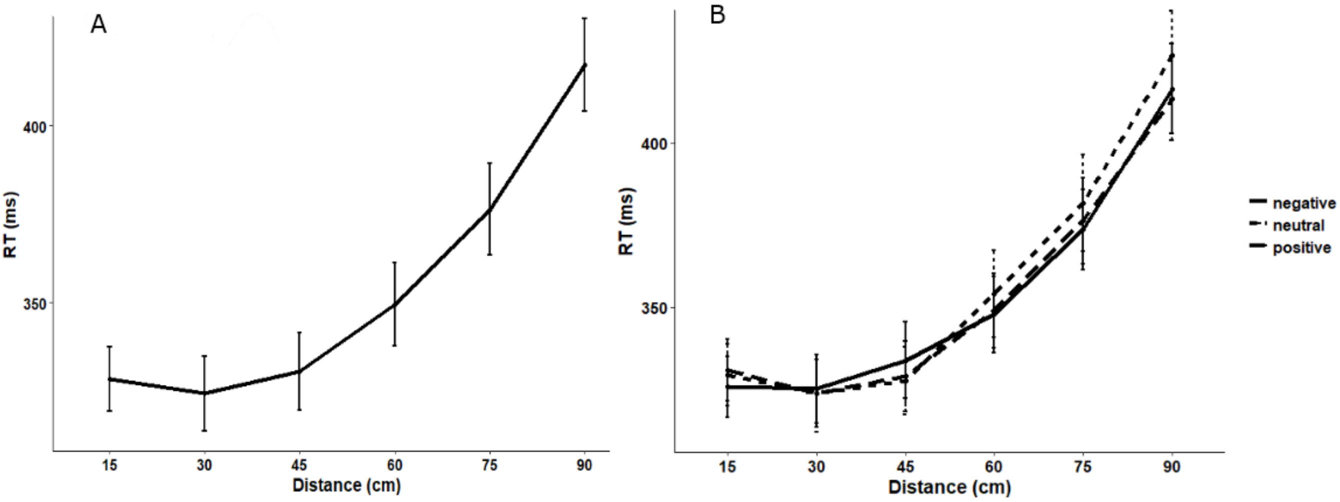

Figure 3. Panel A) Main effect of Distance. Error bars represent the standard errors of the means. Data are better explained by a quadratic function. Panel B) Two-way interaction between Distance and Valence. Error bars represent the standard errors of the means. All values reported are taken from aggregate data.

Visuo-tactile interaction task (Experiment 2). Data from one participant were removed from the analyses due to anticipated responses to the tactile stimulation, exceeding 3 SD from the overall sample (M ± 3 SD =

17.53 ± 87.67 trials). Mean accuracy was 98.34% (± 2.86%) and it was not further analysed, in line with Experiment 1.

We conducted a linear mixed model analysis (LMM) with the same approach described for the approaching trials of Experiment 1. Again, we found that the variable Id significantly increased the fit of the model ($\chi 2_{(1)}$=5064.3, p<.001), at odds with the variable Trial ($\chi 2_{(1)}$=0.6132, p=.43); therefore only Id was used as random effect in the next steps. We found that a quadratic function of Distance improved the fit of the model in respect to a linear relationship ($\chi 2_{(1)}$=343.56; p<.001), by contrast, a cubic ($\chi 2_{(1)}$=1.3502; p=0.25) or quartic ones ($\chi 2_{(2)}$= 1.3521; p=0.51) did not improve the model fit significantly. Differently from Experiment 1, the most parsimonious linear mixed model included all fixed and random factors without any interaction. In this final model, we found a main effect of Distance ($F_{(1,11738)}$=622.855; p<.001) (Figure 4), followed by a significant exponential main effect of Distance2 ($F_{(1,11738)}$=348.9319; p<.001). A trend in the effect of Valence was recorded ($F_{(2,11738)}$=2.3754; p=.09) indicating that participants seem to react slower for neutral stimuli rather than for positive and negative ones (positive: M ± SD = 337.45 ± 54.42; negative: M ± SD= 338.24 ± 55.77; neutral: M ± SD = 340.57 ± 56.14).

In order to discover the effect of Arousal, we ran the second linear mixed model as in Experiment 1. Coherently with Experiment 1, we found that the most parsimonious linear mixed model included all fixed factors without any interactions. A main effect of Distance ($F_{(1,9375.0)}$=514.39; p<.001) was found, followed by a significant exponential main effect of Distance2 ($F_{(1,9375.0)}$=293.81; p<.001) and a main effect of Block ($F_{(3,9375.2)}$=7.5280; p<.001). Arousal ($F_{(1,9375.0)}$=2.0508; p=.15) or Valence ($F_{(1,9375.0)}$=0.0702; p=.79) were not significant.

Overall, these findings suggest that tactile expectancy certainly plays a role in the modulation of the RTs in the visuo-tactile interaction task, however, and crucially to the purpose of the study, the fact that valence only interacts with approaching stimuli, suggests that stimulus valence modulates spatial multisensory interactions and not the mere expectancy of a stimulus.

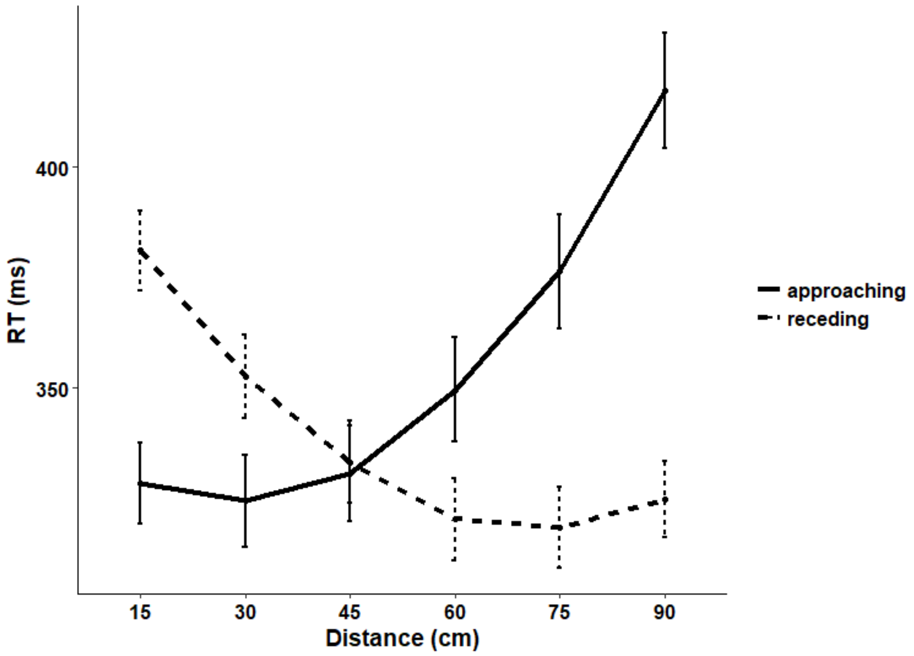

Figure 4. Main effects of Distance. Error bars represent standard errors of the mean. Data are better explained by a quadratic function. Solid line represents approaching trials in Experiment 1, dashed line represents receding trials in Experiment 2.

2. Experiment 3 – Learned valence modulates PPS

The aim of the third experiment was to investigate whether the learned valence of otherwise neutral stimuli can shape the visuo-tactile interactions in the space around us in a similar fashion to the intrinsic valence of looming stimuli.

2.1 Method

2.1.1 Participants

36 new, naive healthy subjects (14 males, mean age 23,58 years, standard deviation 4,96, range: 18-23, all right-handed except for one by self-reported) participated in the experiment. All participants had normal or corrected-to-normal vision. All subjects were students of University of Milano-Bicocca and they were paid for their participation to the study in accordance to the amount of money earned during the conditioning phase (see paragraph 2.1.3). The

monetary refund ranges from 3.5 to 6.5 €. This research was performed in accordance with the Declaration of Helsinki and was approved by the local committee of the Department of Psychology, University of Milano-Bicocca.

2.1.2 Visual stimuli selection and validation

In a pre-experimental stimuli validation session, a first group of subjects (N = 40, 26 females, mean age 22 years, range =19-25) were invited to rate seven stimuli using a Likert scale composed of 9 points. They had to rate the positivity/negativity of the stimulus choosing one out of the 9 alternatives (from -4 "very unpleasant" to +4 "very pleasant", where 0 was the neutral point). The experimental visual stimuli were seven blue geometrical shapes (triangle, star, rhombus, pentagon, hexagon, heptagon and octagon). This procedure allowed us to select the six stimuli used in the main experiment, by classifying them in three valence categories (positive, negative, neutral) according to the recorded scores. The task was run by OpenSesame software 3.1 (Mathôt et al., 2012).

Preliminary visual stimulus validation. We performed a repeated-measure ANOVA in order to compare the different scores obtained by the 7 geometrical shapes during the rating phase. A main effect of geometrical shapes emerged ($F_{(6.264)}$=3.2288; p=.0046), indicating that not all of them were rated with the same pleasantness level. Post-hoc analyses (LSD test) revealed that the star (M ± SD = 5.875±2.19) significantly differs from rhombus (M ± SD = 5.05±1.72), pentagon (M ± SD = 4.75±1.69), octagon (M ± SD = 4.9±1.55), hexagon (M ± SD = 4.575±1.57), heptagon (M ± SD = 4.475±1.55) and triangle (M ± SD = 4.625±2.07) (all p<.05). The other figures were not significantly different from one another. Therefore, the star was discarded, and the other six geometrical shapes were selected as the stimuli for the instrumental conditioning task (see Figure 5 for all the six geometrical shapes used).

2.1.3 Procedure

Instrumental conditioning task. On each trial of the value learning task, a pair of different blue geometrical shapes were projected on a wall in front of the participant. Shapes were vertically aligned above and below a central fixation cross. Participants were requested to choose a shape in order to maximize monetary win (see below). After the participant's choice, made by pressing the "k" key to select the up figure and the "m" key to select the down figure, with a keyboard that subjects kept on their legs, a black frame surrounded the selected geometrical shape and, depending on the reward condition, a message ''WIN'' in green (accompanied by a money win sound), ''LOSS'' in red (accompanied by a money crashed sound) or ''NOTHING'' in black (no sound) was shown (Figure 5, Panel B). All the screens displayed held grey background. Subjects had 2 seconds to choose the shape, after which an out of time screen appeared. Pairs of geometrical shapes always consisted of the same elements. Each pair was associated with a specific type of reward, i.e. win, loss or neutral, thus creating three different reward pairs, i.e. the win pair, the loss pair and the neutral pair (Figure 5, Panel A). Within each pair of positive and negative reward, every shape was associated with a specific probability to be followed by the respective outcome. In the win and loss pairs, there was one shape holding a higher probability (0.8) and the other one a lower probability (0.2) to be followed by the specific outcome, while in the neutral pair each figure was associated with the same probability to be followed by a neutral outcome (1). Monetary wins and losses were always equal to 20 Euro cents and no outcome (0 cent) was the default - that is, the value associated to the reward pair when the participant choice was not the optimal one and that related to the loss pair when the participant choice was the optimal one. Each pair was presented 120 times in a random order, for a total of 360 trials. Assignment of each figure pair to outcome type (win and loss) was counterbalanced across participants in order to eliminate any possible intrinsic valence bias induced by individual shapes. The spatial position of the shape within the pair was also randomized from trial to trial. The total earning was displayed to the participant at the end of the whole experiment together with the overall accuracy and a monetary payout was provided to the participant, which was proportional to the earnings obtained during the experimental task. The conditioning procedure was validated in a pilot experiment, using an Implicit Association Test (Greenwald et al., 1998), a procedure that allows to test for the automatic associations between concepts (see Supplementary Material). The experiment was run using OpenSesame software 3.1 (Mathôt et al., 2012).

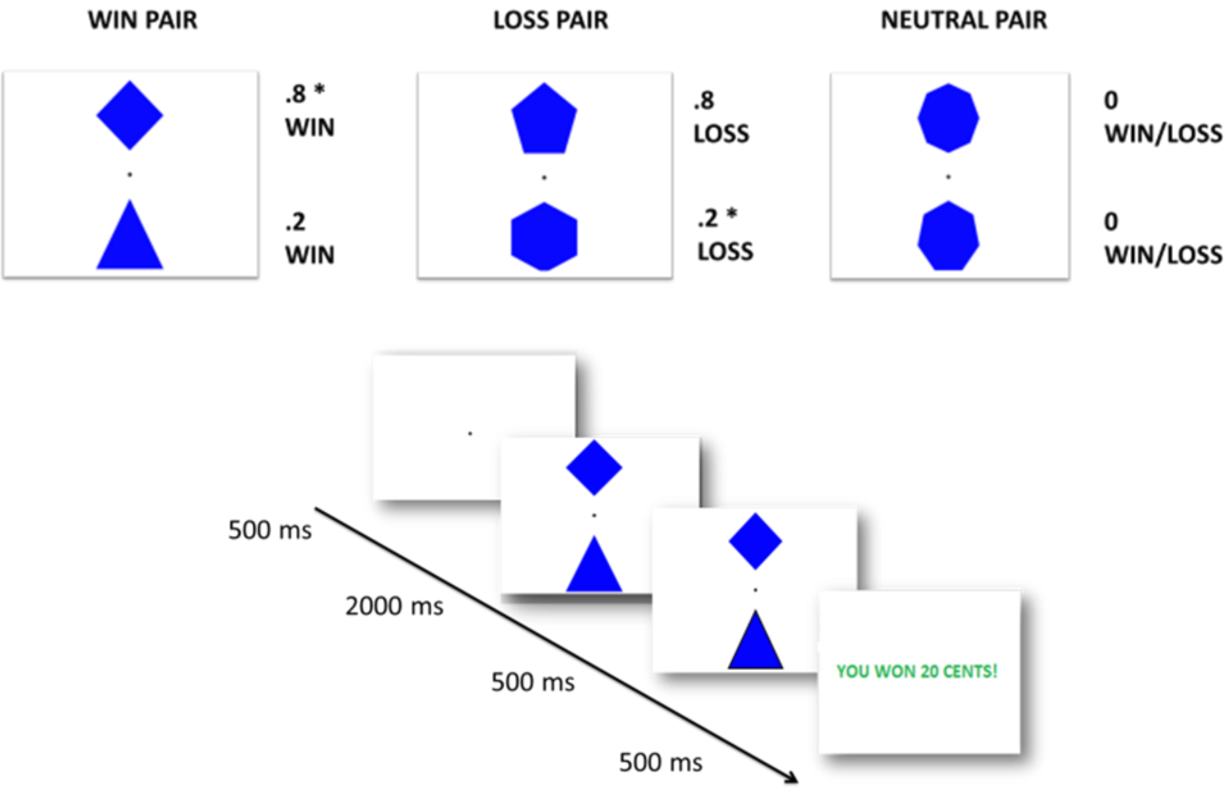

Figure 5. Upper part. Illustration of the 3 geometrical shapes pairs and their probability to be followed by the respective outcome. Asterisks (not seen by participants) represent the two most advantageous shapes to be chosen in order to maximize the final payout. Lower part: Timeline of the instrumental conditioning experiment. A central fixation cross appears for 500 ms followed by the geometrical shapes pair lasting 2 sec or until subject's response. After response, a screen with the selected figure appears for 500 ms followed by the relative outcome lasting 500 ms.

Visuo-tactile interaction task. Just after completing the conditioning task, subjects performed the PPS assessment task. Both the experimental task and set up were identical to that described in Experiment 1 (see Paragraph 1.1.3), except for the following details. Here, the visual stimuli were looming geometrical shapes selected in agreement with the instrumental conditioning phase. In particular, the most rewarded figure, the most punished one and one of the two neutral figures were chosen as experimental stimuli. When presented, they moved at a constant speed of 50 cm/sec, for a total time of 2000 ms and they were spaced out by an inter trial interval of 500 ms. All the geometrical shapes were included in a 180 by 180 pixels square and were projected in a 100x75 cm working area on the wall (Figure 2). Throughout the experiment, 324 trials were presented, consisted of 15 repetitions of each pair for each spatial distance randomly intermingled with 54 catch trials. Stimulus presentation and response collection were controlled by OpenSesame software 3.1.

2.2 Results

Visuo-tactile interaction task. Data from one participant were removed from the analyses due to anticipated responses to the tactile stimulation, exceeding 3 SD from the overall sample (M ± 3 SD = 26.3 ± 79.5 trials). Mean accuracy was 96.96% (± 5.57%) and it was not further analysed according to Experiments 1 and 2. Responses to stimuli at 90 cm were abnormally noisy (SD = 75.26) in respect to all other 5 distances (15 cm: SD = 53.36, 30 cm: SD = 55.72, 45 cm: SD = 55.34, 60 cm: SD = 57.67, 75 cm: SD = 69.04), possibly also due to inter-trial interval that was reduced from Experiments 1 and 2 to Experiment 3 (from 800 ms to 500 ms), to shorten the duration of the experimental session.[4]

We conducted a linear mixed model analysis (LMM) with the same approach described for previous experiments. In order to find the best random intercept, we analysed the effect of Id and Trial and we found out that the inter-individual variability ($\chi^2_{(1)}$=2829.4, p<.001) improved the fit of the model, while the inter-trial variability ($\chi^2_{(1)}$=3.3334, p=.07) does not. Consistently with previous experiment, the random effect was represented by subjects. We put in the model the fixed effects represented by the continuous variables Distance and Win (the total amount of money earned at the end of the

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[4] For this reason, we decided to remove the distance 90cm from the analysis showed in the main text. However, we ran a control analysis including the 90cm that showed that the only significant difference in the results, from those presented here, is the exponential factor of the variable Distance that was cubic instead of quadratic.

conditioning phase, ranging between 3.5 and 6.5 €) together with the nominal variable Valence (positive, negative and neutral conditions). We searched for the model that best fit the data for the continuous variables Distance. Quadratic distance improves the fit in respect to the linear model, ($\chi^2_{(1)}$=4.484, p<.03) while a cubic ($\chi^2_{(1)}$= 0.958, p=.32) or a quartic one ($\chi^2_{(2)}$=1.7951, p=.40) do not. Therefore, the quadratic function of the variable Distance, Valence and Win were treated as the fixed factors in the analysis. The linear mixed model that showed the best fit to the data included all fixed and random factors together with their two and three-way interactions. In this final model, we found a main effect of Distance ($F_{(1,6867.2)}$=11.8297; p<.001) that was followed by a significant main effect of its quadratic function ($F_{(1,6867.1)}$=4.4247; p=.03) (Figure 6) as well as a main effect of Valence ($F_{(2,6867.1)}$=5.0216; p=.006), indicating that participants reacted faster for rewarded than for punished and neutral stimuli (positive: M ± SD= 364.03 ± 62.94; negative: M ± SD= 367.80 ± 65.61; neutral: M ± SD = 369.25 ± 64.07). There were a significant two-way interaction between Distance and Win ($F_{(1,6867.1)}$=5.4448; p<.001) (Figure 7) and a three-way interaction between Distance, Valence and Win ($F_{(2,6867.1)}$=3.7856; p=.02) (Figure 7). A main effect of Win was not significant ($F_{(1,35.7)}$=1.7542; p=.19). Figure 7 shows that the level of Win – that is a measure of the conditioning effect – affects RTs at near distances for all the conditions tested (positive, negative, neutral) as can be seen from the tight shades of colour in the left side of the three panels. At far distances, the level of Win seems to exert a small effect in the reward and punishment conditions (Fig 7, panels a and b), while it is ineffective in the neutral condition (Fig.7c).
Overall, these findings suggest that the conditioning level of positive, negative and neutral stimuli affected performance in a similar way when visual stimuli are located at short distances from the body, while at farther distances, the level of conditioning seems relevant for positive and negative, but not neutral stimulus encoding. Consistent with results of Experiment 1, here we replicated that stimuli associated with a neutral value induce a different response from positive and negative ones as far as the distance from the body increases.

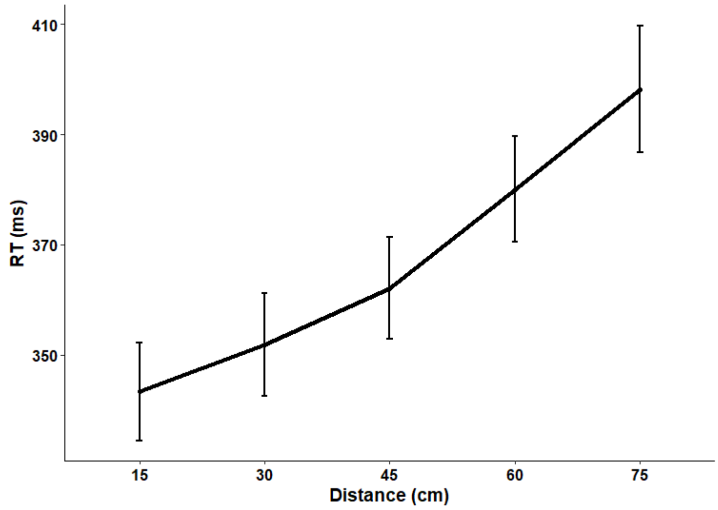

Figure 6. Main effect of Distance. Error bars indicate standard errors of the mean. The values reported are taken from aggregate data. Data are better explained by a quadratic function.

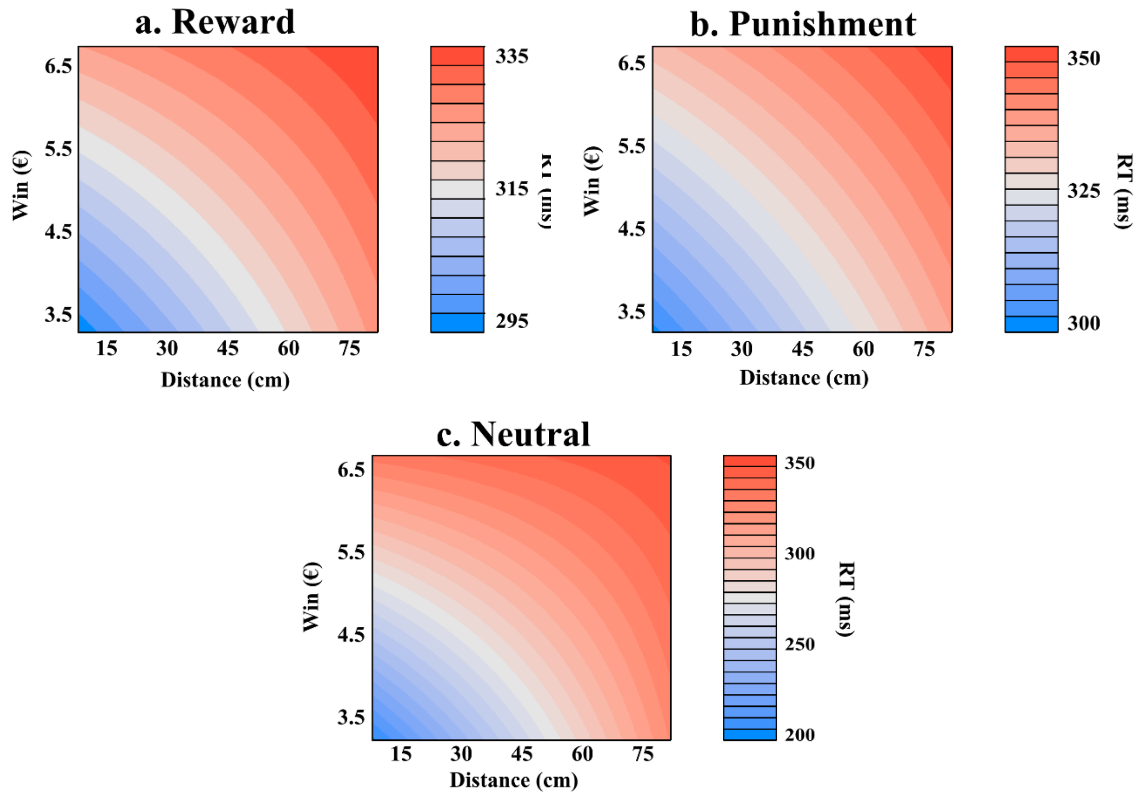

Figure 7. Three-way interaction between Distance, Valence and Win. The three panels illustrate the interaction between Win (y axis) and distance (x axis) as a function of the different valences of the stimuli. a) Reward condition b) Punishment condition c) Neutral condition. Different RTs are represented with different colours from blue (faster) to red (slower). While at shorter distances RTs of all the three valences are modulated by win factor, this remains true at the farthest distances only for stimuli with a connoted valence and not for neutral stimuli, that far from the body are not modulated by the win.

3. Discussion

In this work, we sought to clarify how visuo-tactile integration in space is sensitive to stimulus valence. In particular, we tested whether intrinsic and acquired stimulus valence exerts the same modulation of visuo-tactile interactions across space, controlling for the level of stimulus-induced arousal and the role of tactile expectancy.

We found that approaching visual stimuli with connoted valence (both intrinsic and learned) increase their modulatory effect with the increasing of the distance from the body. Indeed, while at shortest distances valence connoted and neutral stimuli are basically equivalent, at farthest distances positive and negative visual stimuli affect tactile responses more than neutral ones.

