



Body–Space Interactions: Same Spatial Encoding but Different Influence of Valence for Reaching and Defensive Purposes

Chiara Spaccasassi¹, H. Chris Dijkerman², Angelo Maravita³, Oscar Ferrante⁴, and Maartje C. de Jong^{2,5,6,7}

Abstract

■ The space around our body, the so-called peripersonal space, is where interactions with nearby objects may occur. “Defensive space” and “Reaching space”, respectively, refer to two opposite poles of interaction between our body and the external environment: protecting the body and performing a goal-directed action. Here, we hypothesized that mechanisms underlying these two action spaces are differentially modulated by the valence of visual stimuli, as stimuli with negative valence are more likely to activate protective actions whereas stimuli with positive valence may activate approaching actions. To test whether such distinction in cognitive/evaluative processing exists between Reaching and Defensive spaces, we measured behavioral responses as well as neural activations over sensorimotor cortex using EEG while participants performed several tasks designed to tap into mechanisms underlying either Defensive (e.g., respond to touch) or Reaching space (e.g., estimate whether object is within reaching distance). During each task, pictures of objects with either positive or negative valence were presented at different distances from the

participants’ body. We found that Defensive space was smaller for positively compared with negatively valenced visual stimuli. Furthermore, sensorimotor cortex activation (reflected in modulation of beta power) during tactile processing was enhanced when coupled with negatively rather than positively valenced visual stimuli regarding Defensive space. On the contrary, both the EEG and behavioral measures capturing the mechanisms underlying Reaching space did not reveal any modulation by valence. Thus, although valence encoding had differential effects on Reaching and Defensive spaces, the distance of the visual stimulus modulated behavioral measures as well as activity over sensorimotor cortex (reflected in modulations of mu power) in a similar way for both types of spaces. Our results are compatible with the idea that Reaching and Defensive spaces involve the same distance-dependent neural representations of sensory input, whereas task goals and stimulus valence (i.e., contextual information) are implemented at a later processing stage and exert an influence on motor output rather than sensory/space encoding. ■

INTRODUCTION

Peripersonal space (PPS) refers to the region of space directly surrounding our body that may serve as a sensory motor interface between our body and the external world (Graziano & Cooke, 2006; Rizzolatti, Fadiga, Fogassi, & Gallese, 1997; Rizzolatti, Scandolara, Gentilucci, & Camarda, 1981). Integration of visual and tactile stimuli is enhanced when the visual stimulus is closer to the body

rather than far away from it, as revealed by electrophysiological studies in monkey (Graziano, Reiss, & Gross, 1999; Duhamel, Bremner, Hamed, & Graf, 1997; Fogassi et al., 1996) as well as humans (Noel, Serino, & Wallace, 2019; Bernasconi et al., 2018). In humans, there is also considerable behavioral evidence for multisensory enhancement within PPS (Spaccasassi, Frigione, & Maravita, 2021; Spaccasassi, Romano, & Maravita, 2019; Serino et al., 2015; Brozzoli, Cardinali, Pavani, & Farnè, 2010; Makin, Holmes, Brozzoli, Rossetti, & Farne, 2009; Làdavas, Pellegrino, Farnè, & Zeloni, 1998).

The role of PPS is not merely to integrate stimuli coming from different modalities but rather to regulate body–object interactions (di Pellegrino & Làdavas, 2015). This means that objects located inside PPS are represented in terms of potential actions (Bufacchi & Iannetti, 2018). As suggested by de Vignemont and Iannetti (2015), when an appetitive object is close to our body, we can actively try to take it by implementing an approaching, goal-directed, voluntary action. Therefore, a reaching movement, among other actions, acts inside rather than outside

¹Centre for Studies and Research in Cognitive Neuroscience, Department of Psychology, ‘Alma Mater Studiorum’, Bologna University, Cesena, Italy, ²Experimental Psychology, Helmholtz Institute, Utrecht University, The Netherlands, ³University of Milano-Bicocca, Department of Psychology, Milano, Italy, ⁴Centre for Human Brain Health (CHBH), Department of Psychology, University of Birmingham, UK, ⁵Spinoza Centre for Neuroimaging, Royal Netherlands Academy of Sciences, Amsterdam, The Netherlands, ⁶Department of Psychology, University of Amsterdam, The Netherlands, ⁷Amsterdam Brain and Cognition (ABC), University of Amsterdam, The Netherlands

PPS. However, as is evident from the above-mentioned previous literature, PPS size does not overlap with that covered by our reaching movement. Indeed, PPS is not solely a metrical representation of the space around us but includes a more complex (operational) representation of it (di Pellegrino & Làdavas, 2015).

PPS properties are not fixed but can be altered by motor plans, emotional stimuli, and social context (Spaccasassi & Maravita, 2020; Patané, Farnè, & Frassinetti, 2017; Canzoneri et al., 2013; Teneggi, Canzoneri, di Pellegrino, & Serino, 2013). For instance, visuotactile interactions can be extended in space after the active use of a tool, which allows reaching far locations (Farnè, Iriki, & Làdavas, 2005; Maravita, Husain, Clarke, & Driver, 2001). Behavioral measures of PPS based on the strength of multisensory integration were also found to be modulated by the valence of visual stimuli (Spaccasassi et al., 2019; Ferri, Tajadura-Jiménez, Våljamäe, Vastano, & Costantini, 2015). However, although stimulus valence influences action (Saraiva, Schüür, & Bestmann, 2013) and modifies neural activations associated with visual processing (Conroy & Polich, 2007; Schupp et al., 2004; Codispoti, Bradley, & Lang, 2001), neural modulations that reflected the valence of a visual stimulus were not influenced by whether or not the stimulus was estimated to be within reaching distance (Valdés-Conroy, Sebastián, Hinojosa, Román, & Santaniello, 2014).

Here, we hypothesized that these discrepancies in earlier findings are related to differences between “Defensive” space and “Reaching” space, which respectively refer to two opposite poles of interaction between our body and the external environment: protecting the body and performing a goal-directed action. Whether these two spatial systems rely on the same or different neural maps is currently under debate (for a review based on PPS perspective, see de Vignemont & Iannetti, 2015). There are recent attempts to characterize the Defensive space through EEG (Naro et al., 2019) as well as to distinguish it from the Interpersonal space (i.e., the space between individuals) at neuronal level (Vieira, Pierzchajlo, & Mitchell, 2020), but a direct comparison between the Defensive and Reaching spaces is lacking. Here, we provide such direct comparison, recording behavioral as well as neurophysiological measures sensitive to the mechanisms underlying Defensive and Reaching spaces. Reasoning that stimuli with negative valence are more likely to activate protective actions whereas stimuli with positive valence likely activate approaching actions (Saraiva et al., 2013), we hypothesized that mechanisms associated with Defensive space are more strongly activated when objects have negative compared with positive valence, whereas the opposite is true for mechanisms associated with Reaching space.

In a psychophysical experiment, we used explicit questions inquiring into the evaluative components of both Defensive and Reaching spaces. In particular, by adopting a staircase procedure (Cornsweet, 1962), we investigated

whether the cognitive/evaluative aspects of Defensive and Reaching spaces extend to similar regions of space around the body and whether this is similarly modified by stimulus valence. We expect that negative visual stimuli extend Defensive space relative to positive visual stimuli (de Haan, Smit, Van der Stigchel, & Dijkerman, 2016; Ferri et al., 2015), whereas the opposite holds for the Reaching space (Valdés-Conroy et al., 2014; Valdés-Conroy, Román, Hinojosa, & Shorkey, 2012; Balcetis & Dunning, 2010).

Regarding Reaching space, participants were asked to explicitly estimate their own reaching capabilities. This question is used in the scientific literature about PPS as an explicit measure of Reaching space (D’Angelo, di Pellegrino, & Frassinetti, 2019; Patané et al., 2017; Wamain, Gabrielli, & Coello, 2016; Valdés-Conroy et al., 2012, 2014). Regarding Defensive space, participants were asked whether they were comfortable with an object at a certain distance from their body. This method was adopted from research on Interpersonal space, where it is used in reference to humans instead of objects. It was shown that this “comfort” question is sensitive to the valence of avatar facial expression (Ruggiero et al., 2017) and parallels the electrodermal physiological activity pattern (Cartaud, Ott, Iachini, Honoré, & Coello, 2020; Cartaud, Ruggiero, Ott, Iachini, & Coello, 2018). Specifically, an expansion of Interpersonal space as well as a stronger electrodermal response was found when facing an angry face compared with a neutral or happy face, thus revealing the efficacy of the “comfort” question in capturing defensive reactions. In addition, regarding Defensive space, we asked participants to indicate whether they would like to retract their hand away from an object at a certain distance from their body. With the “retract” question, the focus is centered on the motor component of defensive reactions like withdrawal movements (Cooke & Graziano, 2004).

We also recorded activity in sensorimotor cortex using EEG to assess whether tactile anticipation and motor imagery, respectively associated with the mechanisms underlying Defensive and Reaching spaces, are affected by stimulus valence. The same participants performed a tactile discrimination task (i.e., reporting where on their hand they felt a tactile stimulus) and a reaching estimation task (i.e., estimating whether they could reach an object) while they looked at images of valence-connoted objects located at different distances from their hand. Whereas the former task relates to the multisensory perception of space (based on PPS perspective; Serino, 2019; Graziano & Cooke, 2006), the latter, relying on reachability judgments, relates to the motor properties of the action space (de Vignemont & Iannetti, 2015). We reasoned that these cognitive evaluations of valence-connoted visual stimuli tap into both Defensive and Reaching spaces, respectively.

We analyzed modulation of beta rhythm (15–25 Hz) and mu rhythm (8–12 Hz) over sensorimotor cortex, as

these have been associated with tactile processing, tactile anticipation, movement execution, motor preparation, and motor imagery (beta: Gaetz & Cheyne, 2006; McFarland, Miner, Vaughan, & Wolpaw, 2000; Pfurtscheller, 1981, 1986; mu: Coll, Press, Hobson, Catmur, & Bird, 2017; González-Franco, Peck, Rodríguez-Fornells, & Slater, 2014; Braadbaart, Williams, & Waiter, 2013; Llanos, Rodriguez, Rodriguez-Sabate, Morales, & Sabate, 2013; Hari, 2006; Neuper, Scherer, Reiner, & Pfurtscheller, 2005; Muthukumaraswamy & Johnson, 2004; Babiloni et al., 1999; Pfurtscheller & Da Silva, 1999; Salenius, Schnitzler, Salmelin, Jousmäki, & Hari, 1997). Specifically, synchronization and desynchronization of these rhythms over central areas are generally interpreted as an index of sensorimotor cortex inhibition and activation, respectively (McFarland et al., 2000; Pfurtscheller, Stancak, & Neuper, 1996).

Regarding Defensive space, we expect to find stronger somatosensory cortex activation for negatively than positively valenced visual stimuli when occurring close to the body, reflecting actions to protect the body from aversive objects close to the body (de Haan et al., 2016; Ferri et al., 2015). This hypothesis is supported by previous studies showing that somatosensory sensation elicits a defensive response when coupled to a threatening or negative stimulus (Ellena, Starita, Haggard, & Làdavas, 2020; de Haan et al., 2016; Ferri et al., 2015; Taffou & Viaud-Delmon, 2014). In addition, we expect to find modulations of somatosensory activation by visual stimulus valence before delivery of the tactile stimulus, considering that tactile expectation alone is capable of producing somatosensory activations that are associated with upcoming sensory processing (van Ede, de Lange, Jensen, & Maris, 2011; Babiloni et al., 2008, 2010; van Ede, Jensen, & Maris, 2010). Regarding Reaching space, we expect enhanced sensorimotor activity concomitant with visual processing of positively compared with negatively valenced visual stimuli when occurring close to the body, reflecting preparation of goal-directed action toward appetitive nearby objects (Wamain et al., 2016; Valdés-Conroy et al., 2012, 2014).

METHODS

Participants

Thirty healthy right-handed volunteers (21 women, $M_{\text{age}} = 26.3$ years, $SD = 6.8$ years) participated in the study. They had normal or corrected-to-normal vision and normal sense of touch as assessed by a self-report questionnaire. Participants had no (history with) neurological or psychiatric disorders and no abuse of alcohol or drugs, and they gave written informed consent before participation. Five additional participants were excluded from the analysis because of technical problems during EEG recording. Recruitment and testing of participants conformed to the Helsinki Declaration and was approved before data

collection by the local ethics committee the Faculty of Social and Behavioral Sciences of Utrecht University (Study No. FETC17-117). The number of participants was based on a priori power analysis (30 sample size, 0.22 effect size, .05 error probability, .95 power, 8 measurements) conducted by G*Power software (Faul, Erdfelder, Buchner, & Lang, 2009).

Visual Stimuli

Visual stimuli consisted of 20 pairs of images obtained from the Internet showing everyday objects. Each pair consisted of one object with positive valence and one object with negative valence, which were roughly matched on overall shape and semantic value (Figure 1). The two groups of objects (with positive and negative valence) were carefully matched on arousal value and difficulty to grasp (see method in the Behavioral Experiment: Validation of Visual Stimuli section). Also, the two sets of images were carefully matched on overall luminance, contrast, color content and color contrast (using Adobe Photoshop CC 19.1.9). A gamma correction was applied (using MATLAB 2016A, MathWorks, Inc.). Mean luminance of the images as well as the midgray background was 71.1 cd/m^2 . The images were displayed at varying distance from the participant's body along the vertical midline of a big monitor (PH BDL 5530 EL, $133 \times 75 \text{ cm}$ display size, 1920×1080 resolution, 60 Hz refresh rate) that was positioned flat in front of participant's body midline (equivalent to a table surface, see Figure 2). Size of the images was adjusted such that their longest cardinal axis (i.e., height/width) was 12.50 cm.

In the experiments described below, each presentation of an object image was preceded by a fixation stimulus that participants were instructed to fixate on and that consisted of a 21.5-mm wide black dot with a 14.6-mm wide gray dot and a 7.6-mm wide white dot presented concentrically on top of it (Figure 2A). The center of the fixation stimulus was displayed at the same location, that is, distance from the participant's body, as the subsequent object image. The fixation dot appeared 500–800 msec before the visual stimulus, meaning the eye movement toward it was made before the appearance of the visual and tactile stimuli. During the visual and tactile stimuli, the participants were instructed to maintain strict fixation.

General Procedure

Participants were seated in a comfortable chair in a dark room that was acoustically shielded. During all experiments, participants were instructed to place their right hand on the monitor with the dorsal side up, positioning the end of their middle finger on the vertical midline of the monitor, 18 cm from the edge that was close to their body (this position was close to where the nearest object images would appear). Participants put their chin in a chinrest and placed their left hand on a keyboard or computer mouse located out of sight underneath the

Figure 1. Images of everyday objects used as visual stimuli. Each of 20 pairs of objects consisted of one object with positive valence (on the left) and one object with negative valence (on the right), which were roughly matched on overall shape and semantic value. The two groups of objects with positive and negative valence were carefully matched on arousal value and difficulty to grasp, but the valence and likability to touch differed between the objects. The two sets of images were also carefully matched on overall luminance, contrast, color content, and color contrast.



monitor. In case the keyboard was used, participants positioned their left middle and index fingers on two response buttons (Key 1 and Key 2) of which the corresponding meanings were randomly assigned across participants (see following sections). In all experiments, the participants' right hand was used for the experimental manipulation (i.e., tactile imagery/anticipation/stimulation or reaching imagery/estimation), and their left hand was used for responding.