Overall, we observed a reduction of tactile RTs when concurrent visual approaching stimuli were situated near, as compared to far away from the body, compatible with an increased visuo-tactile integration for visual stimuli inside PPS (Haan et al., 2016, Kandula et al., 2017). Looming stimuli are particularly suitable to assess PPS boundaries as compared to receding ones, due to their stronger spatially-dependent effects on tactile processing (Canzoneri et al., 2012, De Paepe et al., 2016, Kandula et al., 2017) as well as to their stronger attentional preference as shown also in monkeys (Maier et al., 2004). Furthermore, in Experiment 2 we tested whether receding stimuli affect tactile responses in a similar way of that recorded in Experiment 1. Experiment 2 shows a different pattern of results, as demonstrated by the clear effect of expectancy of the tactile stimuli (which increases with time delay) in speeding up RTs (Kandula et al., 2017, Van Ede et al., 2011), that adds to the effect of visual stimulus proximity to the body (for a review see Maravita et al., 2003) in speeding up RTs when looming stimuli come closer to the body. The impact of expectancy could have been enhanced in our experiment, also due to the fact that the ratio between the true (visuo-tactile) and catch trials (only visual) was 5:1, a ratio that differs from that of 1:1, recently demonstrated to be optimal for this kind of paradigms (Kandula et al., 2017) and should be implemented in future research. However, and crucially, Experiment 2 also showed that valence of stimuli does not interact with distances when the visual stimuli are moving away from the body. This suggests that valence modulates the response to approaching stimuli, but not to receding ones. This is in agreement with a vision of PPS as a space for interaction (working or defensive), so that the valence of a stimulus moving away from the body becomes less relevant as source of potential interaction. If valence was modulating the expectancy of a sensory event per se (and not PPS multisensory interactions), we should have found the very same interaction between valence and distance with approaching and receding trials (i.e., distance and time are invariantly related in our task) in Experiment 1 and 2.

Another key aspect of our findings is that the distribution of our RTs reflects more a gradient of response rather than an abrupt change at a certain distance. This gradual modification is consistent with the literature in healthy human adults, showing gradual change in the processing of stimuli in space (Cowey et al., 1998, Varnava et al., 2002, Longo & Lourenco, 2006, De Paepe et al., 2016), more than with the idea of a net setting the extension of the PPS (Sambo & Iannetti, 2013). For example, Longo and Lourenco (2006) have shown that participants requested to perform a bisection task on lines at different distances, using a laser pointer, show a bias of the subjective midpoint that gradually shifts from left to right with increasing line distance, suggesting a gradual transition from near to far space. This gradual modulation of PPS representation is reminiscent of the electrophysiological findings in monkeys (Fogassi et al., 1996, Graziano et al., 1997), showing that the probability of discharge to a visual stimulus of visuo-tactile neurons, gradually decreases as the distance between the visual stimulus and the cutaneous RF increases, without any sudden change of response pattern with distance. An alternative method used in the literature to establish the PPS extension, is to fit the responses to a sigmoidal function, assuming that the central point of the function corresponds to the boundary of PPS, and the stipe of the slope indicates how much blurred that limit is (Canzoneri et al., 2012). By adopting this method, previous studies demonstrated how PPS boundaries change after specific experimental manipulations (Teneggi et al., 2013, Serino et al., 2015) as well as they revealed how roughly blurred the transition from PPS to far space is (Stone et al., 2017). However, sigmoidal estimation is grounded in the assumption that the PPS is comprised within the limit of a precise boundary, which indeed was the most important aspect for most of the studies adopting this method of assessment (Canzoneri et al., 2012, Ferri et al., 2015, Serino et al., 2015). Our result, however, stress more the notion that PPS may not be a rigidly defined area with sharp boundaries rather than it is characterized by fuzzy limits, a sort of gradient, reflecting the progressive incremental probability of visual stimuli approaching the body (Graziano et al., 1997), so we did not relay on the aforementioned sigmoidal function to look for a strict limit between PPS and far space.

Consistently with the nature of PPS as a sensory-motor interface between our body and the external environment, a growing number of studies investigated the double nature of PPS as both the locus of reaching/approaching objects of interest and defence/avoidance of threatening ones (for a review see de Vignemont & Iannetti, 2015). In this view, it is likely that stimulus valence is promptly examined, with particular attention to the near space considering its permeability to the intrinsic properties of the object (Ferri et al., 2015) as well as those belonging to the perceiver (Lourenco et al., 2011, Sambo & Iannetti, 2013, Ardizzi & Ferri, 2018).

In the Experiment 1, we found that the presence of a looming visual stimulus located at short distances speeds up the detection of a tactile event regardless of its valence (positive, negative and neutral) or its arousal level. So that when it is close to our body, every kind of stimulus is salient and induce a speeded reaction. At farther distances, arousal level of stimuli seems not to influence the performance significantly. On the contrary, valence becomes relevant as we found that positive and negative stimuli induce faster RTs than neutral ones when far from the body. This result suggests that when stimuli hold a positive or negative valence, and are therefore biologically relevant or salient, they induce a facilitation for crossmodal integration with tactile stimuli even far from the body, although to a less extent respect when they are close to the body. On the other side, when a stimulus is not salient per se, spatial distance from the body may induce the modulation of the crossmodal facilitation.

Interestingly in Experiment 3, it was found that the higher the value of the learning of valence, the slower the response at the nearest distances from the body. Participants showing higher conditioning effect, seem to go through a deeper evaluation of the ongoing stimuli. This is particularly true when the approaching stimulus is located near the participants' body, and much less when it is away from it[5]. Furthermore, it is worth noting that such spatial modulation of the conditioning effect was even weaker for neutral stimuli. In other words, analogously to Experiment 1, stimuli carrying a relevant information due to their positive or negative valence, keep their modulatory effect across the entire space under our investigation, while neutral ones are processed differently according to the actual distance.

Taken together, these results show that visuo-tactile interactions in space can be triggered by the direction of the visual stimulus together with the different intrinsic and acquired valence of stimuli. Indeed, both positive and negative stimuli modulate the motor response to bodily input even when located far from the body. On the contrary, this facilitation is reduced for neutral stimuli in far space. However, given that everything becomes relevant as progressively comes closer to the body and is therefore worth to be promptly processed, the response to all kind of stimuli (positive, negative and neutral) becomes equally efficient. Apparently, our results seem in contrast to previous research investigating the relation between PPS and valence of looming stimuli, which reported the unique advantage for negative stimuli (Ferri et al., 2015). However, as highlighted in the introduction, it is possible to argue that the lack of spatial modulation played by positive stimuli in the above-mentioned study is due to their different arousal level compared to negative stimuli, so that

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[5] As the reviewer suggested, the interpretation of the two-way interaction between Distance and Win reported here could not be consistent with the general notion that all stimuli are salient when close to the body. Therefore, it is fair to underline that this effect could be explained by alternative interpretations (e.g. anxiety level of participants).

arousal and valence were confounded. In the present study, instead, the preliminary weighting of the arousal level of both positive and negative stimuli allowed to assess the role of valence in modulating PPS in a less confounded way.

Next studies may further clarify our results in respect to some methodological aspects. In particular, the above-mentioned balance between real and catch trials may furtherly qualify the contribution of distance and expectancy modulating RTs. Moreover, it would be worth looking into the effect of conditioning on shaping the spatial visuo-tactile interactions depending upon stimulus valence. One could argue that the present reward and punishment were not strong enough to yield effective conditioning, that could well change depending upon contingent factors such as the ecological aspects of stimulus setting or the kind of reward/punishment in determining the effects. For the latter aspect, it is worth mentioning, however, that there are good reasons to believe that the instrumental conditioning paradigm worked. A procedure using implicit measures (IAT) was used in a prior experiment, in which the most rewarded and the most punished geometrical shapes encountered in the previous conditioning phase, were temporarily associated both to positive or negative attributes. Results showed that this association was significantly stronger when the most rewarded and the most punished figures were respectively related to positive and negative attributes, thus supporting the effectiveness of the instrumental conditioning paradigm (see Supplementary Materials for more details). To the same token, the quality of negative valence attributed to a stimulus may produce extremely different effects on visuo-tactile interactions. As suggested by an anonymous reviewer, one could expect that valence-connoted stimuli may exert a stronger modulation closer to the body instead of far from it, because they are more likely to interact with the observer. This could be particularly true when using threatening stimuli (such as those producing or suggesting real physical pain), that may strongly affect RTs in near space as compared to neutral stimuli, even before actually touching the body (for evidence of this, see: Romano et al., 2014). The lack of specific modulation by negative stimuli in near space, found in the present work, may reflect, in facts, the not sufficiently high threatening value of such stimuli. Further studies may clarify this issue by comprising negative stimuli with different biological meaning for the observer.

In summary, these findings suggest that intrinsic and learned valence of looming, but not receding, stimuli shapes visuo-tactile interactions in space in a similar way. While close to the body, all the visual stimuli induce the same facilitation to the tactile detection, at farther bodily distances, neutral stimuli are encoded differently from negative and positive ones either in case of intrinsic or learned valences, entailing longer RTs (Experiment 1) and a null modulation by the conditioning level (Experiment 3). In other words, while salient stimuli tend to activate multisensory integration with bodily stimuli even at farther distances from the body, neutral one becomes salient only when they are close to it, even if the information that is intrinsically or extrinsically related to it is not relevant per se[6]. Further to confirm the plasticity of visuo-tactile interactions in response to specific stimulus properties, these results stress the privileged role of PPS as an interface between body and environment, as showed here by the promptly processing of all kinds of stimuli located near the body, thus highlighting the incredible centrality of our body in the interactions with the external world.

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[6] As the reviewer suggested, the lack of difference in RTs between positive, negative and neutral stimuli at short distances could also reflect the absence of need/possibility to adapt behaviour when the visual stimulus is very close to the body.

Supplementary Material

Everything is worth when it is close to my body: how spatial proximity and stimulus valence affect visuo-tactile integration

Pilot Experiment: Value-Learning Task and IAT (Implicit Association Test)

Introduction: Implicit Association Test (IAT) is an implicit measure test in which subjects are required to categorize as fast and accurate as possible figures or words within specific labels. It is suitable to test the strength of association between concepts (e.g., categories and attributes) stored in memory (Greenwald et al., 1998).

Aim: in order to verify the value-learning task effectiveness, we administered to a pre-experimental group, the value-learning task immediately followed by an Implicit Association Test.

Hypothesis: participants should be faster and more accurate to categorize the most rewarded figure with positive words as well as to categorize the most punished figure with negative words (congruent condition) rather than the reverse situation (incongruent condition).

Participants: 10 subjects took part to the pilot experiment (4 males, mean age ± sd = 24,8 ± 5,98; range 20-41; all right-handed). All subjects (students of University of Milano-Bicocca) were paid in change of their participation to the study and their compensation was related to the amount of money earned during the conditioning phase. This research was performed in accordance with the Declaration of Helsinki and was approved by the local ethical committee of the Department of Psychology, University of Milano-Bicocca.

Procedure: after completing the value-learning task (see value-learning phase of Experiment 2 for details), participants performed the IAT.

A IAT is composed of 5 blocks: 1, 2, 4 are learning blocks while 3 and 5 are test blocks. The total experiment consists of 176 trials, 16 learning trials for each learning block in addition to 64 test trials for each test block. In the learning blocks, participants have to learn to associate a particular word (e.g., cry) or geometrical shape (e.g., pentagon) to its own category (e.g., respectively to the labels "Negative" and "Pentagon"). In the test blocks, instead, categories and attributes are shown together and they are matched, thus forming two possible configurations: congruent trials for the block 3 (e.g., "Positive & Most Rewarded Figure" / "Negative & Most Punished Figure") vs incongruent trials for the block 5 (e.g., "Positive & Most Punished Figure" / "Negative & Most Rewarded Figure"). In these blocks, participants are required to press the "a" keyboard button when a geometrical shape or a word belonging to the first label - located to the high left angle of the screen - appears on the centre of the screen as well as to press the "l" keyboard button when the target is a geometrical shape or a word belonging to the second label - located to the high right angle of the screen. Inter-stimulus interval was 500 ms and participants had no temporal limits to categorize stimuli in the right label, however, they were repeatedly encouraged to be fast in their responses.

This experiment consists of 3 different IAT in which categories are made of geometrical shapes previously conditioned while attributes are positive or negative words (e.g., smile, cry, beautiful, ugly, etc.). The first IAT compares the most rewarded figure with the most punished one, while the second and third IATs respectively compare the most rewarded figure with the neutral one (e.g., the octagon) and the most punished figure with the neutral one. The administration order was counterbalanced between IAT2 and IAT3.

The three IAT tasks lasted overall 15 minutes while the total experiment (value-learning task + IAT) lasted 45 minutes. The IAT experiment was done by OpenSesame 3.1 (Mathôt et al., 2012).

Results: IAT score was calculated by the algorithm developed by Greenwald et al., (2003), that consists in a standardized difference between the mean RTs in blocks 3 and 5, adding a penalization system for incorrect responses (Greenwald' d).

We conducted a series of one-sample t-test against 0, in order to compare each IAT task performance with a default value. It was reported a significant IAT1 vs 0 (d=0,57; t(9)=4,90; p<.001), IAT2 vs 0 (d=0,43; t(9)=3,67; p=.005) and IAT3 vs 0 effects (d=0,27; t(9)=2,77; p=.022). This means that the association between geometrical shapes and attribute was not more neutral.

Discussion: the value-learning task effectively works, thus leading to a positive evaluation of rewarded figures and to a negative evaluation of punished figures.

Study 4

Neuronal oscillations of visuo-tactile integration in space: an EEG study on how stimulus valence affects PPS

Introduction

Peripersonal space (PPS) represents a sensory-motor interface between our body and the external world (Rizzolatti et al., 1981, 1997). This privileged zone around the body allows to promptly respond to every kind of stimulus interacting with us, in order to approach or avoid it (di Pellegrino et al., 1997, Graziano & Cooke, 2006). Based on the different type of motor interaction with nearby objects, recently, it has been proposed a dual model of PPS, with a clear functional distinction between goal-directed action (reaching space) and protection of the body (defensive space). Electrophysiological studies in the monkey revealed that PPS relies on a fronto-parietal network encoding preferentially visual and tactile stimuli occurring near the body (Fogassi et al., 1996, Duhamel et al., 1997, Graziano et al., 1999). A homologous PPS system seems to exist also in humans, as shown by the enhanced processing of tactile stimulation when a task-irrelevant visual stimulus is presented near the body (Spence et al., 2004, Serino et al., 2015, Haan et al., 2016) as well as by the vast amount of studies clearly indicating an overlap between PPS areas in non-human and human primate (Làdavas et al., 1998, Makin et al., 2009, Brozzoli et al., 2011). On the contrary, stimuli located far away from our body activate different neural areas from those responding to near stimuli. Indeed, neuroimaging studies in humans revealed that while the activation of premotor and parietal cortices is linked to actions performed in the near space, the ventral occipital and the medial temporal regions seem instead to be more sensitive to actions executed in far space (Weiss et al., 2000, 2003). This dorsal/ventral dissociation of near vs. far space is consistent with the distinction between the vision for action and perception (Goodale & Milner, 1992) that has been recently confirmed by an electrophysiological study conducted on healthy population (Valdès-Conroy et al., 2014). In this research, participants were asked to estimate their reaching capabilities in relation to valence-connoted visual objects located at nine different distances from their body. Authors found an effect of distance on ERPs, that is an activation of parietal and occipital sites in relation to the processing of visual stimuli located near and far from the body, respectively. Even though the dissociation between near and far space was here confirmed, no effect of stimulus valence on electrical brain activity was recorded. This result is opposed to those reported in literature, in which a different modulation of negative vs positive and neutral stimuli on P300 frontal amplitude has been recorded (Conroy & Polich, 2007). Specifically, the frontal P300 was smaller for negative than positive and neutral stimuli, implicating that affective processing can affect ERPs, even when arousal level is controlled. Moreover, a quick glimpse of emotionally relevant stimuli (e.g. positive and negative pictures) can modulate the early ERP waveform over temporo-occipital areas that starting at around 150 ms after picture onset and reaching its peak around 300 ms compared to neutral stimuli. In the same study, authors found that valence connoted stimuli entail also a late selective processing effect, as indicated by the enlarged LPP amplitudes to emotional compared to neutral images over centro-parietal sensors (Schupp et al., 2004). This result seems to be in line with some studies indicating that briefly presented affective pictures engage appetitive and aversive motivational systems as indexed by specific changes in facial EMG activity, startle reflex modulation and autonomic changes (Codispoti et al., 2001, Globisch et al., 1999).

Interestingly, a recent EEG study using virtual reality revealed that reaching PPS processing elicits mu rhythm desynchronization (8-12 Hz) in the centro-parietal areas of the brain (Wamain et al., 2016). The authors aimed at disentangling whether the mere view of an object located inside PPS can induce motor cortex activation. To this end, they made participants perform two different tasks, a perceptual identification task and a reaching estimation task in which they had to respond to visual stimuli located near, at the border or far from participant's body. A progressively reduction of mu rhythm desynchronization was reported, starting 300 ms after object presentation from peripersonal to extrapersonal space only for the reaching estimation task, thus indicating that motor coding of visual objects not only depends on object's location in space but also on the task goal. Moreover, another EEG study using virtual reality conducted by Gonzalez-Franco and colleagues (2014) observed a mu rhythm desynchronization over the primary sensorimotor areas (C3-C4) in defensive PPS, reflecting motor cortex activation when the embodied virtual hand was threatened by a knife (experimental condition) but not when the table was attacked by a knife (control condition). Given that this result is similar to the mu-ERD (event-related desynchronization) induced when an imaginary hand movement is performed (Pfurtscheller & Lopes Da Silva, 1999, Neuper et al., 2005), the authors concluded that participants behaved as if the real hand was threatened, thus trying to avoid harm. Accordingly, previous studies have revealed signal attenuation within 8-13 Hz frequency range, that is an event-related desynchronization of mu rhythm in situations associated with motor preparation and execution (Babiloni et al., 1999; Llanos et al., 2013; Salenius et al., 1997), movement observation (Cochin et al., 1999; Pineda et al., 2000) and motor imagery (Braadbaart et al., 2013; Hari, 2006; Muthukumaraswamy et al., 2004). However, it is worth noting that also beta band oscillations (13-30 Hz) are subjected to desynchronization over sensorimotor area during motor movement (McFarland et al., 2000) and motor imagery (Pfurtscheller & Neuper, 1997).

In the present EEG experiment, participants performed a tactile discrimination task (i.e. to report where they felt the vibration that could be delivered on two opposite sides of the right hand) while they were asked to look at valence-connoted visual stimuli located at different distances from their body. The main aim of the present study was to replicate Wamain et al. (2016) results through a visuo-tactile task. Indeed, it is reasonable to believe that mu rhythm desynchronization over centro-parietal areas could be stronger for visual stimuli presented in near space than in far space, considering that PPS is encoded by such a visuo-tactile system (Fogassi et al., 1996, Duhamel et al., 1997, Graziano et al., 1999). This expected result could also be corroborated by Evans & Blanke (2013) study, which demonstrated that the visuo-tactile synchrony underlying the illusory hand ownership entails a suppression of frontal-parietal areas like that evoked by the motor imagery during the rubber hand illusion paradigm.

Secondary, we were also interested in investigating if the beta band oscillations are differently modulated by the distance at which the visual stimulus is presented (Pfurtscheller & Neuper, 1997). Considering that nearby visual stimuli constitute attracting poles of interaction for the perceiver, it is possible to speculate that also beta power decrease over sensorimotor cortex could be stronger for visual objects located in PPS rather than outside it (McFarland et al., 2000). Furthermore, van Ede et al. (2010, 2011) found that the expectation of a lateralized tactile target modulates pre-stimulus beta band oscillation, entailing a contralateral suppression of this frequency range that originates at least partly in the primary somatosensory cortex (S1). Even if the modulation of this oscillatory activity was not restricted to attended tactile events, authors found a stronger suppression during state of attentive expectation. Therefore, it is plausible to find a stronger contralateral beta suppression for visual stimuli located near rather than far from the body, before the tactile input delivery (-350 to 0 ms). Indeed, because of the strong connection between visual and tactile sensory modalities in PPS for action purposes, the presence of the visual stimulus located near the body should trigger a preparation towards upcoming bodily events.

In addition to the possible role exerted by distance in the modulation of the mu and beta frequency bands, another aim of this study was to investigate how the different valence of the visual stimuli can shape mu and beta rhythms in relation to space. Despite the explorative nature of this experimental question, we could hypothesize that positive and negative visual stimuli could activate the motor cortex in the same way in near and far space, given that in Studies 1 & 3 we found that valence-connoted visual stimuli entail larger visuo-tactile interactions in space compared to neutral ones. This expected result could reflect the engagement of appetitive (approaching behaviour) and aversive (avoidance behaviour) motivational systems for positive and negative visual stimuli, respectively (Schupp et al., 2004).

Finally, to better understand if the positive and negative valence of the objects differently shapes the reaching and defensive PPS, the same participants underwent two behavioural tasks - staircase procedure (Cornsweet, 1962) – assessing the reaching and defensive PPS, respectively. By using the same visual stimuli as for the EEG task, we were able to to compare the staircase results with those deriving from the neuronal oscillations, in order to explore if the visuo-tactile interactions in near space are more sensitive to a reaching or defensive PPS interpretation (de Vignemont & Iannetti, 2015).

Methods

Participants

35 healthy volunteers (25 females, mean age ± sd = 26.09 ± 6.34 years, range = 18-47) participated in the study. They were all right-handed according to the screening test they underwent upon the arrival at the lab. They had normal or corrected to normal visual acuity and they did not have any problem with their sense of touch as self-reported. Recruitment of participants and testing conformed to the Helsinki Declaration and the local Ethics Committee approved this study. Each subject received monetary compensation for the participation to the study (10 € per hour).

Validation phase. In the first pre-experimental session, a first group of subjects (N = 30, 22 females, mean age ± sd 24,65 ± 4,31 years, range =19-40) was invited to rate 162 visual stimuli through a 9-points Likert scale. They had to rate four stimulus features: valence, arousal, grasp and touch. After the stimulus presentation at the centre of the screen for 1500 ms, participants had to first rate the valence – Rate how negative/positive the picture just displayed is - and the arousal – Rate how arousing the picture just displayed is - choosing among 9 alternatives (from “completely negative/completely unarousing” to “completely positive/very arousing”, where the central point was respectively the neutral/medium point). Then, the visual stimulus appeared again at the center of the screen for other 1500 ms, after that subject had to complete the two remaining scales about grasp – Rate if is it easy or difficult to grasp and lift the object just displayed using only the right hand - and touch – Rate if would you like or dislike to touch the object just displayed - choosing their response among 9 alternatives (from “very easy/dislike very much” to “very difficult/like very much”, where the central point was the neutral point). The experimental visual stimuli were selected from web and they included 81 paires of stimuli with 81 positive and 81 negative images, paired by semantic, color or shape associations. This procedure allowed us to select the 20 stimuli for each category used in the successive experimental step (Figure 1). Stimuli presentation was done through a computer (Lenovo 320-15ABR, 16”). The experiment lasted 45 minutes and was run by OpenSesame software 3.1 (Mathôt et al., 2012).

Results validation phase. We conducted a preliminary descriptive analysis in order to take under control the Valence, Arousal, Grasp and Touch mean scores relative to each visual stimulus. Then, we chose the 40 visual stimuli characterized by appropriate scores on each sub-scale and we divided them in two categories “positive” and “negative”. Then, we performed paired samples t-tests comparing them for Valence, Arousal, Grasp and Touch scores. It was reported a significant effect of Valence ($t_{(29)}$=13,85; p<.001), indicating that the two groups of visual stimuli were rated with a significantly different valence level (positive vs negative: M ± DS = 5.543 ± 0.636 vs M ± DS = 3.04 ± 0.93), as well as a significant effect of Touch ($t_{(29)}$=17.667; p<.001), revealing a different degree of pleasantness to touch the object between the groups (positive vs negative: M ± DS = 5.245 ± 0.83 vs M ± DS = 2.748 ± 1.343). The two remaining factors, Arousal ($t_{(29)}$=1.165; p=.254) and Grasp ($t_{(29)}$=1.846; p=.075) were not significant, respectively suggesting that all the stimuli were judged with the same activation level (positive vs negative: M ± DS = 4.208 ± 0.742 vs M ± DS

= 3.891 ± 0.64) and with the same grasping difficulty (positive vs negative: M ± DS = 1.462 ± 1.035 vs M ± DS = 2.003 ± 1.246).

Figure 1. The 40 stimuli used in the EEG task, staircase procedure and validation session. Positive (left side) and negative stimuli (right side) are paired by color, shape or semantic association.