Before starting the experiments, the reaching distance of the participants' right hand was measured to determine which distances were within and outside this real reaching distance. This distance was measured from the edge of a table at which the participants were sitting (their abdomen touched the table) to the end of their right middle finger while they were asked to stretch their right arm as far as they can. Then, the experiments that are described in the following sections were completed. Participants first completed two experiments during which EEG was recorded: the "Tactile task" involved tactile anticipation and stimulation and was designed to tap into mechanisms underlying Defensive space, whereas the "Reaching task" involved a reaching estimation and was designed to tap into mechanisms underlying Reaching space. With these tasks, we particularly aim to test cognitive/evaluative processing of everyday objects that may occur within and outside Reaching and Defensive spaces. Whether the Tactile task or the Reaching task was completed first was determined randomly per participant. Then, they completed a behavioral experiment in which the boundaries of Defensive and Reaching spaces were determined through explicit evaluative judgments (as described below). After that, they completed another

behavioral experiment in which the valence, arousal level, difficulty to grasp, and likability to touch of each of the 40 object images was assessed. All statistical testing was performed using Jamovi 1.2 (The Jamovi Project, <https://www.jamovi.org>) and included repeated-measures ANOVA or paired *t* tests (unless indicated otherwise; further details are described per experiment below). A Welch's *t* test was performed for post hoc testing of significant two-way interactions resulting from an ANOVA. Response accuracy during the EEG experiments was analyzed using the Wilcoxon test.

EEG Experiments: General Procedure and Recording

Before starting, the Tactile task and Reaching task participants were equipped with an elastic cap (Quickcap, Neuromedical Supplies of Neurosoft, Inc.). EEG was measured using an ActiveTwo System (Biosemi, www.biosemi.com) with 32 silver/silver chloride (Ag/AgCl) flat-type active electrodes positioned at standard locations on the elastic cap. EEG was recorded continuously, with a sampling rate of 2048 Hz, and referenced to an additional active electrode (common mode sense) during recording. Two electrodes in the cap provided an active ground. EOG was also recorded from sub- and supra-orbital regions of the right eye as well as the skin temporal to the outer canthi of the two eyes.

During both the Tactile task and the Reaching task, participants were instructed to minimize their movements and to maintain fixation on the fixation stimulus. Both tasks included the images of objects with either positive or negative valence, displayed with its center at

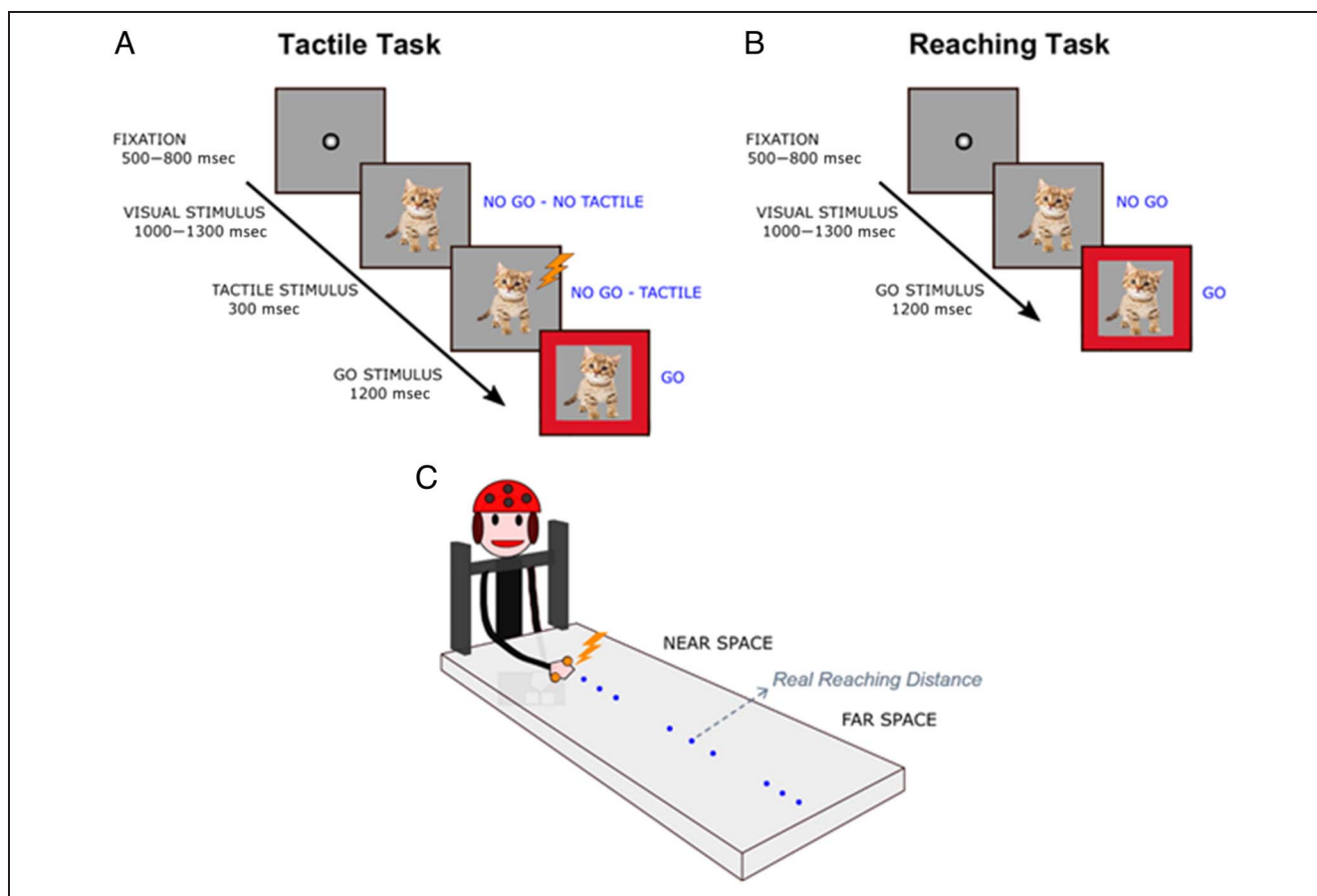


Figure 2. Trial types and experimental setup during the EEG experiments. (A) Trial types and corresponding sequence of events in single trials during the Tactile task. For illustrational purposes, the fixation stimulus and go stimulus are depicted larger than they actually were. The tactile stimulus is indicated by the orange lightning. Blue text represents the names of the trial types. (B) Trial types and corresponding sequence of events in single trials during the Reaching task. Conventions as in A. (C) Illustration of the experimental setup used during the Tactile task and Reaching task. Participants were seated in front of a big monitor that was positioned flat. On the monitor, visual stimuli could appear in one of the nine distances indicated by the blue dots (trials with objects in near space and far space were analyzed and compared; trials with objects close to the real reaching distance were included to increase unpredictability and difficulty of the task but were not analyzed). Orange dots indicate the tactile stimulators used in the Tactile task. The same monitor was used during the behavioral experiments.

one of nine possible distances from the participant's body. Distances were defined relative to the real reaching distance of each participant's right arm as measured before the start of the experiment. Specifically, the distances of the center of the object images were 150.0%, 142.5%, 135.0%, 110.0%, 100.0%, 90.0%, 65.0%, 57.5%, and 50.0% of the real reaching distance. Considering that the averaged reaching distance was 65.83 cm, the shortest (50.0%) and longest (150.0%) distances, on average, corresponded to 32.92 and 98.75 cm from the participant's abdomen, respectively. The closest edge of the nearest visual stimuli was, therefore, on average 8.67 cm away from the end of participant's right middle finger (as this was placed 18 cm from the edge of the monitor and image size was 12.50 cm). The nearest three distances and farthest three distances were analyzed in conjunction and will be referred to as "near space" and "far space," respectively. The middle three distances were included to increase difficulty and unpredictability of the tasks but were not analyzed.

EEG Experiment: Tactile Stimulus Used in Tactile Task

The tactile stimulus was delivered on the more distal phalanx of either the right little finger or the right thumb by means of attaching vibrotactile stimulators to these locations using adhesive tape (Figure 2). The vibrotactile stimulators produced a vibration like that of a mobile phone (eccentric rotating mass in cylindrical casing; Precision Microdrives, model: 308-00, 8-mm diameter, 3.4-mm thick). Per trial, one or none of the stimulators were activated for 100 msec (see trial types in next section). Because of the gradual rise and decay of vibration amplitude in response to onset and offset of the activation, the resulting vibration was perceivable (i.e., >50% of the maximum amplitude) approximately in the time interval of 55–280 msec relative to activation onset. In this time interval, vibration frequency was ~67 Hz (measured with Bosh Sensortec BST-BMI160 inertial measuring unit). Therefore, when interpreting neural activity

relative to onset of the activation of the tactile stimulator (Figure 5), note that the delay between activation and producing a perceivable vibration amplitude was ~ 55 msec. The stimulators produced negligible sound, which was masked by white noise that the participants listened to throughout both the Tactile task and the Reaching task in the EEG experiment using headphones. After completing the Tactile task, participants indicated whether they used audition or touch to determine the location of the vibration on a visual analogue scale that went from “touch only” on the left end to “audition only” on the right end. All participants reported that they discriminated the tactile stimulus mostly by touch ($M = 92$, $SD = 11$; 0 for audition only, 100 for touch only). They also indicated the pleasantness of the tactile stimulus, evidencing that it was not perceived as aversive (visual analogue scale ranging from *very unpleasant* on the left end [score 0] to *very pleasant* on the right end [score 100]; $M = 64$, $SD = 18$).