EEG acquisition

Participants were equipped with an EEG Active Two Biosemi system cap (Amsterdam, The Netherlands, www.biosemi.com), made up of 32 active scalp channels. Their locations observed the International 10-20 EEG system using Ag-AgCl-tipped electrodes. EEG signal was continuously recorded at 2048 Hz sampling rate (bandwidth 417 Hz, Highpass 0.16 Hz, Lowpass 100 Hz, y-scale 100 uv). Electro-oculogram (EOG) was also recorded from a bipolar montage, from the sub and supra orbital regions of the right eye and the outer canthi of the eyes. A reference electrode was put on the mastoid, behind the right ear.

Procedure

EEG task. Upon arrival at the laboratory, participants were screened for the presence of neurological or psychiatric conditions. Left-handed was considered as an exclusion criterion. The consumption of maximal fourteen alcoholic beverages per week was allowed. After completing the screening test, participants were invited to seat in front of a table – different from the experimental one - and to stretch their right arm as far as they can. Experimenter measured the real reaching distance of each participant and put the correspondent value inside the EEG script. EEG recording procedure was then explained to participants and informed consent was obtained.

As soon as participants were equipped with the EEG cap, they were invited to take the experimental seat on a comfortable chair in a dark room adjacent to the control room. During this phase, they were instructed to relax and to keep movements to an absolute minimum. They were also asked to wear headphones throughout the whole experiment and to lean their right hand on a big screen placed flat on a table in front of them with the dorsal side up, positioning the tip of their middle finger at 18 cm from the central edge of the screen. They were also provided of two vibrotactile sensors, located on the first phalanx of their right little finger and of the right thumb, respectively. Finally, they were invited to put their head in a chinrest (height: 41 cm from the table-27 from the monitor) and to place their left hand on a keyboard located under the monitor, positioning the middle and the index finger on the response buttons (1-2, respectively) (Figure 2).

The EEG experiment is a tactile discrimination task. Participants looked at 40 visual stimuli (Figure 1) with different valence (positive vs negative), located at 3 different spatial regions from their right hand (near, at the border, far space) in one of the three distances that correspond to: + 50, 60, 70% (far space), - 50, 60, 70% (near space), -10, 0, + 10% (border space) of the real reaching distance of each subject that was previously measured. Visual images were included inside a 12.5 x 12.5 degrees square and displayed along the central vertical line of the big monitor (PH BDL 5530 EL screen dimension 122 x 68 cm, 1920 x 1080 screen resolution, 60 Hz refresh rate) by standing out on a grey background (RGB 163.163.163) (Figure 2).

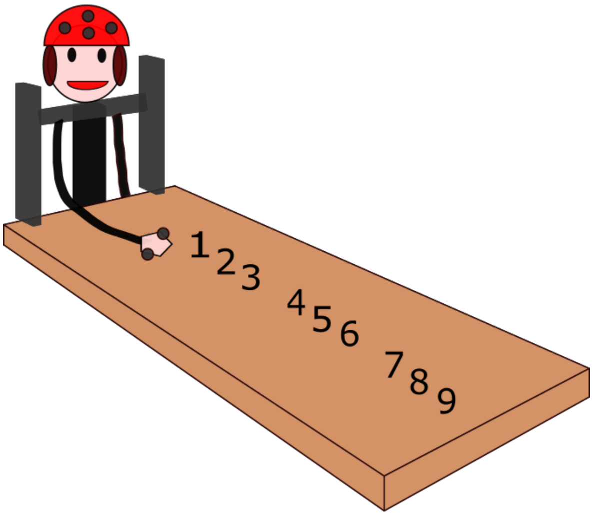

Figure 2. Sketch of EEG experiment. Participant was seated in front of the big monitor in which one of the 40 visual stimuli could appeared in one of the 9 distances displayed by numbers (1,2,3 refer to Near Space, 4,5,6 to Border and 7,8,9 to Far Space)[7]

Every trial started with a fixation dot of a random duration between 500 to 800 ms, that appeared in one of the nine possible locations described above. After that, the visual stimulus appeared for a random duration of 1000-1300 ms in the location previously marked by the fixation. Following stimulus presentation, depending on the characteristic of the trial - if it was a GO or a NO GO trial - a thick red square appeared around the visual stimulus for 1200 ms or the trial stopped, respectively. In the GO trials, participants had to respond as fast as possible indicating where they felt a 300 ms vibrotactile stimulus that was delivered on the little finger or in the thumb of the right hand 100 ms before the red square appearance. Responses were given by pressing with the index and middle finger of the left hand “1” or “2” button of the keyboard located under the monitor (response buttons were counterbalanced

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[7] Please note that the numbers reported in Figure 2 are only for illustrative purposes.

across participants). In the NO GO trials, instead, participants were requested to not respond but simply observe the stimulus (Figure 3).

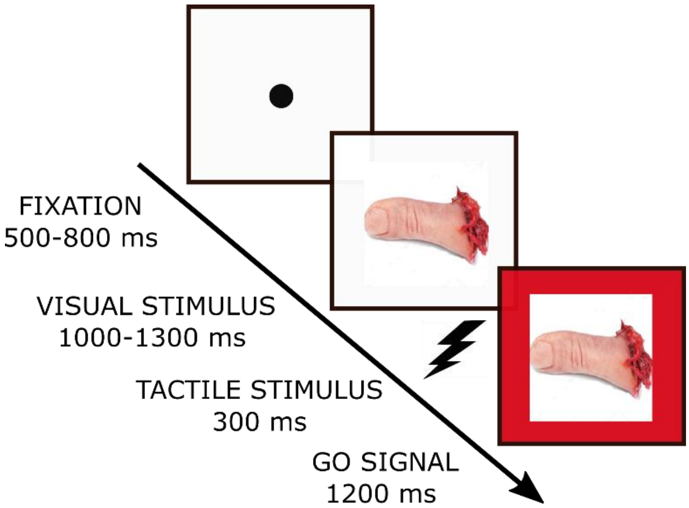

Figure 3. Timeline of the Tactile Discrimination Task. Participant could receive three types of trials: 1) NO GO trial without tactile stimulus 2) NO GO trial with tactile stimulus 3) GO trial with tactile stimulus. Depending on the trial type, the trial stops at three different time points: at the end of visual stimulus (type 1), tactile stimulus (type 2), GO signal (type 3).

It is important to highlight that participants also received a vibration on the right thumb or in the right little finger in a percentage of NO GO trials. In this case, participants were instructed to ignore the tactile vibration and to not respond to it. This allowed to exclude any possible influence of tactile expectancy which has been shown to play a key role in masking the multisensory effect within peripersonal space (Kandula et al., 2017). Taking into account that the optimal ratio of tactile to no-tactile stimuli is 1:1, the vibration was delivered only in the 48% of the trials (for the near and far space: 216 NO GO trials without tactile, 144 NO GO trials with tactile and 36 GO trials with tactile; for the space at the border: 18 NO GO without tactile, 18 NO GO with tactile and 36 GO with tactile for the border region). This task was made up of 864 trials and was divided into three blocks lasting 10 minutes each (288 trials for each block). Between successive blocks, participants were allowed to have a rest. We explored better the near and far regions of space to the detriment of the border, therefore the successive analysis was done only to the far and near regions. At the end of the experiment, subjects were debriefed, filled in a vibrotactile questionnaire in order to check if the stimulus intensity was enough to feel it and received their participation fee. Vibrotactile stimuli were produced by an 8 mm vibrotactile motor (Precision Microdrives, model: 308–00). The experiment lasted 45 minutes and was run by Presentation software.

Staircase. In order to understand if the reaching and defensive PPSs have the same amplitude in relation to positive vs negative visual stimuli, the same experimental group (N = 35, 25 females, mean age ± sd = 26,09 ± 6,34 years, range =18-47) performed the staircase procedure - a psychophysical method used for estimating threshold by adjusting stimulus levels from trial to trial until a stopping rule is reached (Cornsweet, 1962). Their task was to respond as fast as possible to a visual stimulus located at different distances from their right hand, displayed through a big monitor (PH BDL 5530 EL screen dimension 122 x 68 cm, monitor dimension 134 x 80, 1920 x 1080 screen resolution, 60 Hz refresh rate) placed flat on a table. Participants were seated in a dark room at the short end of this screen with their right hand on it, dorsal side up, positioning the tip of their middle finger at 18 cm from the edge of the screen. Their head was fixed with a chinrest (height: 41 cm from the table-27 from the monitor) (Figure 4).

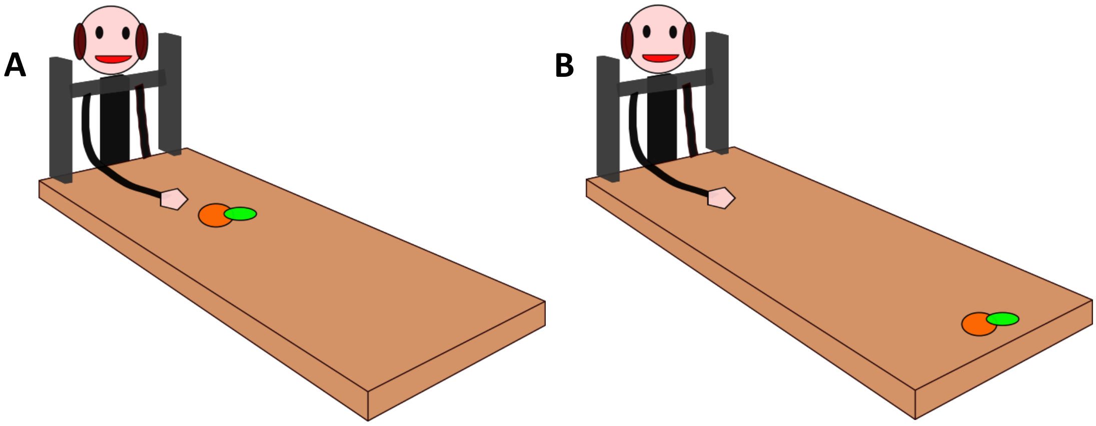

Figure 4. Illustration of staircase procedure. Panel A) Visual stimulus located at the nearest distance – Ascending Series 1. B) Visual stimulus located at the farthest distance – Descending Series 1

Visual stimuli were the same 40 stimuli used in the EEG task (Figure 1) and they were included inside a 12.5 x 12.5 cm square. They were displayed along the central vertical line of the big monitor by standing out on a grey background (RGB 163.163.163). Participants completed four staircases that differ from one another for the type of task – Reaching vs Defensive – and for stimulus valence – Positive vs Negative. The Reaching Positive, Reaching Negative, Defensive Positive, Defensive Negative staircases were made up of 4 blocks each: descending 1, descending 2, ascending 1 and ascending 2. The descending and ascending series differ one another for the starting position of the visual stimulus, located respectively very close (Figure 4, Panel A) and far away (Figure 4, Panel B) to participant's hand, as well as for the movement type of the stimulus, that was respectively approaching vs receding from participant's hand. Each trial started with a 500 ms fixation dot located in the same region of space of the upcoming target, followed by the visual stimulus lasting until the response was recorded. In every single trial, participants had to press one of the two mouse buttons (left vs right) with their left hand that was placed perpendicularly to the right one just below the big monitor. In the Defensive task, participants had to press the left button of the mouse for " feel uncomfortable" and the right button for "feel comfortable" with that object located at that distance from their hand. In the Reaching task, instead, they were instructed to press the left button "if they could reach" and the right button "if they could not reach" that object located at that distance from their hand. As soon as the response was given, visual stimulus disappeared and depending on that response, another visual stimulus appeared located farther away or closer from participant's hand (i.e., if in the Reaching descending series participant pressed "no" to a stimulus located at a certain distance from his/her hand, indicating that he/she could not reach it, the visual stimulus got closer in the very next trial. Conversely, in case of "yes" response, the stimulus moved away in the subsequent trial). In the first descending/ascending series, the staircase step size was 2 cm while in the second ones, it reduced to 0.5 cm. The transition from the first staircase to the second one was determined by the achievement of a fixed numbers of 'reversals', that are stimulus direction changes depending on subject’s response collected inside the very same staircase series. Subjects performed the first series until 6 reversals were recorded, while the second one finished when 12 reversals were registered. In case of 20 equal and consecutive responses recorded while the visual stimulus was located at the shortest distance (“I cannot reach it”/”I feel comfortable”) or farthest distance (“I can reach it”/”I feel uncomfortable”) from participant’s hand, the staircase stopped and the PPS threshold was set at the minimum and maximum distance, respectively. In the first descending/ascending series, the starting position of the visual stimulus – calculated from the center of the image because visual stimuli occupied different space inside the square - was always equal to 98,25 cm and 8,25 cm from subject’s hand, respectively. In the second descending/ascending series, it depended respectively on the highest/lowest spatial distance in which a reversal was recorded during the first series. At the end of this procedure we were able to calculate Reaching and Defensive PPS thresholds for positive vs negative stimuli in a very accurate way, by averaging all the reversal spatial points recorded during the second descending/ascending series. The order of series presentation, the response buttons for ‘yes’ and ‘no’ responses as well as the order of the three tasks were all counterbalanced across participants. The experiment lasted overall 15 minutes and was run by OpenSesame software 3.1 (Mathôt et al., 2012).

EEG data processing

For offline analysis, continuous EEG signal was filtered (basic FIR filter, 1–100 Hz) and recalculated based on average reference using EEGLAB software (Delorme & Makeig, 2004) for MATLAB environment (The Math Works Inc.). Periods with excessive noise artifacts were removed by visual inspection. ICA-based artifact correction was used in order to correct for blink artifacts (Delorme, Sejnowski, & Makeig, 2007) and bad ICA components were automatically removed by using SASICA. The signal was then divided into periods of 2200 ms around the onset of the visual target (700 ms pre-target and 1500 ms post-target onset) as well as into 3200 ms periods around the onset of the tactile input (1900 ms pre-target and 1100 ms post-target).

Epochs still contaminated by muscular contractions or excessive deflection (±75 μV) were automatically detected and were excluded (total rejection rate was about 10% in both the epochs). Event-related changes in the oscillatory activity were quantified using a time-frequency wavelet decomposition of the continuous EEG signals between 1 and 100 Hz (complex Morlet's wavelets, ratio fo/σf = 7) implemented in a "wtools" toolbox (available on request). In order to represent frequency modulation induced by target presentation, the mean spectral power of the pre-event period (visual epochs: from -300 ms to -100 ms, tactile epochs: from – 1500 ms to – 1300 ms) was considered to be a baseline level and was subtracted from each time point for a given frequency and participant for the next 1400 ms (for visual epochs) and 2200 ms (for tactile epochs). Finally, the data were expressed as %-of-baseline by dividing the results of each subtraction by the baseline value. For each participant, mean power of μ (8 Hz–12 Hz) and β rhythm (13-25 Hz) was quantified on the centro-parietal site corresponding to electrodes C3 e C4 (Behmer & Jantzen, 2011, Nyström et al., 2011, Perry & Bentin, 2009, Perry & Bentin, 2011, Pfurtscheller et al., 2006, Pineda et al., 2011, Proverbio, 2012). To quantify the change induced by the visual stimulus presentation per se, we averaged the μ change across the stimulus presentation period (time-window 300–700 ms after stimulus onset), compatibly with Wamain et al. (2016). For the inspection of beta change before tactile stimulus delivery, we averaged the β change across the pre tactile stimulus presentation period (-350 ms to 0) as in van Ede et al. (2010, 2011). Then, for the low frequency band, the difference between C3 and C4 was calculated, in order to detect the Readiness Potential (RP) for the visual epochs. Indeed, we should observe more activation in the left hemisphere than in the right one when there is preparation to move the right hand (Eimer, 1998). To further explore the activation difference over the sensorimotor cortex between the left and right hemisphere, the lateralization index was calculated based on the beta mean power on C3 and C4 electrodes (contralateral-ipsilateral/contralateral+ipsilateral) in relation to the tactile epochs (as in van Ede et al., 2010).

Results

EEG data. EEG data of five participants were discarded from the successive analysis because of technical problems. EEG data of the remaining subjects (N=30) were analysed for each participant, pooling data across the 20 positive stimuli and the 20 negative stimuli. The final values that we used in the following analysis referred to the electrodes C3 and C4, that are those underlying the sensorimotor cortex (in line with Gonzalez-Franco et al., 2014, Evans & Blanke, 2013). The analysis reported below refers to the visual and tactile epochs, respectively.

Visual epochs. Two repeated measures ANOVAs were performed for the mu band (8-12 Hz) and beta band (13-25 Hz), by inserting the variables Distance (near vs. far), Valence (positive vs. negative) and Hemisphere (left vs. right) as factors. For the mu rhythm, a significant main effect of Distance was found ($F_{(1,29)}$= 21,073; $p<0.001$), indicating that the mu rhythm power was less synchronized for the near space processing than for the far space encoding (near: M ± SD= 0,016 ± 0,11; far: M ± SD= 0,069 ± 0,12). This analysis did not reveal any other main effects or significant interactions (all $p > 0.336$). Then, simple t-tests were performed in order to compare the mu power in near and far space with 0. These analysis revealed a non-significant result for the near space ($t_{(29)}$= 0,98; $p=0.336$) and a significant one for the far space ($t_{(29)}$= 3,59; $p>0.001$), thus suggesting that far space processing entails overall a mu rhythm synchronization while this is not true for the near space encoding (Figure 5, panel A).

The same analysis was repeated for the beta band. The repeated measures ANOVA illustrates a significant main effect of Distance ($F_{(1,29)}$= 6,976; $p=0.013$) indicating that the beta rhythm power was significantly more (de)synchronized for the near space processing than for the far space encoding (near: M ± SD= -0,014 ± 0,05; far: M ± SD= 0,001 ± 0,04). This analysis did not reveal any other main effects or significant interactions (all $p > 0.104$). Then, simple t-tests were performed in order to compare the beta power in near and far space with 0. These analyses revealed a significant comparison for the near space ($t_{(29)}$= -2,405; p=0.023) and a non-significant one for the far space ($t_{(29)}$= 0,152; p=0.88), thus suggesting that near space processing entails overall a significant suppression of beta rhythm oscillations while this is not true for the far space encoding (Figure 5, panel B).

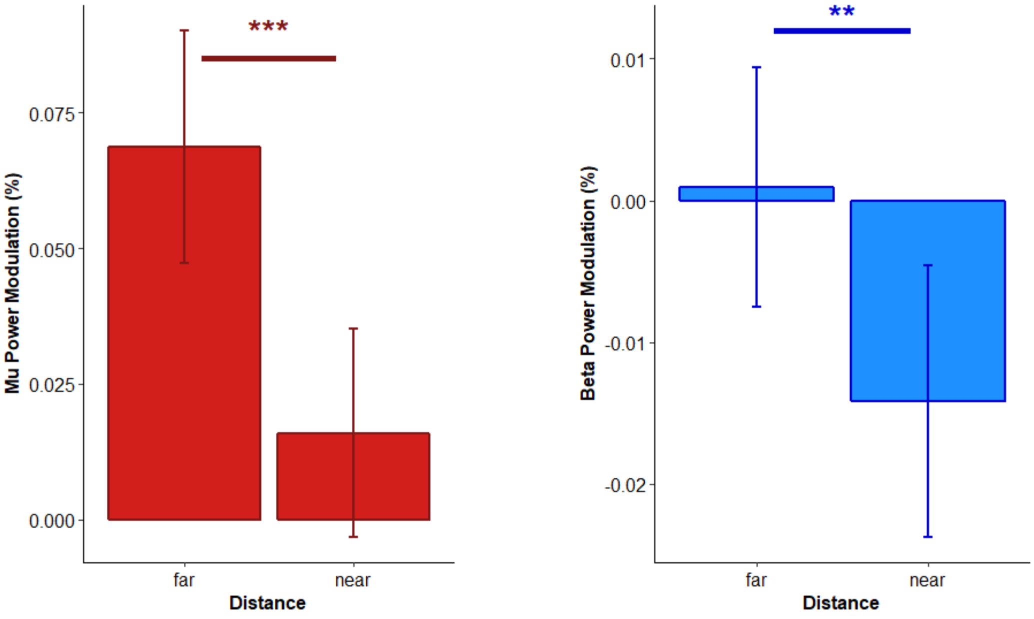

Figure 5. Illustration of the significant main effects of Distance for the mu (panel A) and beta (panel B) power change (expressed in % relative to baseline) in relation to the processing of all the visual stimuli used. Error bars represent the standard error of the mean.

Then, we calculated the readiness potential (RP) by subtracting C3–C4 values (Eimer, 1998) of low frequency range (8-12 Hz) for the 300-700 ms time window following the visual stimulus, in order to further seek for a lateralized movement preparation of the right hand in relation to the different visual stimuli located at different distances from participant's hand. Given that only right hand manipulations were used, we report only one side C3–C4 (in line with Gonzalez-Franco et al., 2014). Here, an increased negativity is expected if a movement is prepared by the contralateral hemisphere. A repeated measures ANOVA was conducted with these values, by inserting the variables Distance (near vs far) and Valence (positive vs negative) as factors but no significant effect was reported (all p> 0.617) (Figure 6, panel A). Despite the absence of any significant result, as can be seen by the graph below, negative visual stimuli located in near space entail a negative RP while all the others do not.

Tactile epochs. Similar to the procedure used with the visual epochs and consistently with van Ede et al. (2010, 2011), a repeated measures ANOVA was performed for the beta mean power (13-25 Hz), by inserting the variables Distance (near vs. far), Valence (positive vs. negative) and Hemisphere (left vs. right) as factors. The analysis revealed no significant main effect or interaction (all p>0.109). Moreover, descriptive analysis showed that none of the experimental conditions has a negative mean beta value, thus indicating an absence of desynchronized beta power. However, simple t-tests against 0 revealed that far space beta power is significantly different from 0 ($t_{(29)}$= 2,86; p=0.008) while that of near space is not ($t_{(29)}$= 1,08; p=0.291) (near: M ± SD= 0,016 ± 0,097; far: M ± SD= 0,06 ± 0,16), thus suggesting that the tactile expectation beta power related to visual stimuli presented in far space is synchronized while it is not true for near visual stimulation. Overall, it is not possible to conclude that tactile expectation entails a different beta band oscillation in relation to the distance and the valence of the concurrent visual stimulus as well as to the stimulation side.

In order to seek for any lateralization of the beta power in anticipation of the somatosensory stimulus applied to the right hand (as in van Ede et al., 2010, 2011), we calculated the lateralization index (contralateral-ipsilateral/contralateral + ipsilateral) on C3 and C4 electrodes for the designated frequency range (13-25 Hz). The Lateralization Index is positive when C3 (left sensorimotor cortex) has a higher power, and it is negative when C4 (topographically corresponding to the right sensorimotor cortex) has a higher power. Then, a repeated measure ANOVA was performed on the lateralization index values by inserting the variables Distance (near vs far) and Valence (positive vs negative) as factors. The analysis did not reveal any significant effect (all p>0.248) (Figure 6, Panel B). As can be seen from the graph above, even if we did not find any significant effect, it seems that the lateralization index is more negative in anticipating the tactile stimulus when concurrently negative visual stimuli are located in near than in far space, consistently with the Readiness Potential described in the paragraph above.

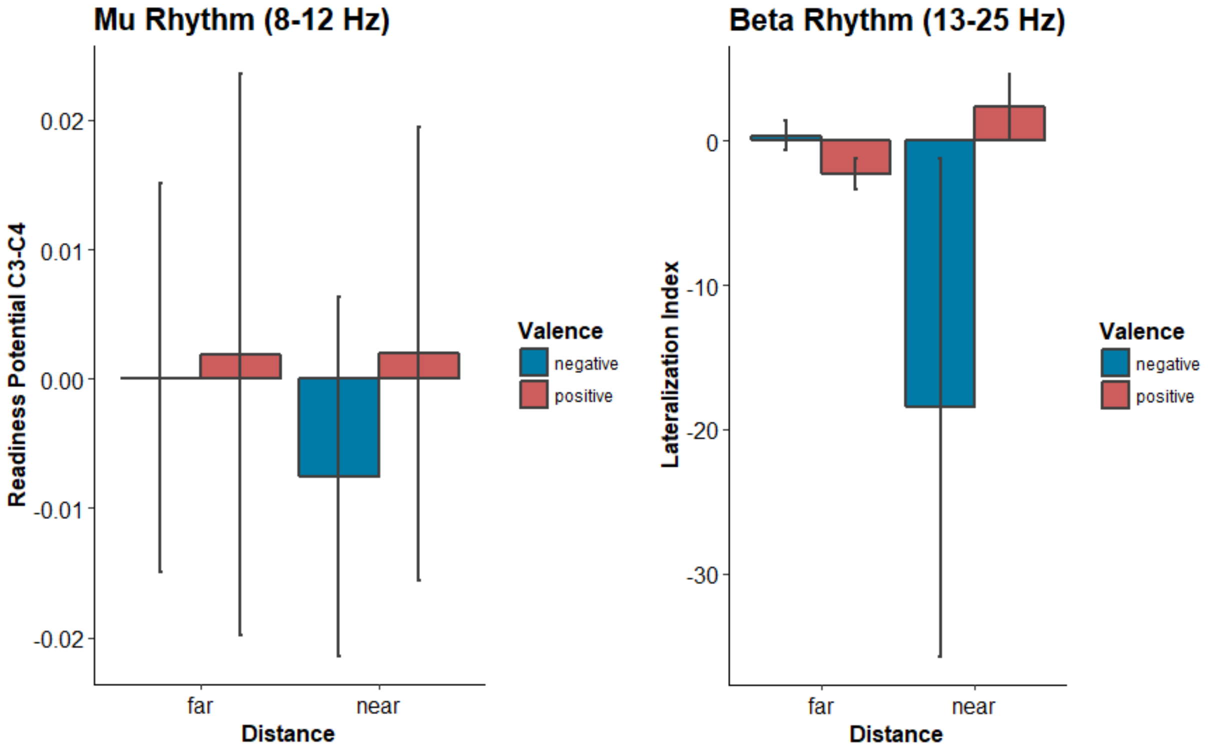

Figure 6. Panel A) Illustration of the Readiness Potential (RP) calculated by on C3 and C4 electrodes (by subtracting C3-C4 mean values) for the mu frequency band (8-12 Hz) in the 300-700 ms time window from the visual stimulus onset. Panel B) Illustration of the Lateralized Index calculated on C3 and C4 electrodes (contralateral-ipsilateral/contralateral+ipsilateral) for the beta frequency (13-25 Hz) relative to the -350-0 ms time window before the tactile stimulus onset.

Staircase data. In the staircase procedure, a 2 (Peripersonal Space) x 2 (Valence) repeated measures ANOVA was performed over the means of ascending and descending series of the overall sample (N=35). A significant main effect of Peripersonal Space ($F_{(2,68)}$= 43,6; p<0.001) and Valence ($F_{(1,34)}$= 56,5; p<0.001) was recorded as well as a significant interaction between Valence and Peripersonal Space ($F_{(1,34)}$=54,6; p<0.001). Tukey contrasts were requested to explore the main effects and interaction. Post hoc test revealed that defensive PPS threshold is reduced compare to the reaching one (defensive PPS: M ± SD=50,01 ± 13,14; reaching PPS: M ± SD=71,81 ± 11,74). This effect indicates that defensive staircase seems to measure a different spatial construct of that relative to the reaching staircase. More in detail, the positive defensive PPS was significantly different from the positive reaching PPS (p<0.001), negative reaching PPS (p>0.001) and negative defensive PPS (p<0.001) (Figure 7). Moreover, exploring the significant main effect of valence, positive stimuli entail a smaller PPS than negative ones (negative: M ± SD=67,76 ± 17,04; positive: M ± SD=54,05 ± 21,24) (p<0.001).

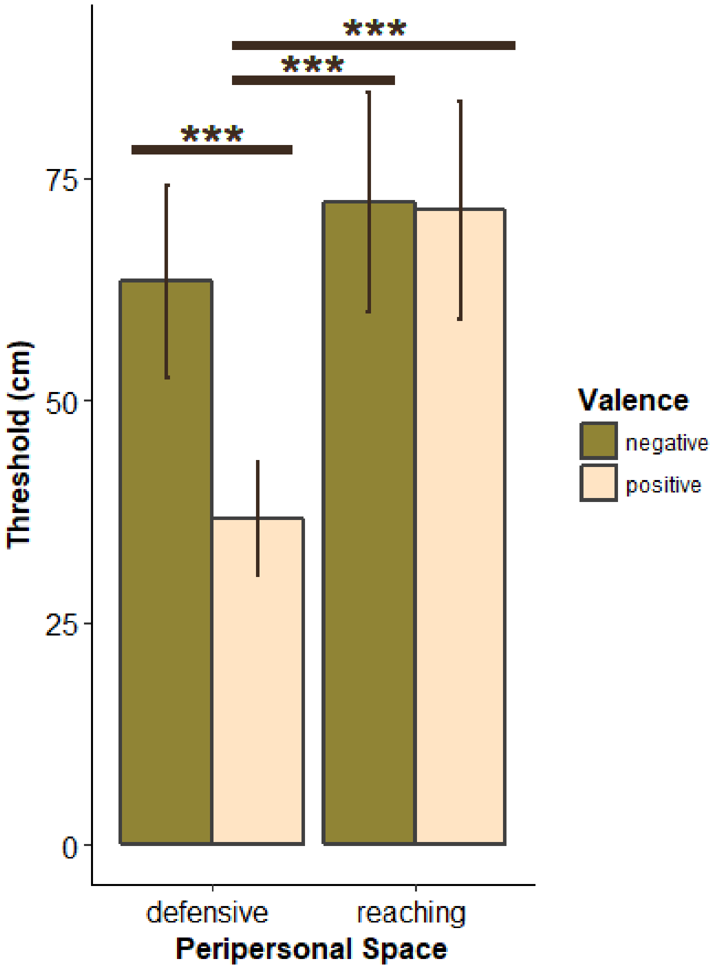

Figure 7. Illustration of the PPS thresholds obtained in the staircase procedure, for both positive (pink bars) and negative stimuli (green bars) related to the Defensive (left side) and Reaching tasks (right side)[8].

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[8] Please note that in most participants (N=25), the amplitude of the Defensive Positive PPS Threshold was set at the minimum value because they reported to feel comfortable with the visual stimulus located at the shortest distance of the staircase for 20 times in a row.

Furthermore, a correlation matrix was performed, comparing each PPS threshold obtained in the staircase procedure to each other, inserting also the actual reaching distance measured at the beginning of the experiment. A significant positive correlation was found between the negative reaching PPS and the positive reaching PPS ($r=0,951$, $p>0.001$) (positive reaching PPS: M ± SD=71,04 ± 12,1, negative reaching PPS: M ± SD=72,02 ± 11,07), negative reaching PPS and the actual reaching distance ($r=0,340$, $p=0.046$) as well as between the positive reaching PPS and the actual reaching distance ($r=0,358$, $p=0.035$) (real reaching threshold: M ± SD=66,06 ± 4,96) (Figure 8).

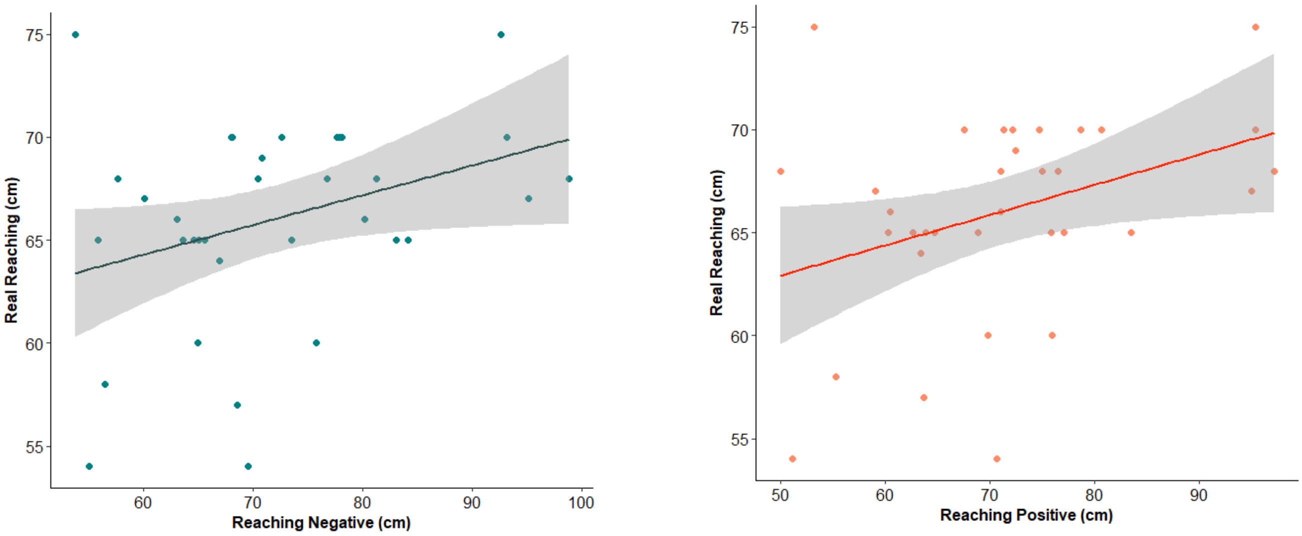

Figure 8. Illustration of the two positive significant correlations between reaching negative (left side) and positive thresholds (right side) of PPS with the real reaching threshold.

The same analyses were then conducted also with the same sample used for EEG analysis (N=30), thus removing the behavioral data of 5 participants who were previously discarded because of bad EEG signal. The RM ANOVA revealed the same significances than the previous one, that are: main effect of Peripersonal Space ($F_{(1,29)}= 31,6$; $p<0.001$), Valence ($F_{(1,29)}= 45,1$; $p<0.001$) and the two-way interaction between Distance and Valence ($F_{(1,29)}= 43,8$; $p<0.001$): Tukey comparison revealed that positive stimuli entail a smaller

PPS than negative ones (negative: M ± SD=66,96 ± 16,60; positive: M ± SD=53,55 ± 20,17) ($p<0.001$). Moreover, exploring the significant main effect of Peripersonal Space, it seems that the defensive PPS threshold is reduced compare to the reaching one (defensive PPS: M ± SD=50,48 ± 21,55; reaching PPS: M ± SD=70,04 ± 10,74). This effect indicates that defensive staircase seems to measure a different spatial construct of that relative to the reaching staircase. More in detail, the positive defensive PPS was significantly different from the positive reaching PPS ($p<0.001$), negative reaching PPS ($p>0.001$) and negative defensive PPS ($p<0.001$). We recorded also the same significant correlations as before even if a little bit weaker: negative reaching PPS and the positive reaching PPS (r=0,935, $p>0.001$) (positive reaching PPS: M ± SD=69,07 ± 12,1, negative reaching PPS: M ± SD=70,04 ± 11,07), negative reaching PPS and the actual reaching distance (r=0,327, p=0.078) as well as between the positive reaching PPS and the actual reaching distance (r=0,354, p=0.055) (real reaching threshold: M ± SD=65,08 ± 4,96).

Relation between Staircase & EEG data. In order to explore if there is a relation between the behavioural data collected by the staircase procedure (N=30) and those recorded through EEG (N=30), we conducted a correlation matrix putting inside the positive and negative PPS thresholds measured through the reaching and defensive staircase procedure as well as the values referring to beta power recorded in near space for the visual epochs[9]. Concerning the reaching staircase, we found an almost significant result. Indeed, the Reaching Positive PPS seems to be negatively related to the Near Positive Visual Beta (r= -0,358; p=0.052) (Figure 9, panel A). This indicates that participants, who overestimate their reaching abilities for positive visual stimuli, show a decreased sensorimotor oscillation in relation to the same positive visual stimuli when these are located in near space. All the other correlations concerning the Reaching Threshold were not significant (all $p>0.185$). Regarding the defensive staircase, instead, a significant negative

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[9] Only the beta power of the visual epochs was put in correlation with the staircase thresholds because it was the unique significant desynchronized power recorded in near space for both type of visual stimuli

correlation between the Defensive Positive PPS and the beta power recorded in near space for negative visual stimuli was recorded (Defensive Positive PPS vs. Near Negative Visual Beta: r= -0,521; p=0.003) (Figure 9, panel B). Participants with bigger safety margin around their body due to the presence of positive visual stimuli had a decreased beta power in near space in relation to negative visual stimuli. It means that who feels more threatened and therefore needs to have a bigger defensive PPS, shows a desynchronized sensorimotor oscillation, suggesting a major activation of the motor cortex in response to nearby visual negative stimuli. However, it is should be pointed out that the Defensive Positive PPS is not a reliable measure because in most cases its amplitude is equal to the first distance tested, that is 8,25 cm from participant's hand which turns into 32,5 cm when calculating the threshold (see Methods section for further details about staircase procedure). Related to this bias, we obtained clear floor effect in the above-mentioned significant correlation, what suggests to be cautious when interpreting the results. All the other correlations were not significant (all p>0.314).

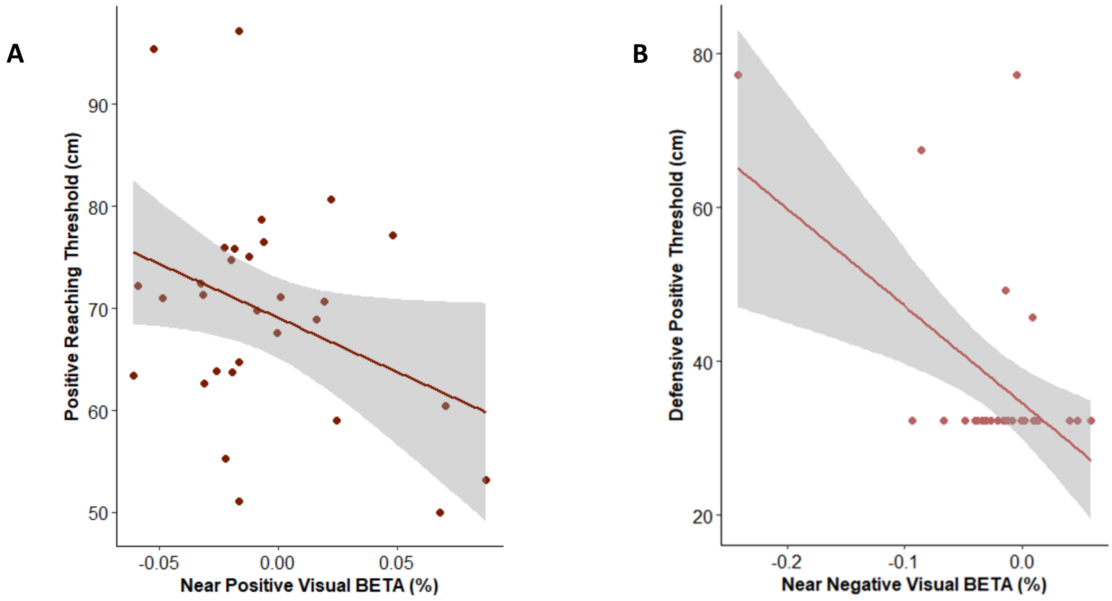

Figure 9. Panel A) Illustration of the almost significant correlation between the Positive Reaching Threshold measured by the staircase procedure and the BETA power recorded in near space for positive stimuli. Panel B) Illustration of the significant correlation between the Positive Defensive Threshold measured by the staircase procedure and the BETA power recorded in near space for negative stimuli.

Discussion

In the present EEG experiment, we wanted to investigate if the motor coding of PPS could be triggered by a visuo-tactile interaction task. Moreover, we were interested to explore whether the processing of valence connoted visual stimuli could entail a different motor cortex activation depending on their spatial distance from the body. Specifically, we tried to answer this question by using a semi-real scenario in which visual stimuli were displayed in near and far space along a monitor positioned horizontally in front of the participant. Along with the presentation of the visual stimulation, in approximately half of the trials, participants also received a tactile stimulus on the thumb or little finger of their right hand and they were requested to discriminate where they perceived it.

As highlighted above, we analyzed the visual and the tactile epochs separately. Regarding the visual epochs, we were unable to find a contralateral motor cortex activation depending on the distance of the visual stimulus presentation as well as on the different affective valence of the picture. Indeed, as revealed by analyses conducted on the mu (8-12 Hz) and beta (13-25 Hz) rhythms, no lateralization effect was found. Specifically, we expected to find a greater mu and beta rhythm desynchronization in near space than in far space over the left sensorimotor cortex, considering that the visual stimuli were presented aligned with the right hand. Instead, we found that the mu rhythm on the overall sensorimotor cortex (right and left S1) was nor synchronized neither desynchronized in near space, thus not allowing to make any inference about activation or deactivation of the motor cortex when visual stimuli are close to the body (as opposed to Wamain et al., 2016). However, the mu rhythm recorded in near space was significantly different from that registered in far space which, in turn, deemed to be synchronized, thus revealing a motor cortex deactivation when valence connoted visual stimuli are not close to our body (Pfurtscheller et al., 1996). Such a motor cortex idling for far visual stimuli is compatible with a reduced motor intention to interact with objects positioned out of our own reach boundaries, thus stressing the notion positing that action planning helps interpreting the external world (Gallese, 2000).

The same analysis conducted on the beta rhythm frequency range, revealed a significant difference between near and far space on the overall sensorimotor cortex (right and left S1). In particular, at higher frequencies, it seems that the sensorimotor cortex is activated in near space but not in far space. Indeed, we recorded a significant decrease of beta power when visual stimuli are located close to our body rather than when they are positioned farther away from it. As highlighted in the introduction, beta suppression over centro-parietal areas has been related to motor imagery (Pfurtscheller & Neuper, 1997) and actual movements performance (McFarland et al., 2000), similarly to mu rhythm desynchronization (Pfurtscheller, 1981). Therefore, this result seems to be in line with that reported by Wamain et al. (2016) who, through a reaching estimation task, observed a motor cortex activation gradient from peripersonal to extrapersonal space, as revealed by the even more attenuated mu rhythm desynchronization over the sensorimotor areas from near to far space. Given that Wamain et al. (2016) did not find the same result in terms of mu rhythm desynchronization by using the same visual stimuli and spatial distances in a perceptual identification task, the conclusion that they have drawn is that motor cortex is not automatically activated by the view of a visual stimulus located in near space, but the goal of the perceiver is necessary for such a motor activation to take place. In the present study, we demonstrate for the first time that a visuo-tactile task is capable to activate motor cortex when visual stimuli are located close to our body but not when they are far away from it. Therefore, this result seems to reinforce the assumption concerning the existence of bimodal visuo-tactile system underlying PPS representation in humans, analogous to that found in the monkey brain as reported by several electrophysiological studies (Fogassi et al., 1996, Duhamel et al., 1997, Graziano et al., 1997, 1999). Indeed, we first proved that pairing a nearby visual stimulus to a tactile one is a sufficient condition to elicit cortical motor responsiveness, which in turns it does not seem to be when the somatosensory stimulation is paired with a far visual stimulus. Moreover, even if it does not reached significance, we found that negative stimuli in near space seem to entail a major readiness potential than those located in far space. Even if it remains speculative, it could be stated that we are probably readier to initiate a motor movement towards nearby rather than distant unpleasant stimuli because of their closer undesirableness. This could be in line with the recent line of research investigating the defensive PPS (Sambo & Iannetti, 2012, 2013, for a review see de Vignemont & Iannetti, 2015).

Concerning the tactile epochs, we were not able to find any significant effect in relation to the tactile stimulus expectancy thus not confirming previous results. Indeed, it was recently found that the more the tactile stimulus is expected, the more it entails a contralateral suppression of beta power in the time interval that goes from -350 ms to the onset of the somatosensory stimulation (van Ede et al., 2010, 2011). Consistently with the major motor activation found for visual stimuli located near the body, we could have found here a greater suppression of beta power in relation to the tactile stimulus expectation for visual stimuli located close rather than far from us. As pointed out in their studies, van Ede et al. (2010, 2011) stress the notion that the contralateral beta suppression over sensorimotor areas is related to sensory preparation, thus excluding any explanation connected to motor preparation. However, even in view of that, it could be highly presumed that near visual stimuli are associated with stronger tactile anticipation than far visual stimuli. Indeed, in a defensive perspective, when an object is coming more in contact with us, we should be more prepared to anticipate any possible resulting bodily consequence with respect to far objects. Instead, we did not found a general desynchronization of beta oscillations in near and far space in relation to tactile stimulus anticipation. Moreover, we were also unable to find a lateralization effect (contrary to van Ede et al., 2011). Even if there was no significance, our results seem to show that tactile expectation on the right hand could be modulated by the valence of the concurrent visual stimulus. Indeed, it would seem that negative stimuli could lead to a suppression of beta power when located in near but not far from the body. This trend could be compatible with the notion of defensive PPS, in which potential threats are constantly monitored in the outer space and become more and more relevant when they approach the body (Graziano et al., 2002, Sambo et al., 2012).

For both visual and tactile epochs, we did not find any kind of modulation exerted by the different valence of the stimuli, neither in near nor in far space. This result is compatible with those recorded in studies 1 and 3 of the present manuscript, in which no valence effect – related to positive and negative stimuli - was found when the visual stimuli were located close to or far away from the body. Therefore, it could be said that visuo-tactile integration are not sensitive to the different valence of the visual stimuli, thus confirming studies already present in literature indicating the vacuity of valence effect when arousal level is controlled (Valdes-Conroy et al., 2012, 2014, Muller et al., 1999, Schupp et al., 2004). Further studies could address the question whatever arousing visual objects can differently modulate visuo-tactile interactions in space by looking at the neural response (in line with Haan et al., 2016).

Nevertheless, by defining the PPS with another method – the staircase procedure – we were able to detect significant differences between the positive and negative thresholds. In particular, we observed that the defensive PPS for positive stimuli entails a smaller amplitude than that recorded for negative stimuli in defensive PPS (in line with Ferri et al., 2015) as well as than those related to positive and negative stimuli in the reaching PPS. As highlighted above, we failed to report a highly differentiated defensive threshold for positive stimuli among participants. It is worth noting that it is reasonable to do not protect themselves from pleasant stimuli, because they do not represent a threat for the organism. However, this data could have a similarity with those recorded for the Readiness Potential and the Lateralization Index, which both show a (non-significant) difference between negative and positive stimuli in near space, with the former entailing an enhanced sensorimotor activation than the latter, as to indicate an intention to perform a defensive movement in order to avoid the close negative stimulus.

In the present study, we also tried to disentangle whether the motor activation related to the visual stimulus located close to the body was better explained by an approaching (reaching purpose) rather than an avoidance movement (defensive purpose) representation. This goal was explored by performing the correlation analysis between the beta power observed in near space and the PPS thresholds recorded through the reaching and defensive staircase procedure. Two significant negative correlations were found with the beta power in near space: the first one between the reaching PPS measured by positive stimuli and the beta power recorded in near space for positive stimuli and the second one between the defensive PPS measured by positive stimuli and the beta power registered in near space for negative stimuli. The first correlation seems to demonstrate that positive stimuli are encoded in reaching terms when located near the body, while the second one would suggest that negative stimuli are processed in a defensive perspective when they are close to the body. Indeed, the more the positive stimulus entails a large reaching amplitude, the more the motor cortex is activated when the same stimulus is presented inside the near space. On the other side, the more inoffensive stimuli induce a large defensive safety margin, the more the motor cortex is responsive when negative aversive stimuli appear in near space. Even if this last correlation did not result to be powerful – because of the floor effect due to the presence of a minimum defensive PPS amplitude for positive stimuli observed in many participants, coupled with the absence of a significant negative correlation between defensive negative PPS and the beta power for near negative stimuli - this interpretation of the data seems to be more in line with the so-called Swiss-Army Knife model rather than the so-called Specialist model of PPS representation. Indeed, here we found that depending on the context, it is possible to activate reaching or defensive motor responses (de Vignemont & Iannetti, 2015) that rely on the same neuronal oscillations recorded in the sensorimotor cortex. Indeed, it would appear that an appetitive stimulus is capable of triggering an approaching movement when located close to the body, while an aversive stimulus is able to provoke an avoiding action in near space, throughout the same experimental task. Therefore, these results seem to cautiously suggest that the visual stimulus could be always mapped onto the same PPS neural representation, regardless of its contextual meaning, which in turns defines the final motor outcome.

Future studies are necessary to deeper investigate if defensive and reaching PPS representations are built on the same neural map or they are founded on two different neural networks. Moreover, it could be interesting to replicate Wamain et al. (2016) experiment, by using our positive and negative visual stimuli, in order to understand if the different valence of stimuli is associated with diverse motor activation in sensorimotor cortex when located close to the body.

In conclusion, our results stress the spatial constraints of visuo-tactile integration (in line with Lloyd, 2007), revealing a sensorimotor activation for visual stimuli close to the body but not far from it. Moreover, we did not find any significant differences in neuronal oscillations in relation to the valence of visual stimuli, thus reinforcing the idea that positive and negative stimuli behave in the same way inside and outside PPS at neuronal level (congruently with the results of Study 1 and 3), when arousal level is taken under control. However, measuring the defensive and reaching PPS amplitude by means of the staircase method, it was possible to gather clues suggesting that positive and negative stimuli in near space are processed in a reaching and defensive fashion, respectively.

Supplementary Material

Neuronal oscillations of visuo-tactile integration in space: an EEG study on how stimulus valence affects PPS

Validation phase 2: rating on stimulus valence, arousal, grasp and touch

Re-validation phase. After the staircase session, the same experimental group of participants (N = 35, 25 females, mean age ± sd 26,09 ± 6,34 years, range = 18-47) was invited to rate through a 9-points Likert scale the valence, arousal, grasp and touch features of the 40 visual stimuli encountered in the EEG task, as in the previous validation phase (see above). This procedure was repeated because following the first stimulus validation, the stimulus background was changed, also the stimulus colour was slightly modified in order to make all visual stimuli equal in luminance. Therefore, this second validation phase allowed us to be sure that the two categories of stimuli used in the previous experimental step were substantially different in valence and touch, but not in arousal and grasp ratings. Stimuli presentation was done through the same large monitor used for the EEG and behavioural task (PH BDL 5530 EL screen dimension 122 x 68 cm, 1920 x 1080 screen resolution, 60 Hz refresh rate). The experiment lasted 15 minutes and was run by OpenSesame software 3.1 (Mathôt et al., 2012).