EEG Experiment: Procedure during Tactile Task

The Tactile task was designed to tap into the evaluative mechanisms underlying Defensive space, particularly with respect to multisensory integration. Participants completed three sessions that were identical, and each lasted 10.5 min. Sessions were separated by a short break. Each trial started with the fixation stimulus at one of the nine possible distances from the participant’s body (see above). After a delay with random duration between 500 and 800 msec, the fixation stimulus was replaced by one of the 40 possible object images displayed at the same distance for a random duration between 1000 and 1300 msec. After that, the sequence of events depended on the trial type. In no-go trials, there was no tactile stimulation; thus, they ended here. For both no-go trials with tactile stimulation and go trials with tactile stimulation (Figure 2A), the tactile stimulator was now activated, and the object image remained visible for an extra 300 msec (the tactile stimulus was perceivable approximately 55–280 msec after activation of the stimulator, see above). A no-go trial with tactile stimulation was then ended, but on go trials with tactile stimulation, a go stimulus that included the object image with a red square around it was then presented for 1200 msec (Figure 2C). The red square had a line thickness of 1.04 cm and subtended 14.65 cm horizontally and vertically. Only on these go trials participants had to indicate as fast as possible whether the tactile stimulus was delivered to the right little finger or right thumb using the keyboard that they operated with their left hand. All go trials were accompanied by tactile stimulation. Note that no-go trials were just shorter versions of a go trial. Thereby, during a no-go trial, the participant did not know yet whether it was a no-go trial or whether a tactile/go stimulus would follow. It has been shown that a low number of go trials is sufficient to elicit task/response-related processing also on no-go trials (e.g., Wamain et al., 2016). The stimuli

were delivered using Presentation (Neurobehavioral Systems, www.neurobs.com).

Per space (near/far space) per valence value (positive/negative), there were in total 18 go trials, 72 no-go trials with tactile stimulation, and 108 no-go trials without tactile stimulation, amounting to 792 trials that were entered in the analysis, which reflected visual stimulation alone (i.e., visual epochs—which stopped at 1000 msec from visual stimulus onset; see the Analysis of EEG Data section for further details). All trials were collapsed in this analysis, because they were identical up to this time point, irrespective of whether they were go or no-go with/without tactile stimulation. For the analysis of tactile processing with simultaneous visual stimulation (i.e., tactile epochs; see the Analysis of EEG Data section for further details), only go trials and no-go trials with tactile stimulation were considered, amounting to 360 trials that were entered in the analysis. As the tactile stimulation increased trial duration, we did not include more no-go trials with tactile stimulation in the experiment than needed to obtain a sufficient amount of trials for analyzing neural oscillation related to tactile processing. As specified above, in both near and far spaces, there were three distances at which images could appear (near: 65.0%, 57.5%, and 50.0% of the real reaching distance; far: 150.0%, 142.5%, and 135.0% of the real reaching distance; Figure 2C). The trials were divided equally over these three distances and analyzed in conjunction. As mentioned above, distances close to the real reaching distance (110.0%, 100.0%, and 90.0%) were included to increase task difficulty and unpredictability but were not analyzed. Therefore, these distances were presented fewer times (in total 36 go trials, 18 no-go trials with tactile stimulation, and 18 no-go trials without tactile stimulation; trials were divided equally over the three distances).

EEG Experiment: Procedure during Reaching Task

The Reaching task was designed to tap into evaluative mechanisms underlying Reaching space. The procedure during the Reaching task was the same as during the Tactile task, with a few exceptions. First, this task did not include tactile stimuli. Therefore, each session lasted somewhat shorter: 9.8 min. There were two trial types: no-go trials and go trials. On go trials, the go stimulus appeared directly after the 1000–1300 msec period designated for the visual stimulus alone. Second, the instruction for go trials was different: Participants were instructed to estimate whether they could reach the displayed objects with their right hand (the same instruction as used for the assessment of Reaching space boundary, see above). They responded by pressing one of two response buttons that were assigned to a “yes” or “no” response, respectively. In total, there were 18 go trials and 180 no-go trials per space (near/far space) per valence value (positive/negative), amounting to 792 trials that were entered in the analysis. Distances close to the real reaching

distance were not analyzed and therefore were presented fewer times (36 go trials and 36 no-go trials in total).

Analysis of EEG Data

During offline analysis, the continuous EEG signal was down-sampled (1024 Hz), filtered (basic finite impulse response filter, 1–100 Hz), and rereferenced to the average signal using EEGLAB software (Delorme & Makeig, 2004) running under MATLAB R2019b. Independent component analysis (ICA)-based artifact correction was used to correct for blink artifacts (Delorme, Sejnowski, & Makeig, 2007), and ICA components falling outside the selection threshold of the EEGLAB plug-in SASICA were automatically removed (Chaumon, Bishop, & Busch, 2015). The signal was then divided into “visual epochs” that contained the periods in which the object images appeared and “tactile epochs” that contained the period in which tactile processing occurred (see specific time intervals used for epoching below). Epochs contaminated by muscular contractions or excessive deflections ($\pm 75 \mu\text{V}$) were excluded (total rejection rate was 11% in visual epochs and 8% in tactile epochs). For each participant, event-related changes in the oscillatory activity were quantified using a time–frequency wavelet decomposition of the EEG signals between 1 and 100 Hz (complex Morlet’s wavelets, ratio $f_0/\sigma_f = 7$) implemented in “WTools” toolbox (Parise & Csibra, 2013). Baseline correction was performed over a -300 to -100 msec time interval relative to onset of the object image/tactile stimulator for visual/tactile epochs, respectively, using Fieldtrip toolbox (fieldtriptoolbox.org; Oostenveld, Fries, Maris, & Schoffelen, 2011) running under MATLAB R2019b (MathWorks, Inc.). Then, the grand average was calculated, and mean power of mu (8–12 Hz) and beta (15–25 Hz) rhythms were extracted from centroparietal electrodes C3, CP1, CP5, and P3 on the left hemisphere and C4, CP2, CP6, and P4 on the right hemisphere (frequency ranges and electrodes of interest based on Proverbio, 2012; Behmer & Jantzen, 2011; Nyström, Ljunghammar, Rosander, & von Hofsten, 2011; Perry, Stein, & Bentin, 2011; Perry & Bentin, 2009; Pfurtscheller, Brunner, Schlögl, & Da Silva, 2006; Pineda, 2005).

Visual epochs included the -700 to $+1500$ msec time interval relative to onset of the object image (including the baseline period that started at -300) as well as the time interval of interest that lasted until $+1000$ msec (see below) and 500 msec extra before and after this interval to account for edge effects resulting from the time–frequency analysis. For the visual epochs, mu power was analyzed in a repeated-measures ANOVA with Distance (near, far), Valence (positive, negative), Hemisphere (left, right) and Task (Reaching, Tactile) as within factors, using the average mu power in the time window 500–1000 msec after visual stimulus onset for both tasks. The time window was chosen because it just

precedes onset of the tactile stimulator and because mu power showed a robust increase within this time window. No statistical analysis was performed on beta power for the visual epochs because scalp maps revealed a clear occipital instead of sensorimotor localization (used scalp maps reflected beta power over the time interval after onset of the object image).