Re-validation phase results. We performed paired samples t-tests comparing them for Valence, Arousal, Grasp and Touch scores. It was reported a significant effect of Valence ($t_{(34)}$=17.09; p<.001), indicating that the two groups of visual stimuli were rated with a significantly different valence level (positive vs negative: M ± DS = 5.946 ± 0.83 vs M ± DS = 2.909 ± 0.7), as well as a significant effect of Touch ($t_{(34)}$=-20.464; p<.001), revealing a different degree of pleasantness to touch the object between the groups (positive vs negative: M ± DS = 5.383 ± 0.696 vs M ± DS = 2.680 ± 0.51). The two remaining factors, Arousal ($t_{(34)}$=0.605; p=.549) and Grasp ($t_{(34)}$=-1.324; p=.194) were not significant, respectively suggesting that all the stimuli were judged with the same activation level (positive vs negative: M ± DS = 3.814 ± 1.407 vs M ± DS = 3.641 ± 1.395) and with the same grasping difficulty (positive vs negative: M ± DS = 1.845 ± 1.109 vs M ± DS = 2.127 ± 1.345).

Study 5

Modulation of visuo-tactile integration by a temporary state of anxiety

Introduction

Our perception of space seems unitary, uniform and harmonious. However, as highlighted in the general introduction, empirical evidence coming from psychology and cognitive neuroscience clearly shows that our mind builds up a collection of multiple representations of space, each related to particular multisensory and motor processes (Holmes & Spence, 2004, Committeri et al., 2006). For instance, the way we represent the space immediately around our body, termed Peripersonal Space (PPS), involves complex multisensory process which integrates bodily (i.e., somatosensory) signals with visual and auditory ones (Canzoneri et al., 2013, Serino et al., 2015). Recently a new method to investigate PPS was proposed, which capitalizes on the rules of integration of visual and tactile stimuli: A revised version of the Temporal Order Judgment (TOJ) task. After receiving a somatosensory, nociceptive cue in one of their two hands, they are presented with pairs of visual stimuli (LEDs) that briefly turn on in rapid succession, either near (40 cm) or far (90 cm) from participant trunk, one to the left and the other to the right of participant body (Filbrich et al., 2017). Their task is to report the temporal order of the two sequential visual stimuli, by indicating the side of the LED perceived as appearing first. Authors reported a multisensory spatial congruency effect consisting in better performance in near space than in far space when the first visual stimulus is congruent with the tactile stimulation side. This effect is likely related to the decisive role played by visuo-tactile integrative mechanism deeply embedded in the brain (e.g. see Maravita et al., 2003).

It is well-known that the multisensory properties underlying PPS can be shaped by contingent factors. For instance, it has been reported that the response of bimodal cells coding for PPS is sensitive to the velocity of the approaching visual stimulus (Fogassi et al., 1996, Noel et al., 2018), tool-use (Iriki et al., 1996, Maravita et al., 2002), stimulus valence (Ferri et al., 2015) and social modulation (Teneggi et al., 2013). Moreover, a recent and promising line of research demonstrates that PPS is affected by the different level of anxiety, that can be described as the feeling of nervousness and worry, usually generalized and unfocused as an overreaction to a situation that is only subjectively perceived as alarming (Bouras & Holt, 2007). Indeed, Lourenco et al. (2011) showed that the line bisection bias is systematically related to individual differences in trait claustrophobic fear (measured by CLQ). Participants with greater claustrophobic fear showed more gradual rightward shifts in attentional bias over distance (logically corresponding to larger near space extension) than those with less claustrophobic fear. This suggests that people with greater anxiety of enclosed spaces and physically restrictive situations represent near space as larger than those showing less anxiety. This result is interpreted according to the defensive role of PPS, suggesting that participants with phobia of close environments may enlarge their peripersonal space in order to feel safer. In another study conducted by Sambo & Iannetti (2012), clear interindividual differences in the extension of PPS emerged. In particular, these differences were positively related to *trait anxiety*: This is the stable trait of anxiety related to the tendency to respond with state anxiety in the anticipation of threatening situations, which is opposed to *state anxiety*, i.e. the unpleasant emotional arousal emerging following threatening or dangerous situations (Spielberger, 1983). People with higher score in trait anxiety tend to have a larger defensive PPS measured through the hand blink reflex (HBR) evoked by the electrical stimulation of the wrist. However, the same study did not find a correlation between the CLQ score and defensive PPS amplitude, thus not corroborating previous results showed by Lourenco et al (2011). Moreover, a correlational study conducted by Iachini et al. (2015) found that the reaching space - assessed by a confederate distance paradigm - was positively correlated to both state and trait anxiety, even if the association was stronger with the latter. This means that people with more anxiety need larger reaching PPS, thus corroborating results found for the defensive PPS reported by Sambo & Iannetti (2012). However, the weaker correlation between PPS and state anxiety may depend at least on the absence of a specific manipulation of anxiety during the experiment. For example, Graydon et al. (2012) showed that reaching and grasping capabilities – which are strictly related to the reaching PPS – are strongly compromised by an induced state of anxiety. Participants were asked to perform a series of tasks assessing their short-term action capabilities (e.g., to reach and grasp blocks located in front of them), just before and after an experimental breathing task (anxiety provoking task) or a control breathing task. The experimental breathing task consisted in breathing in and out with a straw hold between the lips and plugging their nose for two minutes, while the control task requires breathing normally for two minutes. Results indicated that participants who experienced more changes in anxiety underestimated their reaching and grasping ability compared to non-anxious participants. This result seems to implicate that state anxiety affects the perception of affordances in PPS, reducing the perceived extension of one's own arm, possibly due to withdrawal behaviours.

The aim of the present study is to investigate whether a temporary modulation of anxiety may affect visuo-tactile integration in space. To pursue this aim, we took advantage of a TOJ task to measure PPS (Filbrich et al., 2017) as well as to the previously mentioned anxiety manipulation to provoke a temporary state of nervousness and anxiety (Graydon et al., 2012). TOJ task was administered four times to each participant, twice in each of two experimental sessions, just before and after the anxiety manipulation. The two experimental sessions differ each other only for the anxiety manipulation: in one case, participants receive the experimental breathing condition, i.e. a two-minute breathing through a straw between their lips and the nose plugged, in the other, the control breathing condition, they breathe normally. This manipulation has been shown in previous studies to cause mild to moderate levels of anxiety as well as physiological sensations (e.g, smothering sensation), making it a very used in anxiety research (Hofmann et al., 1999, Schmidt & Trakowski, 2004, Teachman et al., 2007, Teachman & Gordon, 2009, Teachman et al., 2010). We expected to find an increase in amplitude of visuo-tactile interactions after the experimental breathing task, but not after the control task, as revealed by differential multisensory congruency effect in space between the two conditions. More specifically, only after the anxiety provoking task, somatosensory stimuli should equally prioritize the perception of near and far visual stimuli presented in the same side of space as the tactile ones. On the contrary, in all the other conditions, we should find that the congruency between tactile and visual stimuli prioritize the perception of near over far visual stimuli (in line with Filbrich et al., 2017). Furthermore, it could be hypothesized that, given the defensive nature of PPS, participants who experience more anxiety during the experimental breathing condition, may show larger extension of the PPS after the anxiety provoking task than those who experienced less state anxiety. Moreover, in the same vein, we could expect that participants with higher trait anxiety scores may generally show a larger PPS than participants with lower trait anxiety scores. This is compatible with the need of a bigger safety margin around our body for those individuals who warn more danger and feel more threatened than for those who feel safe and protected (Lourenco et al., 2011, Sambo & Iannetti, 2013).

Methods

Participants

20 healthy subjects (10 males, mean age 22,4 years, standard deviation 2,21, range: 19-28, all right-handed by self-reported) participated in the experiment. All participants had normal or corrected-to-normal vision and a normal sense of touch as self-reported. All subjects (students of University of Milano-Bicocca) were volunteers and received credits for their participation to the study. This research was performed in accordance with the Declaration

of Helsinki and was approved by the local committee of the Department of Psychology, University of Milano-Bicocca.

Procedure

TOJ. Participants were seated in a barely illuminated room with their arms on a table in front of them and their palms down. Every trial started by turning on a yellow light emitting diode (LED), serving as fixation point. Fixation was positioned 65 cm away from the central body midline of participants trunk and equidistantly from the other four red LEDs that served as experimental visual stimuli, as explained below (Figure 1**).** Participants were instructed to look at the fixation LED throughout the experiment. After 200 ms from the offset of the fixation LED, a tactile cue was delivered to the right or left hand by means of two solenoids attached to the participant's right and left middle finger. The tactile pulse was a clearly perceivable "tap" delivered through a solenoid taped on the participant finger. The solenoid produced a 40-ms stimulation by moving a central 4-mm large magnetic rod. After 200 ms, the tactile stimulus was followed by two sequential 5-ms long visual stimuli, delivered in fast temporal sequence. The two visual stimuli were red LEDs located either at 40 cm (Near Space LEDs) or at 90 cm (Far Space LEDs) from the participant's trunk. Participant's hands were located 2 cm away from LEDs in the near space condition and 52 cm in the far space condition. Both in the near and far space condition, the lateral distance between each pair of visual stimuli was 40 cm. Stimulus Onset Asynchrony (SOA) was randomly selected among 8 different values, namely: ±10, ±30, ±55, ±110 ms (negative values indicate that the left side of space was stimulated first). Participants were invited to report the perceived temporal order of the two visual stimuli, indicating, in the first half of the trials, the side of space in which the red LED was illuminated first, and in the second half of the trials, the side of space in which the red LED was illuminated as second. This response modality was chosen in order to dissociate a genuine perceptual spatial bias from any response/decisional bias (Shore et al., 2001). Participants gave their response by pressing one of two foot pedals located under the table (left pedal for "left", right pedal for "right").

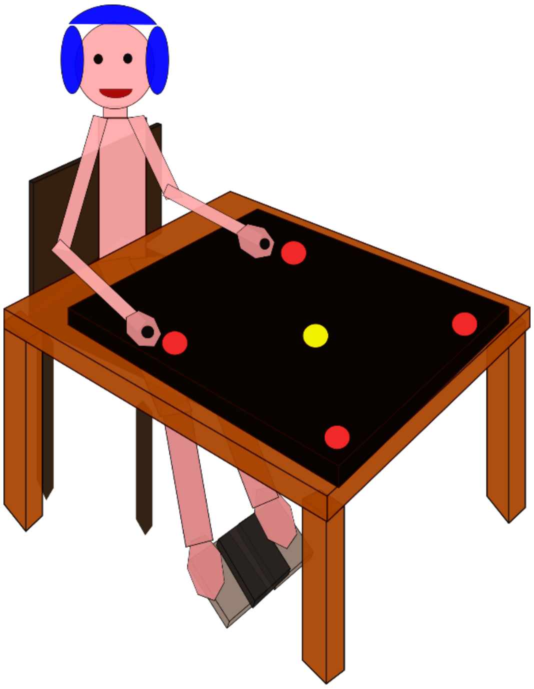

Figure 1. Schematic sketch of the TOJ experimental paradigm. Participant wore two solenoids positioned on the middle finger of the right and left hand. The four red LEDs are located at 2 different distances from participant's trunk: 40 cm (Near Space Condition) and 90 cm (Far Space Condition). The yellow one (Fixation LED) is located at 65 cm from the vertical body midline and at 20 cm from horizontal location of the red LEDs.

As soon as the participant pressed the foot pedal, a new trial started. Participants did not receive any kind of feedback about their performance and were instructed to respond as accurate as possible. The whole experiment consists of 320 trials, divided into 2 blocks of 180 trials each, lasting overall 10 minutes. The experiment was preceded by a training phase made up of 6 trials in which the SOA was always equal to 110 ms. The experiment is a within-subjects design consisting of; 8 SOA (±10, ±30, ±55, ±110) x 2 regions of space (near vs. far) x 2 tactile cue congruency (left vs. right) x 2 response modalities (report first vs. second visual stimulus). Trials were randomly presented within each block of stimulation. The tactile cue was not spatially informative; thus, the location of any forthcoming visual stimulus could not be predicted by the tactile cue. Every single experimental condition was repeated 5 times overall. The two blocks were separated by a break in which the experimenter gave instructions about the upcoming experimental condition. During the entire experiment, patient wore headphones delivering white noise in order to cover the small noise generated by the solenoids. The task was repeated four times by each participant, before and after the experimental breathing condition as well as before and after the control breathing condition (see below for further details). Tactile and LEDs delivery were controlled by an ad-hoc built control relais-box (Tattile Box, s/n Touch15001, EMS, Bologna, Italy) plugged into a computer (Acer P7200i). The stimulus presentation and the response collection were controlled by OpenSesame software 3 (Mathôt et al., 2012).

Anxiety Manipulation. Just after completing the TOJ task, participants were invited to perform an experimental breathing task (anxiety provoking condition) or a control breathing task (no anxiety provoking condition), depending on the experimental session. The experimental breathing task (Figure 2, Panel A) consists of breathing for two minutes through a straw with a diameter of 2 mm positioned between participant's lips, keeping the nose plugged with the right hand and holding the straw with the left hand. The control breathing condition (Figure 2, Panel B) consists of normally breathing for two minutes. The order of administration of the two experimental sessions was randomly assigned to participants, who were invited to come back to the lab to perform the second session after one week. This procedure does not implicate any serious harm or risk to participants (it is taken from the widely used Panic Control Treatment manual by Barlow & Craske, 1994), but a number of studies have shown that the straw breathing task may determine changes on subjective anxiety measures, physiological changes in heart rate and various self-reported bodily sensations (Gordon, 2008, Steinman & Teachman, 2010). Notably, participants were told they were welcome to stop at any point during the manipulation if it became too uncomfortable.

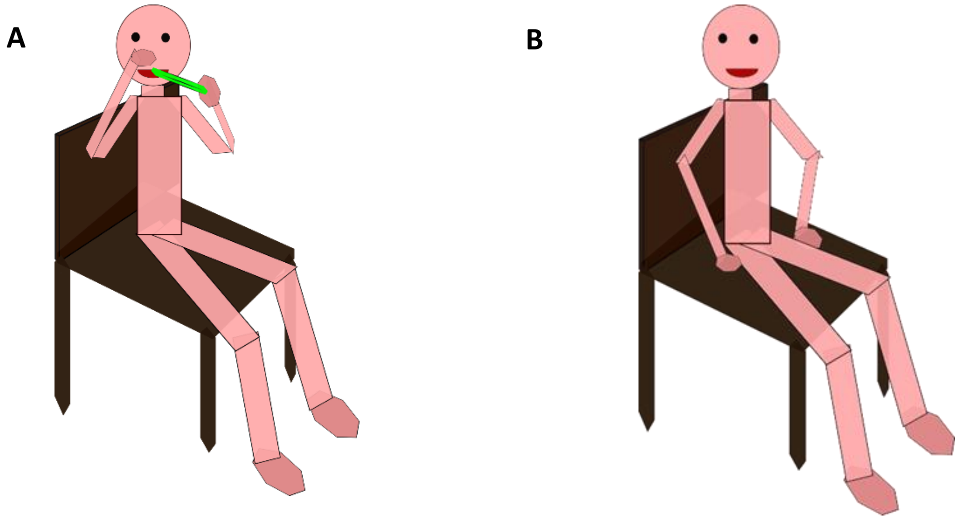

Figure 2. Illustration of the experimental breathing condition (Panel A) and control breathing condition (Panel B). Participant were invited to breath with a straw and the nose plugged for 2 minutes (Panel A) and to breathe normally for 2 minutes (Panel B).

State Trait Anxiety Inventory. The State Trait Anxiety Inventory (STAI, Spielberger & Sydeman 1994) was administered in order to assess anxiety level for each participant. The STAI is a 40 item self-report scale that measures two types of anxiety dimensions: state anxiety (STAI Y1, 20 items), a temporal anxiety or a feeling of tension, apprehension, nervousness, and activation (arousal) of the autonomic nervous system related to an event; trait anxiety (STAI Y2, 20 items), a relatively stable individual difference in anxiety proneness. Each item presented a description, and respondents were asked to indicate the extent to which each item described them on a 4-point scale. STAI Y2 was filled out online by participants before participating to the experiment, while STAI Y1 was administered during the experiment (sessions 1 and 2), just before and after the TOJ tasks.

Anxiety Likert Scale. In order to be sure that the anxiety manipulation really worked, participants were invited to fill out a 10-points Likert scale, just before and after the anxiety manipulation. They had to indicate how they felt at that moment, by choosing one of the 10 alternatives (0-calm enough to fall asleep, 10-feeling as if they may have a panic attack). Contrary to the STAI Y1, the second Likert Anxiety Scale was administered just after the anxiety manipulation because its drawing up is very fast, thus not weakening or interfering at all with the anxiety effect triggered by the prior manipulation.

Measures. The performance of each participant was assessed with two measures: the point of subjective simultaneity (PSS) and the slope. These measures correspond respectively to the α and β parameters of the following logistic function $f(x) = 1/1+ \exp(-\beta (x-\alpha))$. The α defines the threshold of the function, which corresponds to the SOA at which the two visual stimuli are perceived as occurring first equally often (i.e. the 0.5 criterion on the ordinate). This measure corresponds to the PSS, that is the amount of time by which one stimulus has to precede or follow the other in order for the two stimuli to be perceived as occurring simultaneously (Spence et al., 2001). The β parameter describes the slope of the logistic function, which describes the noisiness of the results. Indeed, its steepness depends on the accuracy of participant's responses during the experiment. The average of the PSS values for the cued and the PSS values for the uncued responses was calculated. The proportion of trials in which the visual stimulus presented in the cued side of space was reported as appearing first was plotted as a sigmoid function of SOA (Figure 3).

Data analysis. Regarding TOJ data, before performing statistical analyses, data from the two response modalities ('which is first' vs. 'which is second?') were merged to reduce potential response biases. First, the PSS and slope of each block recorded before the anxiety manipulation (both pre control and pre anxiety breathing task) were unified. Then, simple t-tests were performed, comparing the near and far PSS value to 0, with the aim to characterize potential shifts in the curve to one side of space (in line with Filbrich et al., 2017). The differences between PSS and slope values across conditions were tested using an analysis of variance (ANOVA) for repeated measures with *visual stimuli position* (near vs. far), *treatment* (anxiety vs. control) and *block* (pre vs. post) as within-subject factors. In order to verify how state anxiety influences the perception of space, the same identical ANOVA was repeated once again, by inserting the Likert Anxiety Scale scores divided into two groups (high vs. low) as between-subject factor. In the same vein, another repeated measure ANOVA with Distance (pre near vs. pre far) as within factor and STAI Y2 as covariate was carried out to explore the effect exerted by trait anxiety on space perception. Significance level was set at $p < .05$.

Results

Anxiety Measures. In order to verify if the level of anxiety significantly changed after the experimental breathing condition, a series of paired-sample t-tests was performed. Concerning the Likert Anxiety Scale, there was a significant difference between the pre-anxiety and post-anxiety measures ($t_{(19)}$=-3,387, p=0.003), indicating that after breathing with the straw, participants felt more in anxiety than before doing it (pre: M ± SD= 2,05 ± 1,1, post: M ± SD= 3,65 ± 2,1). Instead, no significant differences were recorded between the pre-control and post-control conditions ($t_{(19)}$=1,926, p=0.069), suggesting that the normal breathing did not produce any anxiety effect (pre: M ± SD= 2,500 ± 1,6, post: M ± SD= 2,15 ± 1,3). Regarding the STAI Y1 scores, no effect was significant, neither between the pre-control and post-control conditions ($t_{(19)}$=-0,038, p=0.970) (pre: M ± SD= 34,25 ± 9,18, post: M ± SD= 34,20 ± 8,79), nor between the pre-anxiety and post-anxiety conditions ($t_{(19)}$=-1,898, p=0.073) (pre: M ± SD= 33,45 ± 6,67, post: M ± SD= 36,75 ± 8,91). This STAI Y1 failure to detect state anxiety modification across the experimental conditions is possibly due to the large time interval between the anxiety task execution and STAI Y1 administration. On the contrary, given its short compilation, Likert Anxiety Scale was administered just before and after the anxiety breathing task, thus making it more suited to assess the real change in anxiety level.

Given the sensibility of the Likert Anxiety Scale to measure the state anxiety changing, only the scores reported in this scale were used in the successive analysis. Thus, in order to verify if TOJ performance is modulated by the different participant’s anxiety levels, the difference between the scores reported in the Likert Anxiety Scale after the anxiety breathing condition and those recorded before the anxiety breathing condition was calculated, then the median of these scores was used as a centre line to categorize participants in high or low state anxiety. The low and high state anxiety group significantly differ each other (-0,25 vs 3,44) as revealed by the independent sample t-test ($p<0.001$).

PSS. Simple t-test showed that PSS values recorded before the control and anxiety breathing conditions, were not significantly different from 0, for both the near space ($t_{(19)}$=-0,498, p=0.624) (near: M ± SD= -2,487 ± 22,4) and far space ($t_{(19)}$=0,239, p=0.814) (far: M ± SD= -0,775 ± 14,5). This means that uncued visual stimuli have not to be presented before than cued ones in both near and far space in order to have the chance to be perceived as occurring simultaneously. Therefore, unilateral tactile cues were not able to produce spatial bias, despite the direction of the near and far PSS is toward the uncued side of space. In order to investigate if the near and far PSS are significantly different from each other, a paired sample t-test was performed. The analysis revealed no significant difference between the near and far PSS ($t_{(19)}$=-0,408, p=0.688), indicating that the visuo-tactile interaction was not different in the two portions of space.

A repeated measures ANOVA was carried out, by putting the variable Visual Stimulus Position (Near, Far), Treatment (Anxiety, Control) and Block (Pre, Post) as within factors. The analysis revealed no significant main effects and interactions (all $p>0.089$), suggesting that the visuo-tactile interactions do not differ before and after the two breathing conditions in near and far space (Figure 3 and 4).

Then, in order to explore the influence of the state anxiety level on visuo-tactile interactions, an identical ANOVA was performed, by adding the variable Likert Anxiety Scale (High Anxiety vs. Low Anxiety) as between subject factor. This ANOVA shows a significant 3-way interaction between Distance, Block and Likert Anxiety Scale ($F_{(1,15)}$=10,70, p=0.005) as well as a significant 4-way interaction between Distance, Block, Treatment and Likert Anxiety Scale

($F_{(1,15)}$=5,20, p=0.038) (Figure 4). Planned comparisons revealed that participants with high state anxiety had a significantly different performance in near space in the pre anxiety condition (M± SD= -2,89 ± 18,21) than in post anxiety condition (M± SD=6,45±15,16) ($t_{(54,4)}$=-2,3280, p=0,024). This indicates that for participants who experienced a more intense temporary anxiety state, the tactile cue seems to prioritize the perception of congruent visual stimuli in near space before the straw breathing task, while it loses its facilitating effect after the experimental breathing condition. Moreover, it was recorded a significant difference in near space after the straw breathing task between participants with high vs low state anxiety ($t_{(81,7)}$=-2,0559, p=0,043). Namely, who experienced more state anxiety showed a more cue-dependant shift of PSS (M± SD= 6,46 ± 15,16) than participants with lower state anxiety scores who instead showed an uncued shifted PSS (M± SD= -5,42 ± 13,25). No other comparisons were significant.

Finally, the last repeated measures ANOVA was performed using the merged PSS values of the first block of each condition (pre control breathing condition and pre experimental breathing condition) with the aim to clarify the role exerted by trait anxiety levels on space perception excluding all the experimental conditions (post control and post experimental breathing condition) that could have influenced the data with the anxiety modulation. Here, the variable Distance was treated as within subject factor (near vs. far) and the scores recorded in STAI Y2 were put as covariate. This analysis showed a nearly significant interaction between Distance and STAI Y2 ($F_{(1,18)}$=4,39, p=0.051) that was furtherly explored by graph (Figure 5).

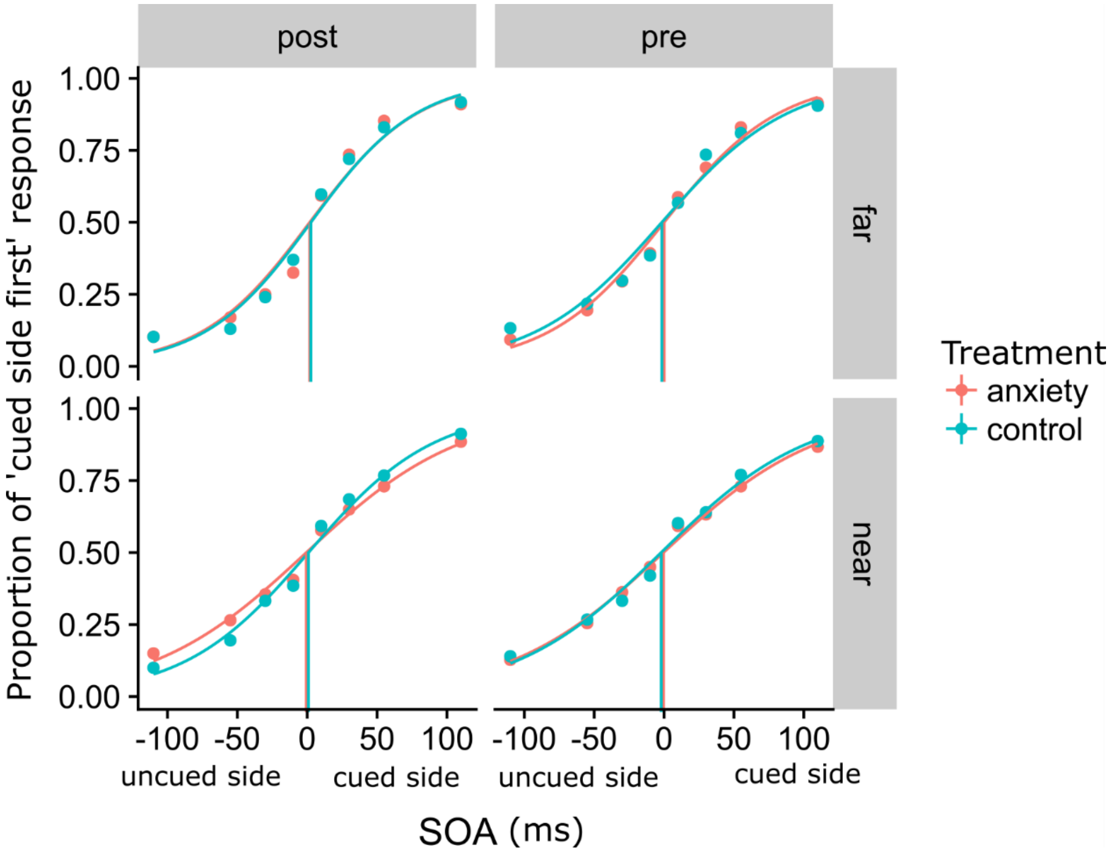

Figure 3. PSS values for each experimental condition. The x-axis represents different hypothetical stimulus onset asynchronies (SOAs) between the two visual stimuli: negative values indicate that the visual stimulus occurring in the uncued side of space was presented first, while positive values indicate that the visual stimulus occurring in the cued side of space was presented first. The y-axis represents the proportion of trials in which the participants perceived the visual stimulus presented in the cued side of space as occurring first. Red curves represent the anxiety treatment (i.e. to breath with a straw), while blue curves represent control treatment (i.e. to breath normally), with the corresponding PSS values indicated by the red and blues vertical solid lines.

Slope. The same analyses were performed for the Slope. A paired sample t-test has been performed in order to verify if participants were more accurate in near or far space. The analysis revealed a significant difference between the two slopes in the two spaces ($t_{(19)}$= -3,55; p=0,002), indicating that participants had a better performance in far space (M± SD=0,058±0,017) that in near space (M± SD=0,042±0,032). The main repeated measures ANOVA with the variables Visual Stimulus Position (Near, Far), Treatment (Anxiety, Control) and Block (Pre, Post) as within factors, showed a significant main effect of visual stimulus position ($F_{(1,19)}$=23,127, p<0,001) and block

($F_{(1,19)}$=5,309, p=0,033). In particular, the slope for the near space (M± SD=0,089±0,038) was smaller than that recorded for the far space (M± SD=0,12±0,062) as well as the slope in the pre anxiety manipulation (M± SD=0,100±0,05) was smaller than that recorded in the post anxiety manipulation (M± SD=0,113±0,051). The main effect of treatment and all the other interactions were not significant (all p>0,198) (Figure 4). The second ANOVA - identical to the previous with the addition of the Likert Anxiety Scale as between subject factor - replicated the two main effects of Distance ($F_{(1,15)}$=18,088, p<0,001) and Block ($F_{(1,15)}$=6,915, p=0,019), but it failed to show other effects or interactions (all p>0,088). The third ANOVA was carried out by putting the variable Distance as within subject factor (pre near vs. pre far) and the scores recorded in STAI Y2 as covariate. Here, neither the main effect nor the interaction was significant (all p> 0,310).

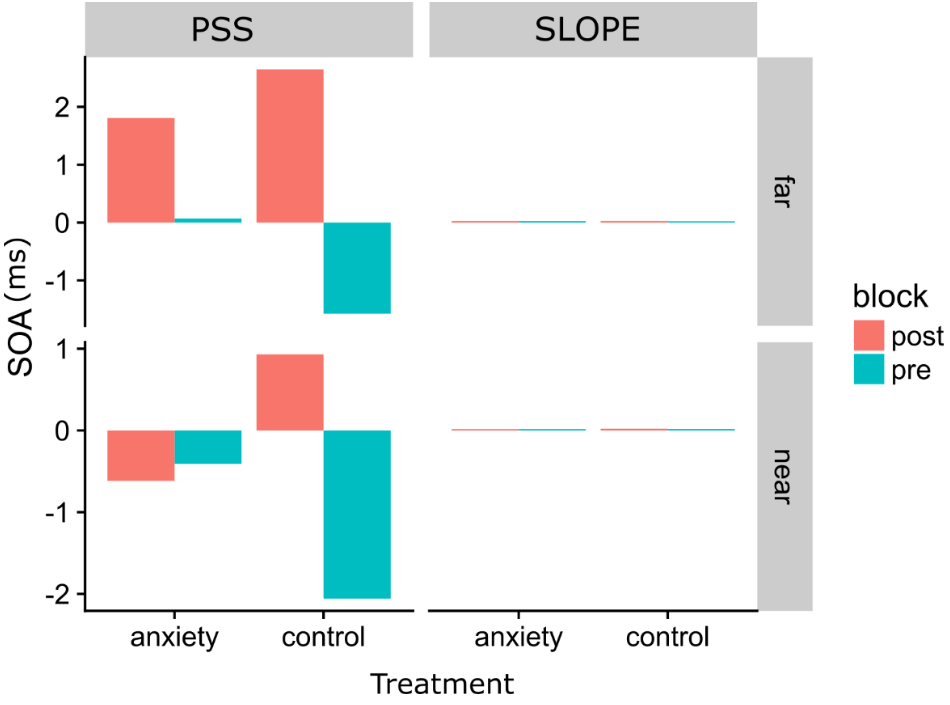

Figure 4. P1) The bars illustrate the mean PSS values for each experimental condition. None of the PSS values were significantly different from each other as well as they were not significantly different from 0. P2) The bars illustrated the slope for all the experimental conditions tested. Blue colour indicates the PPS and slope recorded before the anxiety manipulation (anxiety vs control) while red one refers to PSS and slope recorded after the anxiety manipulation (anxiety vs control). Values referring to the Near Space are reported in the lower part of the graph, while those related to Far Space are shown in the upper part of the graph.

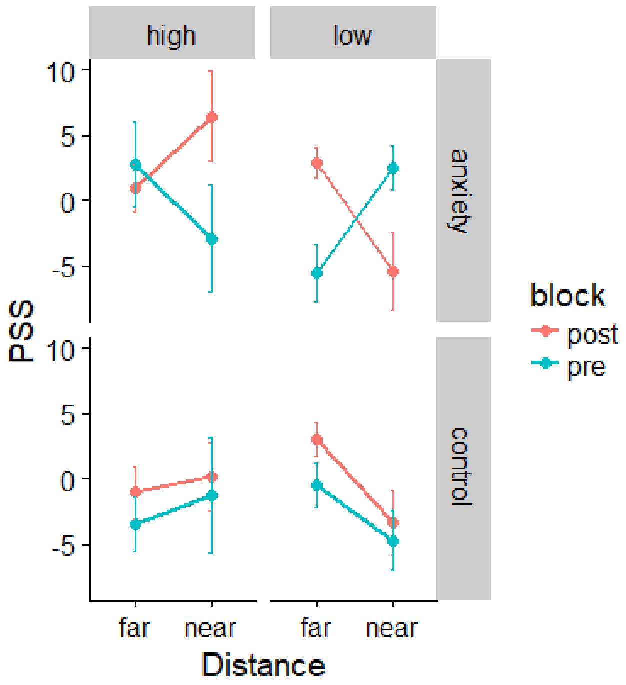

Figure 5. Illustration of the 4-way interaction between Distance, Treatment, Block and Likert Anxiety Scale. The x-axis represents the variable Distance (near and far space) while the y-axis represents the PSS values. Blue line indicates the PPS values recorded before the anxiety manipulation, while red line those registered after the breathing tasks. In the left side, PSS values of participants with high level of state anxiety are plotted, while the right side shows those belonging to low state anxiety subjects. Error bars represent the SEM.

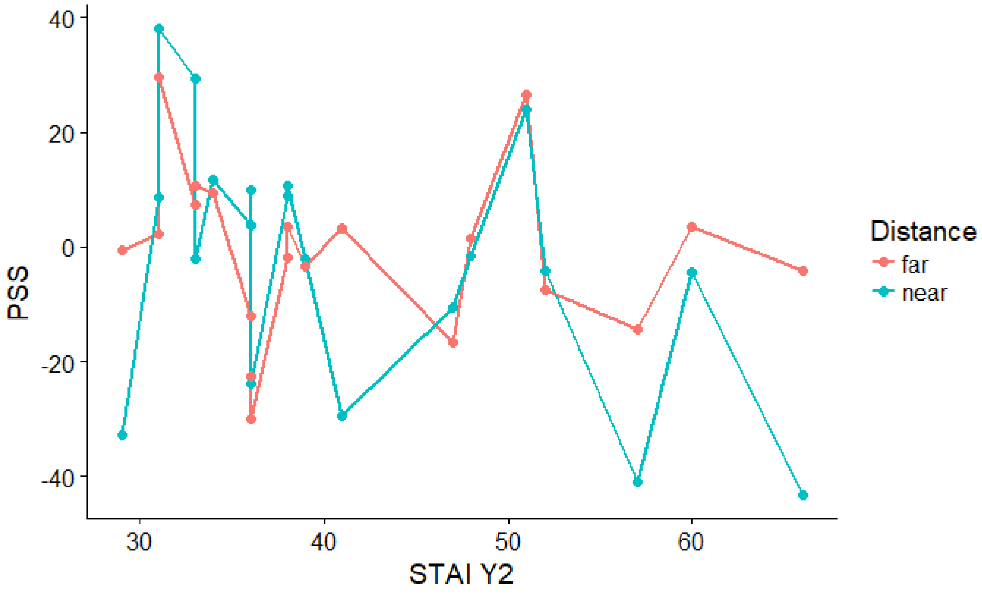

Figure 6. Illustration of the 2-way interaction between Distance and STAI Y2. The x-axis represents the scores recorded in STAI Y2 while the y-axis represents the mean PSS values. Blue line indicates the near space while red line the far space.

Discussion

The aim of the present study was to investigate the role of a temporary state of anxiety on the modulation of PPS representation. More specifically, we sought for evidence that the perception of visual stimuli in space could be differently biased by intervening tactile ones, after inducing a transient state of anxiety. By using a particular version of TOJ task, it is possible to induce spatial biases in the perception of the visual stimuli elicited by somatosensory stimuli applied on one of the two hands, as already demonstrated by Filbrich et al. (2017). Indeed, accordingly to the theory of prior entry (Titchener, 1908, Spence et al., 2001), attended stimuli (i.e. stimuli that are the focus of our attention) are perceived earlier than unattended ones. In this modified version of TOJ task adopted from Filbrich et al. (2017), therefore, the unattended visual stimulus (i.e. the uncued one) has to be presented several milliseconds before the attended one (i.e. the cued one) in order to have the chance to be perceived as appearing at the same time as the attended stimulus. The time interval at which the cued and uncued visual stimuli are perceived as occurring first equally often, is called PSS (i.e. point of subjective simultaneity) and it represents the point at which participants are maximally uncertain about the correct response. The multisensory influence of the tactile cue is indicated by a shift in the PSS.

In this TOJ experiment, participants had to judge the temporal order of two lateralized visual stimuli, either presented near or far from the trunk, which were preceded by a tactile stimulus applied only to one hand that could be spatially congruent or incongruent with the first visual stimulation. Results showed that the presence of the unilateral tactile stimulus does not bias the perception of the visual stimulus presented at the same side of space as the somatosensory input. Consequently, we did not even find a difference between near and far space, given that PSS values were not significantly larger for visual stimuli presented near the trunk than for visual stimuli presented farther away. This unexpected result is in sharp contrast with the abundant evidence coming from attentional studies, which indicate the strong modulation exerted by attended stimuli on the performance in speeded tasks (Posner, 1980, Henderson & Macquistan, 1993, Frischen et al., 2007). Nonetheless, these findings are opposed to those reported by Filbrich et al. (2017), which found a prioritizing effect for the visual stimulus presented in the same side of space as the somatosensory input as well as a greater spatial bias for visual stimuli located in near than far space. The interpretation given by these authors is that the visual space (especially the space close to the body) can be affected by somatosensory stimuli. In order to understand this difference, it is worth noting that the bodily inputs in the experiment by Filbrich and colleagues were nociceptive stimuli. Therefore, it is possible that our failure to replicate these results could be imputable to the different somatosensory stimulation used. Future research could try to answer this question, by replicating the present experimental paradigm using nociceptive stimuli instead of tactile ones. Indeed, considering that the detection of physical threats is an important priority for survival, especially for anxious individuals, it is reasonable to suppose that nociceptive stimulation can strongly interact with the processing of visual stimuli in space. This vision is supported by a vast amount of studies indicating that anxiety is associated with enhanced processing of threatening information (Mathews & MacLeod, 1985, MacLeod et al., 1986, Bishop et al., 2004, for a review see Cisler & Koster, 2010).

An alternative explanation of the non-significant data could be rooted in the time interval used between the tactile and the first visual stimulus presentation, that was set at 200 ms. We decided to replicate this temporal interval as in Filbrich et al., (2017), considering that there is no study in literature investigating the optimal temporal interval between tactile distractor and visual target capable to induce the strongest interaction between the two sensory stimuli. What is known in the literature is that the time window of less than 300 ms is critical for the occurrence of multi-sensory integration (Shimada et al., 2009). Indeed, this short temporal interval is preferable to induce strong sensation of Rubber Hand Illusion, a consolidated experimental paradigm based on visuo-tactile synchrony suitable to study body representation (Botvinick & Cohen, 1998). Moreover, evidence coming from the crossmodal congruency task (i.e. to respond to the tactile target while ignoring the congruent or incongruent visual distractor), seem to suggest that the SOA between the two sensory stimuli is crucial to determine a different amplitude of cross-modal congruency effects (Spence et al., 2004). In particular, when performing a tactile discrimination task while receiving visual distractors, i.e. the opposite combination than the present one, authors showed that by anticipating the visual cue by 30 ms produced the largest cross-modal congruency effects compared to both simultaneous stimulation and – 30 ms. That is, it is harder to ignore visual distractors when they appear briefly before the tactile target rather than simultaneously with it. Of course, in our paradigm the task was the opposite one (judging vision with tactile cues) but it may be that, by using a shorter time interval (even in the opposite direction, i.e. by making the tactile cue following the visual target) may increase crossmodal effects on the TOJ task. Therefore, future studies using this revised version of TOJ task, could manipulate the different temporal intervals between the tactile and visual stimulation in order to find the optimal temporal interval able to produce the strongest multisensory interaction in space.

Despite the lack of the aforementioned main crossmodal spatial effects, the analysis revealed a critical interaction between distance, block, treatment and state anxiety level as measured by the Likert Anxiety Scale. Even if the PSS values were not significantly different from 0, thus not allowing to interpret them unequivocally as cross-modal congruency facilitation effects, visuo-tactile interaction seems to change in relation to the contingent level of anxiety before and after the anxiety task, but not before and after the control task. In particular, it has been found that participants with high state anxiety show different performance in near space before doing the anxiety breathing task than after it. Indeed, the tactile cue seems to prioritize the perception of congruent visual stimuli in near space before breathing with the straw. However, this facilitation due to the congruency with the bodily input is significantly reduced after experiencing a temporary state of anxiety. After the experimental breathing task, indeed, the PSS is shifted toward the cued side, suggesting like an inhibitory effect played by the congruent tactile cue. Moreover, participants who experienced higher levels of state anxiety after the experimental breathing task, show stronger cue-dependant shift of PSS in near space than those with lower state anxiety, thus indicating that the different state anxiety levels impact the way in which visual and tactile stimuli interact in the space around us.

Overall, these effects seem to suggest that a remarkable state of anxiety can alter visuo-tactile interactions in near space. Indeed, in individuals with higher state anxiety, the congruent tactile cue seems to exert a facilitation effect on visual stimulus processing in near space before the anxiety-inducing task, but it loses its advantage after the anxiety manipulation. One possible explanation to this phenomenon is that individuals with greater state anxiety could perceive the tactile input as a threatening stimulus, that would negatively impact on performance. Instead of facilitating the response to the congruent near visual stimulus, it would inhibit its processing, thus resulting in an advantage for the uncued visual targets. Indeed, it is known in the literature how anxiety is strictly connected to the presence of threats. For instance, it was shown that more anxious individuals are slower to pronounce the colour of threat-related words than non-anxious individuals (Mathew & MacLeod, 1984, Mogg et al., 1989) and that high levels of state anxiety are associated with increased threat perception and lower threat thresholds in young population (Muris et al, 2003). Moreover, it was proposed that highly anxious individuals have reduced top-down control over threat-related distractors, as shown by the altered functioning of the regulatory circuitry underlying the processing of task-irrelevant threat-related stimuli (Bishop et al., 2004). The same authors also reported that people with high state anxiety show an increased amygdala response to fearful versus neutral visual stimuli, regardless of the attentional focus (attended vs. unattended), while people with low levels of anxiety showed only increased amygdala response to attended fearful faces (Bishop et al., 2004). Given all these evidence, it is reasonable to believe that the tactile cue was perceived as more threatening in anxious individuals; this distorted perception could have produced a sort of response inhibition, especially in near space where the processing of threats becomes more salient than in far space, due to the proximity with the body.

Despite this interpretation of the data suits very well with the above-mentioned literature, in this work we failed to obtain our primary goal, that was to demonstrate that defensive PPS can be enlarged after an anxiety-provoking task. However, it is worth mentioning that in this paradigm visual targets were static lights and not approaching stimuli, that would have surely entailed a stronger interaction with the body. As suggested by the seminal work in the monkey, by Fogassi et al. (1996), visuo-tactile cells coding PPS respond best to approaching visual stimuli, and they do so earlier the faster the approaching speed of the visual stimulus. Therefore, it could be interesting to replicate the present experiment in the future, assessing PPS with a visuo-tactile interaction task by using looming visual objects (Canzoneri et al., 2012).

Concerning trait anxiety, we found a strong trend between distance and trait-anxiety scores, indicating that participants with higher level of trait anxiety seem to have a greater PSS shift toward the uncued side of the sigmoid in near space than participants with lower level of trait anxiety. Moreover, it seems that high trait anxiety individuals have different visuo-tactile integration in near and far space, with a more notable shift of PSS in the direction of the uncued side at short distance than at far distance. It is possible to argue that, in anxious individuals, visual processing facilitation in near space due to tactile congruency, is due to overall higher, unspecific more readiness, typical of such individuals (Cattel & Scheier, 1961). However, this facilitation effect is not so evident in far space, where PSSs are not so turned toward the uncued side of the curve as in near space, even if they are less shifted towards the cue than those belonging to low trait anxiety individuals. Therefore, our data are too weak to replicate previous findings suggesting an extension of defensive PPS in participants with high trait anxiety (Lourenco et al., 2011, Sambo & Iannetti, 2012).

Interestingly, it seems that the way in which visual and tactile stimuli interact with each other in space is differently modulated by state and trait anxiety. Indeed, high levels of state anxiety entail a more cue-dependant shift of PSS in near space than in far space, while high levels trait anxiety lead to larger shift of PSS in the uncued direction for near than for far space. This observation is consistent with a stronger inhibition played by the congruent tactile cue in near than in far space for participants with higher state anxiety that contrasts with the stronger facilitation played by the congruent tactile cue in near than in far space for participants with higher trait anxiety. This different pattern of visuo-tactile modulation exerted by state and trait anxiety is in line with studies indicating different mechanisms involved in the relationship between state/trait anxiety and attention (Pacheco-Unguetti et al., 2010, Bishop et al., 2007). Indeed, it has been shown that state anxiety modulates the bottom-up attentional processes (alerting and orienting networks), while trait anxiety is more related to top-down attentional biases (executive control network). This dissociation results in a vigilance deficit depending on the salience of the context for state-anxious individuals and a reduced executive control for trait-anxious subjects. These findings could therefore explain why the cross-modal congruency effect was absent after breathing with the straw for high state anxiety participants and, at the same time, they could be predictive for the huge advantage exerted by congruent tactile cue on visual processing in near space for high trait anxiety subjects.

Future studies may further investigate this experimental question by varying some methodological aspects. For instance, it could be a good solution to implement the adaptive PSI method (as in Filbrich et al., 2017) in the TOJ task. This procedure instantly adapts the range of SOAs according to the performance of the participant on all the previous trials. Indeed, one critical aspect of the paradigm used in the present work concerns the few trial repetitions of each experimental condition, in order to limit the duration of each TOJ task, lasting about 10 minutes, thus allowing to test participants before any effect of the anxiety-inducing breathing condition has vanished. Indeed, it seems likely that this kind of manipulation only induces moderate, but short-lasting, increase of anxiety (Graydon et al., 2012, Hofmann et al., 1999).

To conclude, this revised version of the TOJ task resulted to be not ideal to assess visuo-tactile interactions in space, as revealed by the absence of facilitation effect following visuo-tactile stimulus congruency especially in near space. However, despite the absence of this general prioritizing somatosensory congruency effect in near visual space, it has been found that anxiety – both state and trait anxiety - exerts a kind of modulation in near space. Indeed, high state anxiety individuals seem to differently process the congruent tactile cue in near space before and after the experimental anxiety-triggering manipulation. While the tactile stimulus facilitates the encoding of congruent near visual stimulations before the anxiety task, it seems to inhibit it after the experimental breathing task. This suggests that, for high state anxious individuals, the state anxiety manipulation transformed the tactile cue in something threatening, thus inverting the expected, facilitatory effect of the somatosensory stimulation on visual space processing. On the other hand, high level of trait anxiety seems to entail a stronger facilitating effect of congruent tactile cue in near space than low trait anxiety levels. These findings are compatible with evidence in the literature indicating a marked susceptibility to bottom-up attentional processing (i.e. greater sensitivity to the context) for high state anxiety individuals and to top-down attentional control (i.e. inhibition process) for high trait anxiety subjects.

General Discussion

In the present thesis, I addressed the issue of how visuo-tactile integration in space is sensitive to emotional states. More specifically, a large part of the present work is devoted to understanding how intrinsic (Studies 1 and 4) and learned valence of visual stimuli (Study 3) affect the processing of bodily inputs while they are located at specific distances from participants' body. While in Study 1 and 3 I collected behavioural evidence disentangling the role exerted by positive, negative and neutral approaching visual stimuli on PPS processing, Study 4 aimed to investigate the neuronal oscillations underlying PPS representation in relation to static valence-connoted visual stimuli. Moreover, Study 5 sheds light on how a temporary state as well as a stable trait of anxiety could modify the interaction between tactile and static spatially defined visual stimuli, taking advantage of the prioritizing congruency effect on multisensory stimulation in near space (Filbrich et al., 2017).

The overall results seem to emphasise the suitability of visuo-tactile interactions to assess PPS representation as well as their plasticity in response to the above-mentioned experimental manipulations. Indeed, in Studies 1 and 3, we found that intrinsic and learned valence-connoted approaching stimuli are capable of enhancing the multisensory integration in space, while neutral ones do not. Interestingly, it is possible to state that this effect is not ascribed to the mere tactile expectation, because we found that neither positive nor negative stimuli are capable of exerting any kind of spatial effect when receding away from participant's body, as described in Study 2. Moreover, both positive and negative visual stimuli coupled with tactile ones are effective in triggering motor cortex activation when they are located in near space, but this is not true when the same stimuli are positioned in far space. Indeed, as can be seen from the beta band oscillations (13-25 Hz) recorded in Study 4, we found a significant desynchronization of this frequency range for nearby valence-connoted visual stimuli, thus revealing that both positive and negative stimuli are coded in motor terms when they are close to the body, as if they are potential poles of physical interactions with the observer. Finally, as can be found in the last experiment here reported, the congruent interaction between visual and tactile stimuli in near space is differently modulated by state and trait anxiety levels. Indeed, participants who experienced a higher temporary state of anxiety show a marked inhibitory effect of the congruent tactile cue on the near visual stimulus processing compared to those participants who were less upset by the state anxiety inducing task. On the other side, high trait anxiety participants' response to the multisensory congruency stimulation seems to be more facilitated in near than in far space. This result confirms the special status hold by the visuo-tactile coupling in near space, thus revealing how this portion of space is sensitive to distinct features of human personality. In particular, Study 1 investigates the influence exerted by the intrinsic valence of looming visual stimuli on visuo-tactile interactions across space, by keeping the level of stimulus-induced arousal under control. Indeed, previous research on this topic has not adequately controlled for the psychophysiological activation elicited by the stimulus itself when interpreting results on how valence affects PPS (Ferri et al., 2015). Here, it has been found that approaching visual stimuli with intrinsic affective valence increase their modulatory effect with increasing distance from the body. Indeed, while at shortest distances, valence-connoted and neutral stimuli are basically equivalent, at farthest distances positive and negative visual stimuli affect tactile responses more than neutral ones. Unexpectedly, arousal level seems not to be relevant in visuo-tactile interaction's modulation, thus not confirming theories postulating a strong link between arousal and motor readiness (Frijda et al., 1989), as well as those stressing the influence of arousing stimuli on cognitive functions (Lang, 1995). However, this null effect could be explained by the choice of not sufficiently high arousing visual stimuli chosen from the validation phase. Indeed, in order to create the two no statistically different categories of valence-connoted visual stimuli with high arousal, we necessarily selected those stimuli with a similar arousal score for the positive and negative group, thus discarding a lot of threatening images for the latter category, which were associated with high arousal score. If threatening visual stimuli had been used, arousal effects could have probably been reported. Moreover, an overall reduction of tactile RTs when concurrent visual approaching stimuli were situated close to the body, as compared to far away from it, was observed (in line with Serino et al., 2015, Haan et al., 2016, De Paepe et al., 2016, Kandula et al., 2017). This effect is compatible with an increased visuo-tactile integration for visual stimuli inside PPS (for a review see Maravita et al., 2003), thus stressing the multimodal structure of the external space (Grusser, 1983).