Tactile epochs included the -1900 to $+1100$ msec time interval relative to onset of the tactile stimulator. This interval started early because we wanted to enable visual inspection of the tactile epochs with baseline correction applied over the period before onset of the object image instead of the period before onset of the tactile stimulator (this inspection corroborated results described in the Results section regarding power differences that were present during tactile processing, but that already emerged before onset of the tactile stimulator). For the tactile epochs, mu and beta power were analyzed in a repeated-measures ANOVA with Distance (near, far), Valence (positive, negative), and Hemisphere (left, right) as within factors. For mu and beta power, respectively, we used the average power in the time window 400–1000 and 300–700 msec after activation of the tactile stimulator. These time windows were based on previous literature (Singh et al., 2014; Hu, Peng, Valentini, Zhang, & Hu, 2013; Cheyne et al., 2003). Note that on some trials, the tactile epoch and the window used for mu rhythm lasted beyond the end of the trial (the shortest no-go trials lasted only until 800 msec after onset of the tactile stimulator). However, when we repeated our analysis of mu power using a shorter time window (400–700 msec), we found equivalent results.

Behavioral Experiment: Assessment of Spatial Boundary

We asked participants to make explicit judgments for both Defensive and Reaching spaces using a staircase procedure that included the two groups of object images (with positive and negative valence) and three different experimental questions. To explicitly assess Reaching space, we asked participants to answer as fast as possible: “Could you reach that object at that distance with your right hand?” To explicitly assess Defensive space, we asked two questions in separated runs, one related to a feeling of comfort and the other related to action, in this case, an avoidance response. The respective questions were as follows: “Do you feel uncomfortable with that object at that distance from your right hand?” and “Would you like to retract your right hand away from that object at that distance from your right hand?” For each question, four runs with positively valenced images and four runs with negatively valenced images were completed. Per question per valence value, the starting position of the object image on the first trial of a run alternated between being close to the participant’s right hand (ascending series) or being far from the participant’s right hand

(descending series). The specific object that was displayed on a single trial within a run was selected randomly from the respective group of 20 images. Each trial started with 500-msec presentation of the fixation stimulus followed by presentation of an object image that lasted until response (using OpenSesame 3.1; Mathôt, Schreij, & Theeuwes, 2012). Participants responded by pressing one of two possible response buttons on a computer mouse (left button for “yes,” right button for “no”). A “yes”/“no” answer resulted in the position of the object image on the following trial being farther away/closer to their body, respectively. In the first run of each series, step size was 2.22 cm, whereas in the second run, a more precise estimation of the extent of the respective space was obtained using a step size of 0.56 cm. The final runs ended when the participant’s answer (and thereby the distance of the object image) went back-and-forth between the two possibilities for 12 times in a row (this was six times for the runs with 2.22 cm precision). The spatial boundary determined by explicit judgments was then computed by averaging all the object positions that elicited response change across the final run of both descending and ascending series. For statistical analysis, a repeated-measures ANOVA over participants was performed, with Space (Reaching, Defensive “comfort,” Defensive “retract”), and Valence (positive, negative) as within factors.

Behavioral Experiment: Validation of Visual Stimuli

After the other experiments were completed, participants performed a short behavioral experiment in which they rated the valence, arousal level, difficulty to grasp, and likability to touch regarding each of the 40 images of objects used in the completed experiments. Valence (“Rate how NEGATIVE/POSITIVE the picture just displayed is”) and arousal level (“Rate how AROUSING the picture just displayed is”) of the displayed object were rated using a 9-point Likert scale that ran from *completely negative/completely unarousing* to *completely positive/completely arousing*, with the central point marked as *neutral/medium arousing* (using OpenSesame 3.1; Mathôt et al., 2012). The images were displayed at the center of the same screen used for the EEG task for 1500 msec preceded by a 500-msec fixation stimulus, and the Likert scales remained visible until response. The response was made using a computer mouse held in the right hand. The procedure was then repeated with two different questions that assessed difficulty to grasp and likability to touch (respective instructions were “Rate if is it difficult or easy to GRASP/LIFT the object just displayed using only the right hand” and “Rate if would you like or dislike to TOUCH the object just displayed”; Likert scale was labeled *very easy/dislike very much* on the left end and *very difficult/like very much* on the right end, with the label *neutral* in the middle). The two categories of 20 images (positive/negative valence) differed in rated valence and likability to touch but not in rated arousal value and

difficulty to grasp: valence, $t(29) = 17.0, p > .001$; likability to touch, $t(29) = 20.4, p > .001$; arousal, $t(29) = 1.1, p = .3$; difficulty to grasp, $t(29) = -0.9, p = .4$. The 20 pairs of images used in the experiments were selected from a larger set of 81 pairs of images that was assessed in a pilot test using the same protocol as describe above. Based on the results of the pilot test, 20 of the 81 pairs of images were selected such that they differed in valence but not in arousal value and difficulty to grasp, and this was confirmed for the current group of participants (see statistical results above).

RESULTS

Explicit Assessment of Spatial Boundary

The boundary of Defensive space, but not Reaching space, is farther from the body for objects with negative compared to positive valence. A significant interaction between Space and Valence, $F(2, 58) = 20.7, p < .001$, revealed that valence had no effect in Reaching space, $t(81.9) = -0.21, p \approx 1.0$, whereas it had a strong effect on Defensive space (Defensive “comfort” space, $t(81.9) = -7.4, p < .001$; Defensive “retract” space, $t(81.9) = -7.3, p < .001$; main effect of Valence, $F(1, 29) = 54.8, p < .001$; Figure 3). The effect of Valence on Defensive space was mainly expressed as a profound reduction of its threshold when positive visual stimuli were presented: objects with positive valence, Reaching space versus Defensive “comfort” space, $t(102.9) = 8.1, p < .001$; Reaching PPS versus Defensive “retract” space, $t(102.9) = 8.1, p < .001$; Real Reaching versus Defensive “comfort” space, $t(29) = 11.266, p < .001$; Real Reaching versus Defensive “retract” space, $t(29) = 8.1, p < .001$. Regarding negative visual stimuli, Defensive space was also slightly smaller than Reaching space, but they did not significantly differ from each other: objects with negative valence, Reaching space versus Defensive “comfort” space, $t(102.9) = 1.7, p = .5$; Reaching space versus Defensive “retract” space, $t(102.9) = 1.9, p = .4$; overall main effect of Space, $F(2, 58) = 24.3, p < .001$. There were no differences between our two measures of Defensive space regarding these effects (difference between the two Defensive spaces, $F(1, 29) = 0.02, p = .9$; interaction with valence, $F(1, 29) = 0.01, p = .9$), and overall, the results of the two defensive staircases were positively correlated ($r = .620, p < .001$), thus suggesting they were indeed measuring the same type of space.

Behavioral Results EEG Experiment

Responses are faster and more accurate for nearby objects, but they are not influenced by stimulus valence. In both tasks, participants responded faster when objects were located near rather than far from the body, $F(1, 29) = 15.4, p < .001$. This difference between near and far space was even stronger in the Reaching task

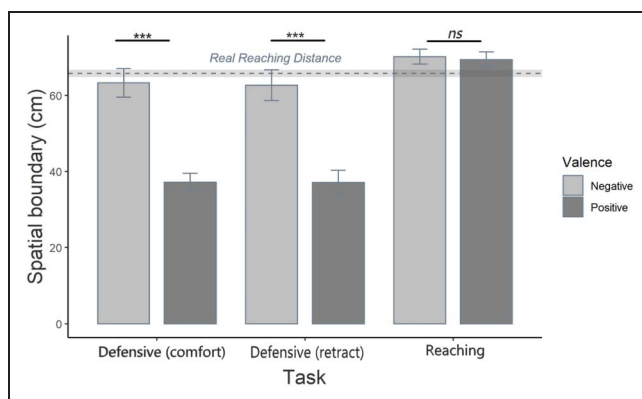


Figure 3. Explicit assessment of spatial boundary: The boundary of Defensive space, but not Reaching space, is farther from the body for objects with negative compared with positive valence. The boundary of Defensive space (both Defensive “comfort” and Defensive “retract”) was much closer to the body for objects with positive valence (dark gray bars) than for objects with negative valence (light gray bars). For the Defensive “comfort” measure, participants indicated whether they felt comfortable with objects at a certain distance from their hand. For the Defensive “retract” measure, participants indicated whether they wanted to retract their hand farther away from the objects. The size of Reaching space, as assessed by asking participants to indicate whether objects were within reaching distance, was not influenced by the valence of the objects. Error bars indicate *SEM*. The dashed horizontal line indicates the actual reaching distance of the participants (shading indicates *SEM*). Asterisks represent the difference between objects with positive and negative valence ($***p < .001$; *ns* indicates no significant difference).

(69 msec difference), $F(1, 29) = 17.4, p < .001$, than in the Tactile task (22 msec), $F(1, 29) = 4.9, p = .04$; Distance \times Task, $F(1, 29) = 6.3, p = .02$; overall mean RT was 622 msec. RTs were particularly fast for objects in near space in the Reaching task (difference between the tasks: 90 msec), $F(1, 29) = 6.9, p = .01$, whereas RTs for objects in far space were more similar (42 msec), $F(1, 29) = 1.5, p = .2$; overall main effect of Task, $F(1, 29) = 4.3, p < .05$. No main effects of Valence or interactions with Valence were found, all $F(1, 29) < 1.2$, all $p \geq .3$.

Responses were more accurate for near than for far objects in the Reaching task, $\chi^2(1) = 6.0, p = .01$ (near: $M = 96\%$, $SD = 12\%$; far: $M = 93\%$, $SD = 9\%$), but not in the Tactile task, $\chi^2(1) = 0.1, p = .7$ (near: $M = 91\%$, $SD = 9\%$; far: $M = 90\%$, $SD = 11\%$). Valence of the object did not influence response accuracy: Reaching task, $\chi^2(1) = 0.2, p = .7$; Tactile task, $\chi^2(1) = 0.3, p = .6$.

Visual Processing

Bilateral mu synchronization is weaker for nearby objects, and this effect is not influenced by stimulus valence. In both tasks, bilateral mu synchronization was larger when objects were far from the body than when objects were near the body (Figure 4): Distance, $F(1, 29) = 34.0, p < .001$; mu power relative to baseline for far, $t(29) = 6.4, p < .001$; for near, $t(29) = 23.8, p = .008$; hemisphere, $F(1, 29) = 2.5, p = .1$; Distance \times Hemisphere,

$F(1, 29) = 1.3, p = .3$. The difference between near and far objects was significant in the Reaching task, $F(1, 29) = 17.8, p < .001$, as well as in the Tactile task, $F(1, 29) = 41.9, p < .001$, but in the Tactile task, the enhanced mu synchronization for far objects was particularly strong (Figure 4): difference between the tasks for far objects, $F(1, 29) = 20.6, p < .001$; for near objects, $F(1, 29) = 2.6, p = .1$; Distance \times Task, $F(1, 29) = 11.0, p = .002$; task, $F(1, 29) = 13.2, p < .001$. Object valence did not influence these effects, Distance \times Valence, $F(1, 29) = 0.2, p = .7$; Valence, $F(1, 29) \approx 0.0, p \approx 1.0$; other interactions with Valence, all $F < 3.5$, all $p > .07$. Note that visual stimuli had a larger retinal size when closer to the body, which might have contributed to the main effect of Distance.

Tactile Processing

Beta desynchronization is enhanced for objects with negative compared with positive valence. In line with expectation, there was a bilateral desynchronization of mu and beta power after the tactile stimulus was delivered, which was stronger in the contralateral than in the ipsilateral hemisphere: mu, $F(1, 29) = 8.8, p = .006$; beta, $F(1, 29) = 5.6, p = .03$ (contralateral and ipsilateral power for mu: $M = 0.84 \mu V^2, SD = 0.14$ and $M = 0.87 \mu V^2, SD = 0.13$; for beta: $M = 0.89 \mu V^2, SD = 0.08$ and $M = 0.91 \mu V^2, SD = 0.07$). In both hemispheres, desynchronization of beta rhythm was stronger when objects had negative compared with positive valence (Figure 5A–C), valence, $F(1, 29) = 4.9, p = .03$; Valence \times Hemisphere, $F(1, 29) = 0.3, p = .6$. There was a marginally significant Valence \times Distance interaction, $F(1, 29) = 3.1, p = .09$, and Valence \times Distance \times Hemisphere, $F(1, 29) = 0.9, p = .3$ (Figure 5D). The effects of Hemisphere and Valence were not significant before onset of the tactile stimulus (analysis over 800–1000 msec time interval after visual stimulus onset, all $F(1, 29) \leq 1.5$; all $p > .2$), indicating they emerged during tactile processing. Note that vibration amplitude increased gradually after onset of the tactile stimulator and that it reached a perceivable level after approximately 55 msec (see Methods). Also note that, even if their onset was asynchronous, the tactile stimulus was delivered when the visual stimulus was still present. Therefore, these results may reflect coupling of visuotactile stimuli, rather than tactile stimulation alone.

There was a difference in beta power between objects in near and far space (Figure 5C), $F(1, 29) = 20.2, p < .001$. However, this difference may, at least partly, reflect a difference in visual processing, because it was already present before onset of the tactile stimulus and may thereby have affected the time interval used for baseline correction (analysis over 800–1000 msec time interval after visual stimulus onset, $F(1, 29) = 5.1, p = .03$; $-0.014 \mu V^2 \pm 0.006$ difference). Similarly, mu power also differed for objects in near and far space, $F(1, 29) = 16.2, p < .001$ (near: $M = 0.88 \mu V^2, SD = 0.12$, far: $M = 0.83 \mu V^2, SD = 0.14$), but a difference with similar scalp