Study 2 was carried out in order to exclude that confounding factors (i.e. tactile expectation) could explain the modulation exerted by the intrinsic valence of visual stimuli found in Study 1. Looming stimuli are particularly suitable to assess PPS boundaries as compared to receding ones, due to their stronger spatially-dependent effects on tactile processing (Canzoneri et al., 2012, De Paepe et al., 2016, Kandula et al., 2017) as well as to their stronger attentional preference as shown also in the monkey (Maier et al., 2004). However, the more the visual stimulus travels towards participant’s body without being accompanied by the tactile input, the higher is the expectation to receive the tactile stimulus in the participant (Kandula et al., 2017, Van Ede et al., 2011). This high tactile expectancy implies higher motor readiness in responding to the tactile stimulus (Umbach et al., 2012) and could mask the effect of visual stimulus proximity to the body in speeding up RTs to the bodily inputs (Maravita et al., 2003). In this study, the experimental set-up was identical to that used in the previous experiment, except for the direction of the visual stimuli that now recede away from participant’s body rather than moving towards it. Experiment 2 shows a different pattern of results, as demonstrated by the clear facilitation effect played by tactile stimulus expectancy in speeding up RTs (Kandula et al., 2017, van Ede et al., 2011), that adds to the already known effect exerted by the visual stimulus proximity to the body in accelerating the motor response (for a review see Maravita et al., 2003). The impact of tactile expectancy increased with the time-delay of tactile stimulus delivering, namely tactile RTs were significantly faster for visual stimuli located far away from participant’s body than for visual stimuli positioned close to it. However, this effect could have been enhanced in this experiment, also due to the fact that the ratio between the true (visuo-tactile) and catch trials (only visual) was 5:1. In the literature, instead, it has been shown that the optimal ratio to study multisensory integration in space is 1:1 (Kandula et al., 2017), meaning that the amount of catch trials should match that of true trials. However, and crucially, Experiment 2 showed that stimulus valence does not interact with distance when visual stimuli are moving away from the body. This result suggests that valence modulates the response to approaching stimuli, but not to receding ones. This finding is in agreement with a vision of PPS as a space for interaction (working or defensive), so that the valence of a stimulus moving away from the body becomes less relevant as source of potential interaction. If valence was modulating the expectancy of a sensory event per se (and not PPS multisensory interactions), we should have found the very same interaction between valence and distance with approaching and receding trials (i.e., distance and time are invariantly related in the task) in Experiment 1 and 2.

In Experiment 3, it has been investigated if the learned valence of visual stimuli could exert the same effect on visuo-tactile integration in space as in Experiment 1. Indeed, it is well-known in literature that the consequences of a value-learning task can strongly affect human cognition (Raymond & O'Brien, 2009), similarly to stimuli holding intrinsic valence (Delgado et al., 2006). Therefore, after learning the association between geometrical shapes and monetary value, participants were requested to perform a visuo-tactile interaction task by using the same rewarded, punished and neutral visual stimuli encountered in the previous experimental phase. It was found that the higher the value of the learned valence, the slower the response at the nearest distances from the body. Participants showing higher conditioning effect, seem to go through a deeper evaluation of the ongoing stimuli which led to a speeding cost as revealed by the RTs. This is particularly true when the approaching stimulus is located near the participants' body, and much less when it is away from it. Furthermore, it is worth noting that such spatial modulation of the conditioning effect was even weaker for neutral stimuli. In other words, analogously to Experiment 1, stimuli carrying a relevant information due to their positive or negative valence, keep their modulatory effect across the entire space under investigation, while neutral ones are processed differently according to the actual distance.

Taken together, these results (Experiments 1, 2, 3) show that visuo-tactile interactions in space can be modulated by the intrinsic and acquired valence of stimuli as well as by the direction of the visual stimulus. Indeed, both positive and negative approaching stimuli shape the motor response to bodily input even when located far from the body. On the contrary, this facilitation is reduced for neutral stimuli in far space. However, given that everything becomes relevant as progressively comes closer to the body and is therefore worth to be promptly processed, the response to all kind of stimuli (positive, negative and neutral) becomes equally efficient when located at short distances. Apparently, our results seem in contrast to previous research investigating the relation between PPS and valence of looming stimuli, which reported the unique advantage for negative stimuli (Ferri et al., 2015). However, as highlighted in the introduction, it is possible to argue that the lack of spatial modulation played by positive stimuli in the aforementioned study is due to their different arousal level compared to negative stimuli, so that arousal and valence were possibly confounded. In the present study, instead, the preliminary weighting of the arousal level of both positive and negative stimuli allowed to assess the role of valence in modulating PPS in a less confounded way.

Another key aspect of these findings is that the distribution of RTs reflects more a gradient of response rather than an abrupt change between peripersonal and far space at a precise distance. This gradual modification is consistent with the literature in healthy human adults, showing gradual change in the processing of stimuli in space (Cowey et al., 1998, Varnava et al., 2002, Longo & Lourenco, 2006, De Paepe et al., 2016), more than with the idea of a threshold exactly setting the extension of the PPS (Canzoneri et al., 2012). For example, Longo and Lourenco (2006) have observed that participants show a bias of the subjective midpoint that gradually shifts from left to right with increasing line distance, when requested to perform a bisection task using a laser pointer on segments located at different distances from participants' body. This gradual modulation of PPS representation is reminiscent of the electrophysiological findings in monkeys (Fogassi et al., 1996, Graziano et al., 1997), showing that the probability of discharge to a visual stimulus of visuo-tactile neurons, gradually decreases as the distance between the visual stimulus and the cutaneous RF increases, without any sudden change of response pattern with distance. Therefore, this result suggests that PPS may not be a rigidly defined area with sharp boundaries rather than PPS is characterized by fuzzy limits, a sort of gradient, reflecting the progressive incremental probability of visual stimuli approaching the body (Graziano et al., 1997). This way to define PPS is also supported by recent works conducted by Hunley & Lourenco (2018) and Noel et al. (2018), indicating how gradual is the transition between PPS and extrapersonal space. Despite this shaded representation of the limit between the near and far space, many studies converge on the preferential encoding of the former rather than the latter space (for a review see Cléry et al., 2015). Moreover, at neuronal level, it was recently demonstrated by Wamain et al. (2016), that prototypical objects in near space entail a greater motor cortex activation than that elicited by the same visual stimuli when are located in far space. This finding is supported by the even more attenuated mu rhythm desynchronization over the sensorimotor areas from near to far space. In Study 4, we stressed Wamain and colleagues (2016) results, in accordance with a significant decrease of beta power when valence-connoted visual stimuli are located close to our body rather than when they are positioned farther away from it. As highlighted in the introduction of Study 4, beta suppression over centro-parietal areas is related to motor imagery (Pfurtscheller & Neuper, 1997) as well as it is recorded during actual movements (McFarland et al., 2000), in a similar way to mu rhythm desynchronization (Pfurtscheller, 1981). Therefore, the result that of Study 4 indicates that both positive and negative visual stimuli trigger a consistent activation of motor cortex only when they are close to our body, thus stressing the interpretation of PPS as a sensory-motor interface between the body and the external environment (Berti & Frassinetti, 2000). Moreover, the great novelty introduced by this work is that we replicated Wamain et al. (2016) results through a visuo-tactile interaction task. Indeed, as highlighted in the chapter describing the Study 4, Wamain et al. (2016) reported the presence of such a motor cortex activation gradient from peripersonal to extrapersonal space only by using a reaching estimation task, in which participants were asked to indicate if they could reach that stimulus by imaging to extend their arm. On the contrary, when they were asked to identify the nature of the visual stimulus, authors failed to replicate their previous results despite the same visual stimuli and spatial distances have been used as in the reaching task. The conclusion that they have drawn is that the goal of the task is fundamental to encode the nearby stimulus in motor terms. It follows that seeing a visual stimulus close to the body does not automatically activate a motor response. Given all these premises, the present study demonstrated for the first time that pairing visual and tactile stimuli in near space is a sufficient condition to elicit a motor activation in the perceivers. This integration processes which combine vision and touch lead to a preferential representation of near space (in line with Macaluso & Maravita, 2010), by encoding objects falling inside its fuzzy boundaries in motor terms (Sedda et al. 2018). This electrophysiological finding seems to confirm the existence, in humans, of an inter-sensory integrative system representing space through the combination of visual and tactile stimuli, as already abundantly discovered in monkey's brain (Rizzolatti et al., 1981, Graziano et al., 1997).

In this study, I also tried to disentangle if the motor activation related to the nearby visual stimulus was more linked to an approaching (reaching purpose) or an avoiding movement (defensive purpose), by doing a correlation analysis between the beta power observed in near space and the defensive and reaching PPS thresholds recorded by means of the staircase procedure. Two significant negative correlations were found with the beta power in near space: the first one between the reaching PPS measured by positive stimuli and the beta power registered in near space for positive stimuli and the second one between the defensive PPS measured by positive stimuli and the beta power registered in near space for negative stimuli. The first correlation seems to demonstrate that positive stimuli are encoded in reaching terms when located near the body, while the second one would suggest that negative stimuli are encoded in a defensive perspective when they are close to the body. Indeed, the more the positive stimulus entails a big reaching margin, the more the motor cortex was activated when the positive stimulus was presented inside the near space. On the other side, the more inoffensive stimuli cause a large defensive margin, the more the motor cortex was responsive when negative aversive stimuli appear in near space. Even if this last correlation is not so powerful – indeed, it has not been found a significant negative correlation between defensive negative PPS and the beta power for near negative stimuli - this interpretation of the data seems to be more in line with the Swiss-Army Knife model rather than the Specialist model of PPS representation, both described in the introduction. Indeed, here we found that depending on the context, it is possible to activate reaching or defensive motor responses (de Vignemont & Iannetti, 2015) that rely on the same neuronal oscillations recorded in the sensorimotor cortex. For instance, an appetitive stimulus is capable of triggering an approaching movement when located close to the body while an aversive stimulus seems to be able to provoke an avoiding action in near space, throughout the same experimental task. Therefore, these results seem to suggest that the visual stimulus could always be mapped onto the same PPS neural map, regardless of its contextual meaning, which in turns determines the final motor outcome. However, it is worth noting that a deeper investigation needs to be done regarding this point, considering that some of the effects above-mentioned are not so statistically powerful, as highlighted in the result section of the Study 4 and, then, this interpretation remains highly speculative.

Finally, in Study 5, we tried to investigate if the defensive PPS is sensitive to different anxiety conditions, namely the state vs the trait anxiety. In literature, it is known that higher trait anxiety levels entail a bigger safety margin around the body than lower trait anxiety levels. Here, we failed to replicate this result because of a more general defeat regarding the Temporal Order Judgment revised paradigm used to assess PPS. Indeed, we found that the time interval of 200 ms between the tactile cue and the visual target did not prioritize the processing of congruent near stimuli, as conversely reported for the nociceptive stimulation in Filbrich et al. (2017). However, we found that a remarkable temporary as well as a more stable anxiety condition can alter visuo-tactile interactions in near space. Indeed, it has been reported that participants who experienced a higher temporary state of anxiety showed a marked inhibitory effect of the congruent tactile cue on the near visual stimulus processing compared to those participants who were less susceptible to the state anxiety provoking task. This effect seems to suggest that for short-term anxious individuals, the congruent tactile cue seems to exert a disruptive effect on visual stimulus processing in near space after the anxiety provoking task. Maybe, individuals with greater state anxiety could perceive the tactile stimulus as a threatening one, which negatively interfere with the performance. Instead of facilitating the response to the congruent near visual stimulus, it inhibits its processing thus resulting in an advantage for uncued visual targets. This result is compatible with those reported in literature showing that high levels of state anxiety entail a reduced top-down control over threat-related distractors (Bishop et al., 2004). On the other side, high trait anxiety participants' response to the congruent multisensory stimulation seems to be more facilitated in near than in far space, compatibly with previous studies indicating a reduced executive control for trait anxious subjects (Pacheco-Unguetti et al., 2010).

Taken together, the five studies illustrated in the present thesis stress the privileged integration of visual and tactile stimuli inside PPS and its permeability to emotional related states. On one side, it has been demonstrated that the intrinsic and learned positive and negative valence of visual stimuli forge visuo-tactile interactions in space in a similar way, entailing an extending multisensory process (Studies 1 and 3) as well as a motor cortex activation when located close to the body (Study 4). On the other side, we showed that the visuo-tactile congruency in near space is particularly susceptible to different kinds of anxiety: its facilitation effect is disrupted when experiencing a high temporary anxiety state while it is enhanced when suffering from high trait anxiety condition (Study 5).

In conclusion, these results reinforce the notion that PPS is a multisensory representation of the environment around the body in relation to the motor system, which allows to efficiently interact with the physical world in order to manipulate objects of interest as well as to avoid potential threats. Every object appearing in this space is able to activate specific motor responses as well as it seems to acquire relevance because of its proximity to the body. Therefore, the present thesis stresses the strict relationship between body and space, in which the former, being considered as "Leibe" (lived body) and not as "Korper" (material organism), shall preponderantly contribute to the phenomenological constitution of the latter (Husserl, 1934/1937). In conclusion, it seems appropriate to mention the philosopher Merleau-Ponty (1945) who wrote: "*Inside and outside are inseparable. The world is wholly inside and I am wholly outside of myself*" (p. 407). These valuable thoughts are still relevant today for the study of the phenomenology of body and space relationships, as well as for many fields of human knowledge.

Conclusions

Experimenting space is one of the most fundamental experience in our life. It is so a natural and deep-rooted process, that human beings take it for granted. However, this capability involves specific and complex brain mechanisms that have been under scientific investigation for many years. Specifically, in this thesis I wondered if the multisensory integration underlying the processing of the space immediately surrounding our body, namely the Peripersonal Space (PPS), is sensitive to the valence of nearby objects as well as to temporary states and stable traits of anxiety. Moreover, I was also interested to look at the neuronal oscillations underpinning the valence connoted visual stimulus processing in near space in relation to the tactile one.

Taken together, the findings here reported add three novelties to the existing scientific literature:

1. Intrinsic and learned valence connoted visual stimuli enlarge visuo-tactile interactions in space;
2. The visuo-tactile pairing is capable of triggering motor cortex activation when valence connoted visual stimuli are located inside PPS;
3. State and trait anxiety lead to a different modulation of congruent visuo-tactile integration in near space.

These results discussed in the above paragraph shed light on how PPS is sensitive to different emotional features of surrounding objects as well as to those belonging to the perceiver. Consequently, the constant “dialogue” between the body and space masterfully emerges from this work, really suggesting that the body - with its peculiarities - can significantly affect the external world and vice versa.

Apollo and Daphne

Gian Lorenzo Bernini (1622/1625)

“But even now in this new form Apollo loved her; and placing his hand upon the trunk, he felt the heart still fluttering beneath the bark. He embraced the branches as if human limbs, and pressed his lips upon the wood. But even the wood shrank from his kisses. And the god cried out to this: "Since thou canst not be my bride, thou shalt at least be my tree. My hair, my lyre, my quiver shall always be entwined with thee, 0 laurel. ... And as my head is ever young and my locks unshorn, so do thou keep the beauty of thy leaves perpetual.” Ovid, Metamorphoses (pages 553-65)

REFERENCES

Ardizzi, M., & Ferri, F. (2018). Interoceptive influences on peripersonal space boundary. *Cognition, 177*, 79-86.

Avenanti, A., Annela, L., & Serino, A. (2012). Suppression of premotor cortex disrupts motor coding of peripersonal space. *Neuroimage*, *63*(1), 281-288.

Babiloni, C., Carducci, F., Cincotti, F., Rossini, P. M., Neuper, C., Pfurtscheller, G., & Babiloni, F. (1999). Human movement-related potentials vs desynchronization of EEG alpha rhythm: a high-resolution EEG study. *Neuroimage*, *10*(6), 658-665.

Balcetis, E., & Dunning, D. (2010). Wishful seeing: More desired objects are seen as closer. *Psychological science*, *21*(1), 147-152.

Barlow, D. H., Craske, M. G., & Meadows, E. A. (1994). Mastery of your anxiety and panic. Graywind Publications.

Battaglini, P. P., Muzur, A., Galletti, C., Skrap, M., Brovelli, A., & Fattori, P. (2002). Effects of lesions to area V6A in monkeys. *Experimental Brain Research*, *144*(3), 419-422.

Behmer Jr, L. P., & Jantzen, K. J. (2011). Reading sheet music facilitates sensorimotor mu-desynchronization in musicians. *Clinical Neurophysiology*, *122*(7), 1342-1347.

Beisteiner, R., Altenmuller, E., Lang, W., Lindinger, G., & Deecke, L. (1994). Musicians processing music: Measurement of brain potentials with EEG. *European Journal of Cognitive Psychology*, *6*(3), 311-327.

Berti, A., & Frassinetti, F. (2000). When far becomes near: Remapping of space by tool use. *Journal of cognitive neuroscience*, *12*(3), 415-420.

Bishop, S., Duncan, J., Brett, M., & Lawrence, A. D. (2004). Prefrontal cortical function and anxiety: controlling attention to threat-related stimuli. *Nature neuroscience, 7*(2), 184.

Bishop, S. J., Jenkins, R., & Lawrence, A. (2007). The neural processing of task-irrelevant fearful faces: effects of perceptual load and individual differences in trait and state anxiety. *Cereb. Cortex*, *17*, 1595-1603.

Bonnier, P. (1905). *L'aschématie*.

Botvinick, M., & Cohen, J. (1998). Rubber hands 'feel'touch that eyes see. *Nature*, *391*(6669), 756.

Bouras, N., & Holt, G. (2007). Psychiatric and behavioural disorders in developmental and intellectual disabilities.

Braadbaart, L., Williams, J. H., & Waiter, G. D. (2013). Do mirror neuron areas mediate mu rhythm suppression during imitation and action observation?. *International Journal of Psychophysiology*, *89*(1), 99-105.

Brain, W. R. (1941). Visual orientation with special reference to lesions of the right cerebral hemisphere. *Brain: A Journal of Neurology*.

Brozzoli, C., Pavani, F., Urquizar, C., Cardinali, L., & Farnè, A. (2009). Grasping actions remap peripersonal space. *Neuroreport*, *20*(10), 913-917.

Canzoneri, E., Magosso, E., & Serino, A. (2012). Dynamic sounds capture the boundaries of peripersonal space representation in humans. *PloS one*, *7*(9), e44306.

Canzoneri, E., Marzolla, M., Amoresano, A., Verni, G., & Serino, A. (2013). Amputation and prosthesis implantation shape body and peripersonal space representations. Scientific reports, 3, 2844.

Canzoneri, E., Ubaldi, S., Rastelli, V., Finisguerra, A., Bassolino, M., & Serino, A. (2013). Tool-use reshapes the boundaries of body and peripersonal space representations. *Experimental Brain Research*, *228*(1), 25-42.

Cardinali, L., Brozzoli, C., & Farne, A. (2009). Peripersonal space and body schema: two labels for the same concept?. *Brain topography*, *21*(3-4), 252-260.

Cattell, R. B., & Scheier, I. H. (1961). The meaning and measurement of neuroticism and anxiety.

Chao, L. L., & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *Neuroimage*, *12*(4), 478-484.

Childs, E., Astur, R. S., & de Wit, H. (2017). Virtual reality conditioned place preference using monetary reward. *Behavioural brain research*, *322*, 110-114.

Cléry, J., Guipponi, O., Wardak, C., & Hamed, S. B. (2015). Neuronal bases of peripersonal and extrapersonal spaces, their plasticity and their dynamics: knowns and unknowns. *Neuropsychologia*, *70*, 313-326.

Cisler, J. M., & Koster, E. H. (2010). Mechanisms of attentional biases towards threat in anxiety disorders: An integrative review. *Clinical psychology review*, *30*(2), 203-216.

Codispoti, M., Bradley, M. M., & Lang, P. J. (2001). Affective reactions to briefly presented pictures. *Psychophysiology*, *38*(3), 474-478.

Coello, Y., Bourgeois, J., & Iachini, T. (2012). Embodied perception of reachable space: how do we manage threatening objects?. *Cognitive processing*, *13*(1), 131-135.

Committeri, G., Pitzalis, S., Galati, G., Patria, F., Pelle, G., Sabatini, U., ... & Pizzamiglio, L. (2006). Neural bases of personal and extrapersonal neglect in humans. *Brain*, *130*(2), 431-441.

Conroy, M. A., & Polich, J. (2007). Affective valence and P300 when stimulus arousal level is controlled. *Cognition and emotion*, *21*(4), 891-901.

Cooke, D. F., & Graziano, M. S. (2003). Defensive movements evoked by air puff in monkeys. *Journal of Neurophysiology*, *90*(5), 3317-3329.

Cooke, D. F., Taylor, C. S., Moore, T., & Graziano, M. S. (2003). Complex movements evoked by microstimulation of the ventral intraparietal area. *Proceedings of the National Academy of Sciences*, *100*(10), 6163-6168.

Cornsweet, T. N. (1962). The staircase-method in psychophysics. *The American journal of psychology*, *75*(3), 485-491.

Cowey, A., Small, M., & Ellis, S. (1998). No abrupt change in visual hemineglect from near to far space. *Neuropsychologia, 37*(1), 1-6.

Critchley, M. (1949). THE PHENOMENON OF TACTILE IN ATTENTION WITH SPECIAL REFERENCE TO PARIETAL LESIONS. *Brain*, *72*(4), 538-561.

Cutting, J. E., & Vishton, P. M. (1995). Perceiving layout and knowing distances: The integration, relative potency, and contextual use of different information about depth. In *Perception of space and motion* (pp. 69-117).

de Borst, A. W., Sanchez-Vives, M. V., Slater, M., & de Gelder, B. (2018). First person experience of threat modulates cortical network encoding human peripersonal space. *bioRxiv*, 314971.

De Paepe, A. L., Crombez, G., & Legrain, V. (2016). What's Coming Near? The Influence of Dynamical Visual Stimuli on Nociceptive Processing. *PloS one*, *11*(5), e0155864.

De Paepe, A. L., Crombez, G., Spence, C., & Legrain, V. (2014). Mapping nociceptive stimuli in a peripersonal frame of reference: Evidence from a temporal order judgment task. *Neuropsychologia*, *56*, 219-228.

De Renzi, E. (1982). Disorders of space exploration and cognition. *JOHN WILEY & SONS, INC., 605 THIRD AVE., NEW YORK, NY 10158. 1982.*

de Vignemont, F., & Iannetti, G. D. (2015). How many peripersonal spaces?. *Neuropsychologia*, *70*, 327-334.

di Pellegrino, G., Làdavas, E., & Farné, A. (1997). Seeing where your hands are. *Nature*, *388*(6644), 730.

Delgado, M. R., Labouliere, C. D., & Phelps, E. A. (2006). Fear of losing money? Aversive conditioning with secondary reinforcers. *Social cognitive and affective neuroscience*, *1*(3), 250-259.

Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of neuroscience methods*, *134*(1), 9-21.

Delorme, A., Sejnowski, T., & Makeig, S. (2007). Enhanced detection of artifacts in EEG data using higher-order statistics and independent component analysis. *Neuroimage*, *34*(4), 1443-1449.

Duhamel, J. R., Bremmer, F., Hamed, S. B., & Graf, W. (1997). Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature*, *389*(6653), 845.

Eimer, M. (1998). The lateralized readiness potential as an on-line measure of central response activation processes. *Behavior Research Methods, Instruments, & Computers*, *30*(1), 146-156.