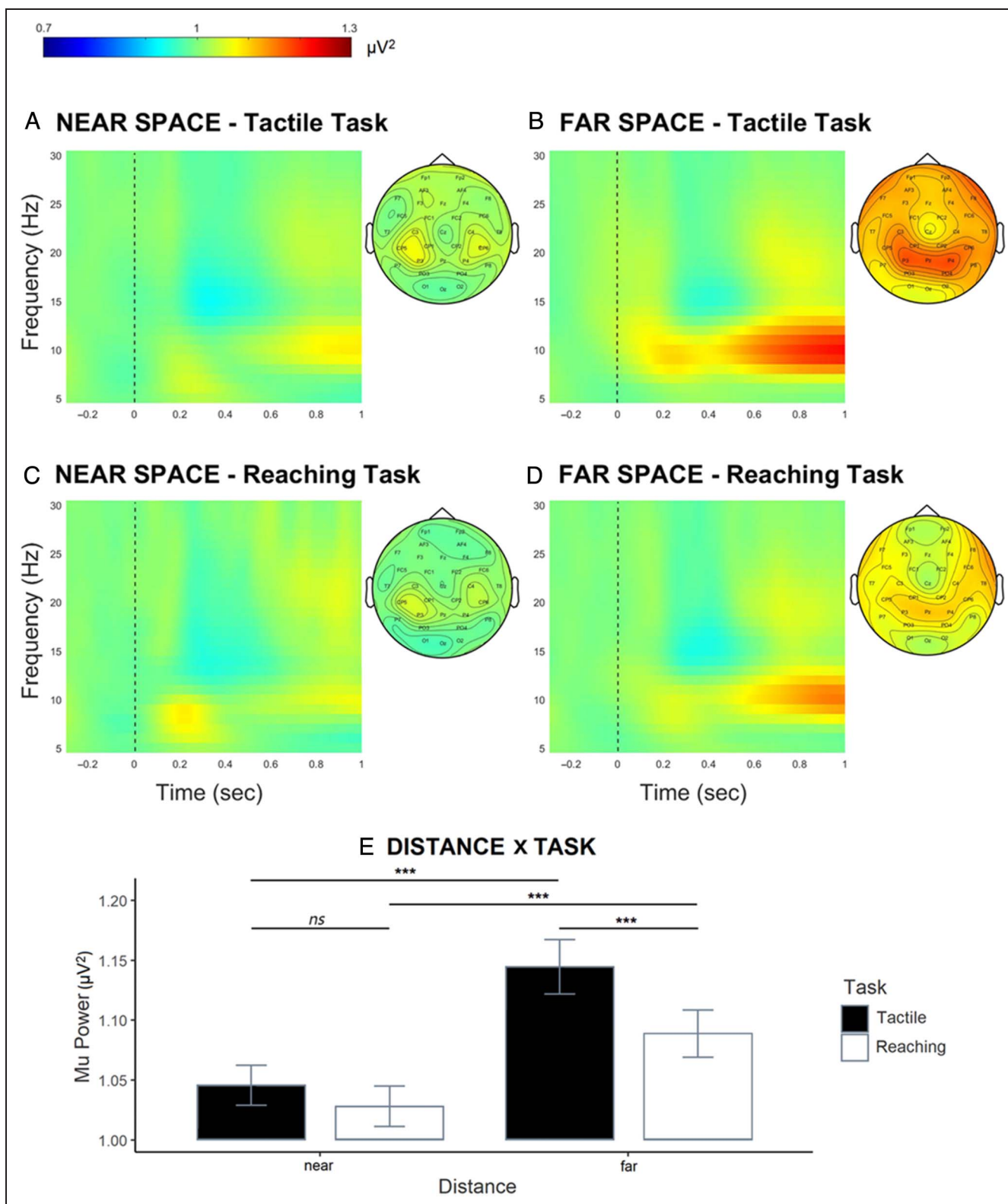


Figure 4. Visual processing: Bilateral mu synchronization is weaker for nearby objects than for far objects in the Tactile task as well as in the Reaching task. (A) Time–frequency (TF) spectrum relative to onset of the visual stimulus and scalp map of mu power (8–12 Hz) for the time interval 500–1000 msec after visual stimulus onset for near space in the Tactile task. Mu power is indicated by colors (see color bar in top left corner), with blue and red symbolizing μV^2 desynchronization and synchronization relative to baseline, respectively. (B) TF spectrum and scalp map for far space in the Tactile task. (C) TF spectrum and scalp map for near space in the Reaching task. (D) TF spectrum and scalp map for far space in the Reaching task. (E) Mu power (8–12 Hz) for the time interval 500–1000 msec after visual stimulus onset, illustrating the main effect of Distance in both tasks. Error bars represent *SEM*. Asterisks represent difference between conditions ($***p < .001$; *ns* indicates no significant difference).

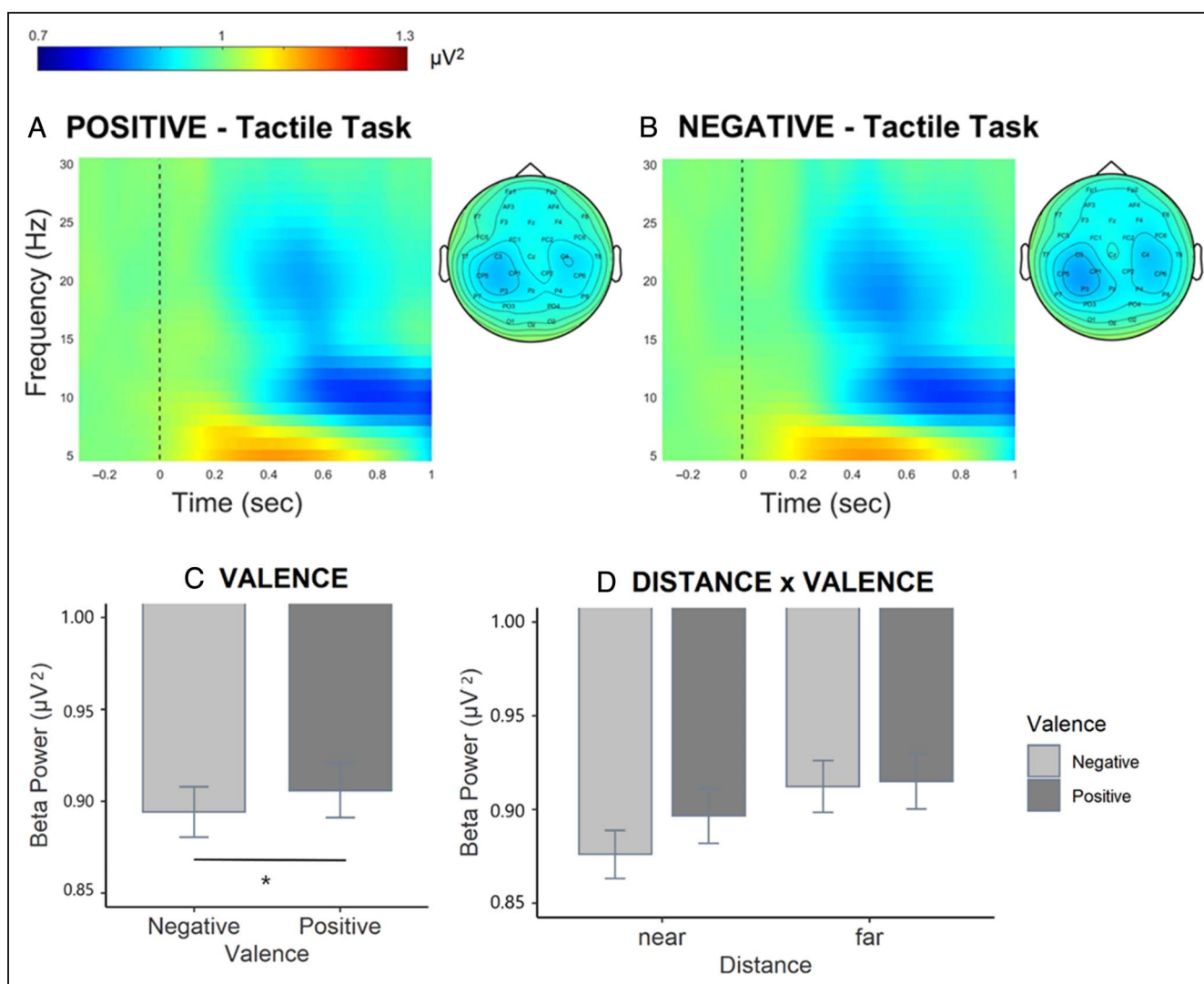


Figure 5. Tactile processing: Beta desynchronization is enhanced for objects with negative compared with positive valence. (A) Time–frequency (TF) spectrum relative to onset of the tactile stimulator and scalp map of beta power (15–25 Hz) for the time interval 300–700 msec after tactile stimulator onset for objects with positive valence (near and far spaces are averaged). Note that vibration amplitude increased gradually after onset of the tactile stimulator and that it reached a perceivable level after approximately 55 msec (see Methods). Beta power is indicated by colors (see color bar in top left corner), with blue and red symbolizing desynchronization and synchronization relative to baseline, respectively. (B) Same as A, but here for objects with negative valence. (C) Beta power (15–25 Hz) for the time interval 300–700 msec after tactile stimulus onset, illustrating the main effect of valence. There was also a main effect of distance, but this was not related to tactile processing specifically, because it was already present before onset of the tactile stimulus. (D) Same data as in C, but here presented for near and far space separately (the two-way interaction Distance \times Valence was only marginally significant). Error bars represent *SEM*. Asterisks represent difference between conditions ($*p < .05$).

location and magnitude was already present before onset of the tactile stimulus, indicating it probably reflected tactile anticipation rather than tactile processing (Figure 4). Desynchronization of mu rhythm was not influenced by Object Valence, $F(1, 29) = 0.01$, $p = .9$, and no other main effects or interactions were found (all $F \leq 0.8$, $p \geq .4$).