Evans, N., & Blanke, O. (2013). Shared electrophysiology mechanisms of body ownership and motor imagery. *Neuroimage*, *64*, 216-228.

Farnè, A., & Làdavas, E. (2000). Dynamic size-change of hand peripersonal space following tool use. *Neuroreport*, *11*(8), 1645-1649.

Farnè, A., Dematté, M. L., & Làdavas, E. (2005). Neuropsychological evidence of modular organization of the near peripersonal space. *Neurology, 65*(11), 1754-1758.

Ferri, F., Tajadura-Jiménez, A., Väljamäe, A., Vastano, R., & Costantini, M. (2015). Emotion-inducing approaching sounds shape the boundaries of multisensory peripersonal space. *Neuropsychologia*, *70*, 468-475.

Filbrich, L., Alamia, A., Burns, S., & Legrain, V. (2017). Orienting attention in visual space by nociceptive stimuli: investigation with a temporal order judgment task based on the adaptive PSI method. *Experimental brain research, 235*(7), 2069-2079.

Filbrich, L., Alamia, A., Blandiaux, S., Burns, S., & Legrain, V. (2017). Shaping visual space perception through bodily sensations: Testing the impact of nociceptive stimuli on visual perception in peripersonal space with temporal order judgments. *PloS one*, *12*(8), e0182634.

Fogassi, L., Gallese, V., Fadiga, L., Luppino, G., Matelli, M., & Rizzolatti, G. (1996). Coding of peripersonal space in inferior premotor cortex (area F4). *Journal of neurophysiology*, *76*(1), 141-157.

Fowles, D. C. (1980). The three arousal model: Implications of Gray's two-factor learning theory for heart rate, electrodermal activity, and psychopathy. *Psychophysiology*, *17*(2), 87-104.

Frijda, N. H., Kuipers, P., & Ter Schure, E. (1989). Relations among emotion, appraisal, and emotional action readiness. *Journal of personality and social psychology*, *57*(2), 212.

Frischen, A., Bayliss, A. P., & Tipper, S. P. (2007). Gaze cueing of attention: visual attention, social cognition, and individual differences. *Psychological bulletin, 133*(4), 694.

Gallese, V. (2000). The inner sense of action. Agency and motor representations. *Journal of Consciousness studies*, *7*(10), 23-40.

Gamberini, L., Seraglia, B., & Priftis, K. (2008). Processing of peripersonal and extrapersonal space using tools: Evidence from visual line bisection in real and virtual environments. *Neuropsychologia*, *46*(5), 1298-1304.

Gentilucci, M., Fogassi, L., Luppino, G., Matelli, M., Camarda, R., & Rizzolatti, G. (1988). Functional organization of inferior area 6 in the macaque monkey. *Experimental brain research*, *71*(3), 475-490.

Globisch, J., Hamm, A. O., Esteves, F., & Öhman, A. (1999). Fear appears fast: Temporal course of startle reflex potentiation in animal fearful subjects. *Psychophysiology*, *36*(1), 66-75.

Goldstein, R. Z., Cottone, L. A., Jia, Z., Maloney, T., Volkow, N. D., & Squires, N. K. (2006). The effect of graded monetary reward on cognitive event-related potentials and behavior in young healthy adults. *International Journal of Psychophysiology*, *62*(2), 272-279.

González-Franco, M., Peck, T. C., Rodríguez-Fornells, A., & Slater, M. (2014). A threat to a virtual hand elicits motor cortex activation. *Experimental brain research*, *232*(3), 875-887.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in neurosciences*, *15*(1), 20-25.

Gordon, T. L. (2008). Ethnic variations in anxiety triggers and responses. ProQuest.

Grafton, S. T., Fadiga, L., Arbib, M. A., & Rizzolatti, G. (1997). Premotor cortex activation during observation and naming of familiar tools. *Neuroimage*, *6*(4), 231-236.

Graydon, M. M., Linkenauger, S. A., Teachman, B. A., & Proffitt, D. R. (2012). Scared stiff: The influence of anxiety on the perception of action capabilities. *Cognition & emotion, 26*(7), 1301-1315.

Graziano, M. S., & Cooke, D. F. (2006). Parieto-frontal interactions, personal space, and defensive behavior. *Neuropsychologia*, *44*(6), 845-859.

Graziano, M. S., Hu, X. T., & Gross, C. G. (1997). Visuospatial properties of ventral premotor cortex. *Journal of Neurophysiology, 77*(5), 2268-2292.

Graziano, M. S., Reiss, L. A., & Gross, C. G. (1999). A neuronal representation of the location of nearby sounds. *Nature*, *397*(6718), 428.

Graziano, M. S., Taylor, C. S., & Moore, T. (2002). Complex movements evoked by microstimulation of precentral cortex. *Neuron*, *34*(5), 841-851.

Greenwald, A. G., McGhee, D. E., & Schwartz, J. L. (1998). Measuring individual differences in implicit cognition: the implicit association test. *Journal of personality and social psychology, 74*(6), 1464.

Greenwald, A. G., Nosek, B. A., & Banaji, M. R. (2003). Understanding and using the implicit association test: I. An improved scoring algorithm. *Journal of personality and social psychology*, *85*(2), 197.

Grüsser, O. J. (1983). Multimodal structure of the extrapersonal space. In *Spatially oriented behavior* (pp. 327-352). Springer, New York, NY.

Haan, A. M., Smit, M., Stigchel, S., & Dijkerman, H. C. (2016). Approaching threat modulates visuotactile interactions in peripersonal space. *Experimental brain research*, *234*(7), 1875-1884.

Halligan, P. W., Fink, G. R., Marshall, J. C., & Vallar, G. (2003). Spatial cognition: evidence from visual neglect. Trends in cognitive sciences, 7(3), 125-133.

Halligan, P. W., & Marshall, J. C. (1991). Left neglect for near but not far space in man. *Nature*, *350*(6318), 498.

Hari, R. (2006). Action–perception connection and the cortical mu rhythm. *Progress in brain research*, *159*, 253-260.

Head, H., & Holmes, G. (1911). Sensory disturbances from cerebral lesions. *Brain*, *34*(2-3), 102-254.

Head, H., & Holmes, G. (1912). Researches INTO SENSORY DISTURBANCES FROM CEREBRAL LESIONS. *The Lancet*, *179*(4612), 144-152.

Hediger, H. (1955). Studies of the psychology and behavior of captive animals in zoos and circuses.

Henderson, J. M., & Macquistan, A. D. (1993). The spatial distribution of attention following an exogenous cue. *Perception & Psychophysics, 53*(2), 221-230.

Hunley, S. B., & Lourenco, S. F. (2018). What is peripersonal space? An examination of unresolved empirical issues and emerging findings. *Wiley Interdisciplinary Reviews: Cognitive Science*, e1472.

Hunley, S. B., Marker, A. M., & Lourenco, S. F. (2017). Individual differences in the flexibility of peripersonal space. *Experimental psychology*.

Husserl, E. (1993). Die Krisis der europaischen Wissenschaften und die transzendentale Phänomenologie. Ergänzungsband. Texte aus dem Nachlass 1934–1937. *Dordrecht: Kluwer Academic Publishers*.

Iriki, A., Tanaka, M., & Iwamura, Y. (1996). Coding of modified body schema during tool use by macaque postcentral neurones. *Neuroreport, 7*(14), 2325-2330.

Jewell, G., & McCourt, M. E. (2000). Pseudoneglect: a review and meta-analysis of performance factors in line bisection tasks. *Neuropsychologia*, *38*(1), 93-110.

Kandula, M., Van der Stoep, N., Hofman, D., & Dijkerman, H. C. (2017). On the contribution of overt tactile expectations to visuo-tactile interactions within the peripersonal space. *Experimental brain research, 235*(8), 2511-2522.

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2015). lmerTest: tests in linear mixed effects models. R package version 2.0-20. *URL: https://cran. rproject. org/web/packages/lmerTest. Accessed*, *15*, 2016.

Làdavas, E. (2002). Functional and dynamic properties of visual peripersonal space. *Trends in cognitive sciences, 6*(1), 17-22.

Làdavas, E., Di Pellegrino, G., Farnè, A., & Zeloni, G. (1998). Neuropsychological evidence of an integrated visuotactile representation of peripersonal space in humans. *Journal of Cognitive Neuroscience*, *10*(5), 581-589.

Lang, P. J. (1995). The emotion probe: studies of motivation and attention. *American psychologist*, *50*(5), 372.

Llanos, C., Rodriguez, M., Rodriguez-Sabate, C., Morales, I., & Sabate, M. (2013). Mu-rhythm changes during the planning of motor and motor imagery actions. *Neuropsychologia*, *51*(6), 1019-1026.

Lloyd, D. M. (2007). Spatial limits on referred touch to an alien limb may reflect boundaries of visuo-tactile peripersonal space surrounding the hand. *Brain and cognition*, *64*(1), 104-109.

Longo, M. R., & Lourenco, S. F. (2006). On the nature of near space: Effects of tool use and the transition to far space. *Neuropsychologia, 44*(6), 977-981.

Longo, M. R., Musil, J. J., & Haggard, P. (2012). Visuo-tactile integration in personal space. *Journal of Cognitive Neuroscience*, *24*(3), 543-552.

Lourenco, S. F., Longo, M. R., & Pathman, T. (2011). Near space and its relation to claustrophobic fear. *Cognition*, *119*(3), 448-453.

Macaluso, E., & Maravita, A. (2010). The representation of space near the body through touch and vision. *Neuropsychologia*, *48*(3), 782-795.

MacKay, W. A., & Crammond, D. J. (1987). Neuronal correlates in posterior parietal lobe of the expectation of events. *Behavioural brain research, 24*(3), 167-179.

Makin, T. R., Holmes, N. P., Brozzoli, C., Rossetti, Y., & Farne, A. (2009). Coding of visual space during motor preparation: approaching objects rapidly modulate corticospinal excitability in hand-centered coordinates. *Journal of Neuroscience*, *29*(38), 11841-11851.

Maier, J. X., Neuhoff, J. G., Logothetis, N. K., & Ghazanfar, A. A. (2004). Multisensory integration of looming signals by rhesus monkeys. *Neuron*, *43*(2), 177-181.

Maravita, A., Husain, M., Clarke, K., & Driver, J. (2001). Reaching with a tool extends visual–tactile interactions into far space: Evidence from cross-modal extinction. *Neuropsychologia*, *39*(6), 580-585.

Maravita, A., Spence, C., Clarke, K., Husain, M., & Driver, J. (2000). Vision and touch through the looking glass in a case of crossmodal extinction. *Neuroreport*, *11*(16), 3521-3526.

Maravita, A., Spence, C., & Driver, J. (2003). Multisensory integration and the body schema: close to hand and within reach. *Current biology*, *13*(13), R531-R539.

Mathews, A., & MacLeod, C. (1985). Selective processing of threat cues in anxiety states. *Behaviour research and therapy*, *23*(5), 563-569.

Mathôt, S., Schreij, D., & Theeuwes, J. (2012). OpenSesame: An open-source, graphical experiment builder for the social sciences. *Behavior research methods, 44*(2), 314-324.ù

Merleau-Ponty, M. (1963). Phénoménologie de la perception (Paris: Gallimard, 1964). *Google Scholar*, 174.

Mogg, K., Mathews, A., & Weinman, J. (1989). Selective processing of threat cues in anxiety states: A replication. *Behaviour research and therapy, 27*(4), 317-323.

Müller, M. M., Keil, A., Gruber, T., & Elbert, T. (1999). Processing of affective pictures modulates right-hemispheric gamma band EEG activity. Clinical Neurophysiology, 110(11), 1913-1920.

Muris, P., Rapee, R., Meesters, C., Schouten, E., & Geers, M. (2003). Threat perception abnormalities in children: the role of anxiety disorders symptoms, chronic anxiety, and state anxiety. *Journal of Anxiety Disorders, 17*(3), 271-287.

Muthukumaraswamy, S. D., & Johnson, B. W. (2004). Primary motor cortex activation during action observation revealed by wavelet analysis of the EEG. *Clinical Neurophysiology*, *115*(8), 1760-1766.

Neppi-Mòdona, M., Rabuffetti, M., Folegatti, A., Ricci, R., Spinazzola, L., Schiavone, F., ... & Berti, A. (2007). Bisecting lines with different tools in right brain damaged patients: the role of action programming and sensory feedback in modulating spatial remapping. *Cortex*, *43*(3), 397-410.

Neuper, C., Scherer, R., Reiner, M., & Pfurtscheller, G. (2005). Imagery of motor actions: Differential effects of kinesthetic and visual–motor mode of imagery in single-trial EEG. *Cognitive brain research*, *25*(3), 668-677.

Noel, J. P., Blanke, O., Magosso, E., & Serino, A. (2018). Neural Adaptation Accounts for the Dynamic Resizing of Peri-Personal Space: Evidence from a Psychophysical-Computational Approach. *Journal of neurophysiology*.

Nyström, P., Ljunghammar, T., Rosander, K., & von Hofsten, C. (2011). Using mu rhythm desynchronization to measure mirror neuron activity in infants. *Developmental science*, *14*(2), 327-335.

Pacheco-Unguetti, A. P., Acosta, A., Callejas, A., & Lupiáñez, J. (2010). Attention and anxiety: Different attentional functioning under state and trait anxiety. *Psychological science*, *21*(2), 298-304.

Pavani, F., Spence, C., & Driver, J. (2000). Visual capture of touch: Out-of-the-body experiences with rubber gloves. *Psychological science*, *11*(5), 353-359.

Perry, A., & Bentin, S. (2009). Mirror activity in the human brain while observing hand movements: a comparison between EEG desynchronization in the μ-range and previous fMRI results. *Brain research*, *1282*, 126-132.

Perry, A., Stein, L., & Bentin, S. (2011). Motor and attentional mechanisms involved in social interaction—Evidence from mu and alpha EEG suppression. *Neuroimage*, *58*(3), 895-904.

Pfurtscheller, G. (1981). Central beta rhythm during sensorimotor activities in man. Electroencephalography and clinical neurophysiology, 51(3), 253-264.

Pfurtscheller, G., Brunner, C., Schlögl, A., & Da Silva, F. L. (2006). Mu rhythm (de) synchronization and EEG single-trial classification of different motor imagery tasks. *NeuroImage*, *31*(1), 153-159.

Pfurtscheller, G., & Da Silva, F. L. (1999). Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clinical neurophysiology*, *110*(11), 1842-1857.

Pfurtscheller, G., & Neuper, C. (1997). Motor imagery activates primary sensorimotor area in humans. *Neuroscience letters*, *239*(2-3), 65-68.

Pfurtscheller, G., Stancak Jr, A., & Neuper, C. (1996). Event-related synchronization (ERS) in the alpha band—an electrophysiological correlate of cortical idling: a review. International journal of psychophysiology, 24(1-2), 39-46.

Pineda, J. A., Allison, B. Z., & Vankov, A. (2000). The effects of self-movement, observation, and imagination on/spl mu/rhythms and readiness potentials

(RP's): toward a brain-computer interface (BCI). *IEEE Transactions on Rehabilitation Engineering*, *8*(2), 219-222.

Pineda, J. A., Giromini, L., Porcelli, P., Parolin, L., & Viglione, D. J. (2011). Mu suppression and human movement responses to the Rorschach test. *Neuroreport*, *22*(5), 223-226.

Ponty, M. M. (1945). Phénoménologie de la perception.

Posner, M. I. (1980). Orienting of attention. *Quarterly journal of experimental psychology, 32*(1), 3-25.

Previc, F. H. (1998). The neuropsychology of 3-D space. *Psychological bulletin*, *124*(2), 123.

Proverbio, A. M. (2012). Tool perception suppresses 10–12 Hz μ rhythm of EEG over the somatosensory area. *Biological psychology*, *91*(1), 1-7.

Ratcliff, R. (1993). Methods for dealing with reaction time outliers. *Psychological bulletin, 114(3)*, 510.

Raymond, J. E., & O'Brien, J. L. (2009). Selective visual attention and motivation: The consequences of value learning in an attentional blink task. *Psychological Science*, *20*(8), 981-988.

Rizzolatti, G., Fadiga, L., Fogassi, L., & Gallese, V. (1997). The space around us. *Science*, *277*(5323), 190-191.

Rizzolatti, G., Matelli, M., & Pavesi, G. (1983). Deficits in attention and movement following the removal of postarcuate (area 6) and prearcuate (area 8) cortex in macaque monkeys. *Brain*, *106*(3), 655-673.

Rizzolatti, G., Scandolara, C., Matelli, M., & Gentilucci, M. (1981). Afferent properties of periarcuate neurons in macaque monkeys. I. Somatosensory responses. *Behavioural brain research*, *2*(2), 125-146.

Rizzolatti, G., Scandolara, C., Matelli, M., & Gentilucci, M. (1981). Afferent properties of periarcuate neurons in macaque monkeys. II. Visual responses. *Behavioural brain research*, *2*(2), 147-163.

Romano, D., Gandola, M., Bottini, G., & Maravita, A. (2014). Arousal responses to noxious stimuli in somatoparaphrenia and anosognosia: clues to body awareness. *Brain, 137*(4), 1213-1223.

Rossetti, A., Romano, D., Bolognini, N., & Maravita, A. (2015). Dynamic expansion of alert responses to incoming painful stimuli following tool use. *Neuropsychologia*, *70*, 486-494.

Salenius, S., Schnitzler, A., Salmelin, R., Jousmäki, V., & Hari, R. (1997). Modulation of human cortical rolandic rhythms during natural sensorimotor tasks. *Neuroimage*, *5*(3), 221-228.

Sambo, C. F., Forster, B., Williams, S. C., & Iannetti, G. D. (2012). To blink or not to blink: fine cognitive tuning of the defensive peripersonal space. *Journal of Neuroscience*, *32*(37), 12921-12927.

Sambo, C. F., & Iannetti, G. D. (2013). Better safe than sorry? The safety margin surrounding the body is increased by anxiety. *Journal of Neuroscience*, *33*(35), 14225-14230.

Sambo, C. F., Liang, M., Cruccu, G., & Iannetti, G. D. (2011). Defensive peripersonal space: the blink reflex evoked by hand stimulation is increased when the hand is near the face. *Journal of neurophysiology*, *107*(3), 880-889.

Sanchez-Vives, M. V., & Slater, M. (2005). From presence to consciousness through virtual reality. *Nature Reviews Neuroscience*, *6*(4), 332.

Schenkenberg, T., Bradford, D. C., & Ajax, E. T. (1980). Line bisection and unilateral visual neglect in patients with neurologic impairment. *Neurology*, *30*(5), 509-509.

Schmidt, N. B., & Trakowski, J. (2004). Interoceptive assessment and exposure in panic disorder: A descriptive study. *Cognitive and Behavioral Practice, 11*(1), 81-92.

Schupp, H. T., Öhman, A., Junghöfer, M., Weike, A. I., Stockburger, J., & Hamm, A. O. (2004). The facilitated processing of threatening faces: an ERP analysis. *Emotion*, *4*(2), 189.

Sedda, A., Ambrosini, E., Dirupo, G., Tonin, D., Valsecchi, L., Redaelli, T., ... & Bottini, G. (2018). Affordances after spinal cord injury. *Journal of neuropsychology*.

Serino, A., Canzoneri, E., Marzolla, M., Di Pellegrino, G., & Magosso, E. (2015). Extending peripersonal space representation without tool-use: evidence from a combined behavioral-computational approach. *Frontiers in Behavioral Neuroscience*, *9*, 4.

Serino, A., Noel, J. P., Galli, G., Canzoneri, E., Marmaroli, P., Lissek, H., & Blanke, O. (2015). Body part-centered and full body-centered peripersonal space representations. *Scientific reports*, *5*, 18603.

Shimada, S., Fukuda, K., & Hiraki, K. (2009). Rubber hand illusion under delayed visual feedback. *PloS one, 4*(7), e6185.

Shore, D. I., Spence, C., & Klein, R. M. (2001). Visual prior entry. *Psychological science, 12*(3), 205-212.

Slater, M., Pérez Marcos, D., Ehrsson, H., & Sanchez-Vives, M. V. (2009). Inducing illusory ownership of a virtual body. *Frontiers in neuroscience*, *3*, 29.

Spence, C., Pavani, F., & Driver, J. (2004). Spatial constraints on visual-tactile cross-modal distractor congruency effects. *Cognitive, Affective, & Behavioral Neuroscience*, *4*(2), 148-169.

Spence, C., Pavani, F., Maravita, A., & Holmes, N. (2004). Multisensory contributions to the 3-D representation of visuotactile peripersonal space in humans: evidence from the crossmodal congruency task. *Journal of Physiology-Paris*, *98*(1), 171-189.

Spence, C., Shore, D. I., & Klein, R. M. (2001). Multisensory prior entry. *Journal of Experimental Psychology: General, 130*(4), 799.

Spielberger, C. D. (1983). Manual for the State-Trait Anxiety Inventory STAI (form Y)("self-evaluation questionnaire").

Spielberger, C. D., Gonzalez-Reigosa, F., Martinez-Urrutia, A., Natalicio, L. F., & Natalicio, D. S. (2017). The state-trait anxiety inventory. *Revista Interamericana de Psicologia/Interamerican Journal of Psychology*, *5*(3 & 4).

Spielberger, C. D., & Sydeman, S. J. (1994). State-Trait Anxiety Inventory and State-Trait Anger Expression Inventory. Lawrence Erlbaum Associates, Inc.

Steinman, S. A., & Teachman, B. A. (2010). Modifying interpretations among individuals high in anxiety sensitivity. *Journal of Anxiety Disorders, 24*(1), 71-78.

Stone, K. D., Kandula, M., Keizer, A., & Dijkerman, H. C. (2018). Peripersonal space boundaries around the lower limbs. *Experimental brain research*, *236*(1), 161-173.

Taffou, M., & Viaud-Delmon, I. (2014). Cynophobic fear adaptively extends peri-personal space. *Frontiers in psychiatry*, *5*, 122.

Teachman, B. A., & Gordon, T. (2009). Age differences in anxious responding: Older and calmer, unless the trigger is physical. *Psychology and Aging, 24*(3), 703.

Teachman, B. A., Marker, C. D., & Clerkin, E. M. (2010). Catastrophic misinterpretations as a predictor of symptom change during treatment for panic disorder. *Journal of Consulting and Clinical Psychology, 78*(6), 964.

Teachman, B. A., Smith-Janik, S. B., & Saporito, J. (2007). Information processing biases and panic disorder: Relationships among cognitive and symptom measures. *Behaviour research and therapy*, *45*(8), 1791-1811.

Teneggi, C., Canzoneri, E., di Pellegrino, G., & Serino, A. (2013). Social modulation of peripersonal space boundaries. *Current biology, 23*(5), 406-411.

Titchener, E. B. (1908). Lectures on the elementary psychology of feeling and attention. Macmillan.

Tzschentke, T. M. (1998). Measuring reward with the conditioned place preference paradigm: a comprehensive review of drug effects, recent progress and new issues. *Progress in neurobiology, 56*(6), 613-672.

Vagnoni, E., Lourenco, S. F., & Longo, M. R. (2012). Threat modulates perception of looming visual stimuli. *Current biology*, *22*(19), R826-R827.

Valdés-Conroy, B., Román, F. J., Hinojosa, J. A., & Shorkey, S. P. (2012). So far so good: Emotion in the peripersonal/extrapersonal space. *PloS one*, *7*(11), e49162.

Valdés-Conroy, B., Sebastián, M., Hinojosa, J. A., Román, F. J., & Santaniello, G. (2014). A close look into the near/far space division: a real-distance ERP study. *Neuropsychologia*, *59*, 27-34.

van Ede, F., de Lange, F., Jensen, O., & Maris, E. (2011). Orienting attention to an upcoming tactile event involves a spatially and temporally specific modulation of sensorimotor alpha-and beta-band oscillations. *Journal of Neuroscience, 31*(6), 2016-2024.

van Ede, F., Jensen, O., & Maris, E. (2010). Tactile expectation modulates pre-stimulus β-band oscillations in human sensorimotor cortex. *Neuroimage*, *51*(2), 867-876.

Varnava, A., McCarthy, M., & Beaumont, J. G. (2002). Line bisection in normal adults: direction of attentional bias for near and far space. *Neuropsychologia, 40*(8), 1372-1378.

Wamain, Y., Gabrielli, F., & Coello, Y. (2016). EEG μ rhythm in virtual reality reveals that motor coding of visual objects in peripersonal space is task dependent. *Cortex*, *74*, 20-30.

Weiss, P. H., Marshall, J. C., Wunderlich, G., Tellmann, L., Halligan, P. W., Freund, H. J., ... & Fink, G. R. (2000). Neural consequences of acting in near versus far space: a physiological basis for clinical dissociations. *Brain*, *123*(12), 2531-2541.

Weiss, P. H., Marshall, J. C., Zilles, K., & Fink, G. R. (2003). Are action and perception in near and far space additive or interactive factors?. *Neuroimage*, *18*(4), 837-846.

Yamamoto, S., & Kitazawa, S. (2001). Reversal of subjective temporal order due to arm crossing. *Nature neuroscience*, *4*(7), 759.

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