DISCUSSION

Inspired by the literature on PPS, we aimed to explore the electrophysiological and behavioral signature of the mechanisms underlying the two spatial representations—Reaching and Defensive spaces—and their modulation

by the valence of visual stimuli. We recorded EEG while participants performed a Reaching task (Reaching space) and a Tactile task (Defensive space) in which they viewed visual stimuli with positive or negative valence. In a separate experiment that included the same visual stimuli as the EEG experiment, spatial boundaries were probed using explicit judgments about evaluative mechanisms in a staircase procedure. We obtained three main results: (i) The boundary of Defensive space, but not Reaching space, was influenced by valence: The boundary was closer to the body for visual stimuli with positive compared with negative valence. (ii) Electrophysiological results support an influence of valence in Defensive space: During tactile

processing in the Tactile task, desynchronization of beta rhythm over the sensorimotor cortex was smaller for positively compared with negatively valenced visual stimuli. (iii) Visual processing in both Defensive and Reaching spaces was influenced by object distance, but not valence: In both the Tactile task and the Reaching task, presentation of the visual stimulus elicited weaker synchronization of mu power when the visual stimulus was presented close to rather than far from the body. Thus, to summarize, both EEG and psychophysical data reveal an effect of valence for Defensive space, whereas no effects of valence were found for Reaching space. Our results regarding Defensive space suggest that valence (i.e., contextual information) influences late processing stages rather than initial object/space encoding, because tactile processing (beta rhythm) and explicit measure of spatial boundary were influenced by valence, but visual processing was not.

Valence Encoding Modulates Defensive Space Boundaries and Beta Rhythm Oscillations during Tactile Processing

Using two different questions that relate to Defensive space (i.e., “Are you uncomfortable with that object at that distance?” and “Would you like to retract your right arm with that object at that distance?”) in a staircase procedure, we obtained a clear effect of valence on explicit judgments of Defensive space boundary. In particular, we found that positively valenced stimuli entail a smaller Defensive space than negatively valenced stimuli for both the questions used. This makes sense, considering that it is not necessary to implement protective actions when encountering pleasant stimuli. Valence of the visual stimulus did not influence the boundary of Reaching space (“Could you reach, with your right hand, that object located at that distance?”).

Although the estimation of own reaching capabilities is often used in the scientific literature to explicitly assess Reaching space (D’Angelo et al., 2019; Patané et al., 2017; Wamain et al., 2016; Valdés-Conroy et al., 2012, 2014), to date, there is no standard explicit measurement of Defensive space. In the context of PPS, a physiological response to threat is typically employed when indexing Defensive space, measured both through the hand–blink reflex (Sambo, Liang, Cruccu, & Iannetti, 2012) and skin conductance (Rossetti, Romano, Bolognini, & Maravita, 2015). Therefore, we developed a novel paradigm to explicitly characterize Defensive space by using two different questions tapping into the mechanisms underlying this space, the “comfort” question and the “retract” question.

So far, most studies about PPS investigated the influence of negatively valenced stimuli by comparing them to stimuli with neutral valence (de Haan et al., 2016; Ferri et al., 2015; Taffou & Viaud-Delmon, 2014). These studies, using multisensory stimulation paradigms, showed an expansion of PPS boundaries for visually

threatening stimuli (Ferri et al., 2015, Taffou & Viaud-Delmon, 2014). The influence of stimuli with positive valence on PPS boundaries has received less attention. Using a visuotactile interaction task, Spaccasassi et al. (2019) showed faster RTs to both positively and negatively valenced stimuli (regardless of their arousal value) compared with neutral stimuli in far space, although this distinction disappeared in near space. This was interpreted as evidence for high saliency of all visual stimuli that are close to the body as well as nonneutral stimuli farther away from the body. However, this study did not assess changes in PPS boundary.

In the current study, we assessed the influence of visual stimulus valence in relation to the distinction between Defensive and Reaching spaces and found that valence influenced the mechanisms underlying Defensive space but not those underlying Reaching space. Defensive space boundary measured by explicit judgments about positively valenced stimuli was much closer to the body than both explicit judgments about Reaching space and the actual reaching distance of the participants, whereas there were no significant differences regarding positively valenced stimuli (we did not include a neutral stimulus). Without claiming that Defensive space, Reaching space and actual reaching distance are the same for negatively valenced stimuli, these results suggest that the modulation of Defensive space by valence mainly comprises a reduction in Defensive space for positively valenced stimuli. It would be interesting to see whether this holds if affirmative questions are asked instead, that is, asking whether the participant is “comfortable” (instead of uncomfortable) and asking whether the participant would like to “keep the hand in place” (instead of asking about retraction). Neurolinguistic studies indicated that negative and affirmative sentences are processed differently, with the latter being associated with better mnemonic and semantic processing (Christensen, 2009; Cornish & Wason, 1970). Note that our staircase methodology inevitably resulted in a measure of a boundary, but this reflects the methodology used, and we therefore consider the boundaries found in the current study not to be in contradiction with a recent proposal that PPS is a set of graded fields than as a sharp boundary (Bufacchi & Iannetti, 2018).

This influence of stimulus valence on the properties of Defensive space was supported by modulations of beta oscillations that occurred bilaterally centered on the sensorimotor cortices during tactile processing in the Tactile task (bilateral occurrence is in line with previous literature: Genna et al., 2017; using the same tactile stimulus as in this study: de Jong & Dijkerman, 2019). Beta desynchronization was reduced for concurrent visual stimuli with positive compared with negative valence. Previous studies have shown a link between aversive tactile stimuli and modulations of beta oscillations (Michail, Dresel, Witkovský, Stankewitz, & Schulz, 2016; Mancini, Longo, Canzoneri, Vallar, & Haggard, 2013) as well as between

processing unpleasant visual stimuli and modulations of beta oscillations (Güntekin & Başar, 2010). Our study extends these findings by showing that the valence of a “visual” stimulus modulates beta oscillations that reflect “tactile” processing. We suggest that the observed difference in beta desynchronization could be linked to unpleasant bodily consequences (Valentini, Liang, Aglioti, & Iannetti, 2012) implied by negatively valenced visual stimuli (Dijkerman & Medendorp, 2021; Kandula, Hofman, & Dijkerman, 2015). This interpretation relates to the influence of valence on the explicit judgments measuring Defensive space boundary that we found using the “comfort” question (“Are you uncomfortable with that object at that distance?”). Alternatively, the difference in beta desynchronization could be related to subthreshold motor activation like an avoidance response (DeLaRosa et al., 2014), considering the effect on Defensive space boundary observed using the “retract” question (“Would you like to retract your right arm with that object at that distance?”).

Interestingly, the bilateral valence effect observed for beta oscillations was not (or only weakly) modulated by object distance. It could be that the influence of object distance would have been stronger if the objects had had a larger difference in valence or a higher arousal level (being threatening or dangerous), if the tactile stimulus would have been aversive or nociceptive (as in De Paepe, Crombez, Spence, & Legrain, 2014; Sambo et al., 2012) or if the experiment would have included more participants and/or more trials. However, even if object distance (marginally) influences the modulation of beta by object valence, our findings largely suggest that near space encoding occurs separately from—perhaps before—valence encoding as indicated by the different modulation of oscillations in near versus far space before tactile stimulation. This is in line with the “Swiss Army knife model” of PPS (de Vignemont & Iannetti, 2015), which describes a single cortical map underlying Reaching PPS and Defensive PPS.

We had hypothesized that positively valenced stimuli evoke enhanced neural processing in the Reaching task and a more distant Reaching space boundary than negatively valenced stimuli because of their high desirability (Valdés-Conroy et al., 2012; Balçetis & Dunning, 2010). However, valence of the visual stimulus influenced neither behavioral measures nor EEGs related to Reaching space. This suggests that visual stimulus valence does not modulate the mechanisms underlying Reaching space when the arousal level of the visual stimuli is carefully matched, in line with a previous report that showed that ERPs recorded with EEG are not modulated by the valence of visual stimuli displayed either inside or outside Reaching space (Valdés-Conroy et al., 2014). Moreover, this result is also consistent with our validation ratings where the reachability scores of the stimuli with positive and negative valence were similar. Here, we considered Reaching space to be characterized best by asking for a

subjective estimation of reaching ability (indicate if you *could* reach the object with your right arm; in line with D’Angelo et al., 2019; Patané et al., 2017), as reaching is the most straightforward way of proactively interacting with an object close to our hand. Note that this methodology does not equate Reaching space to actual Reaching space, because rather than an objective measure of reaching ability, we analyzed subjective estimates and neural processing associated with concomitant motor imagery. Still, it could be that the lack of modulation by valence is inherent to the context of reaching ability (“could”) rather than reaching preference (“would”). In addition, it would be interesting to more thoroughly test (with more go trials) whether RTs and accuracy in the EEG task are indeed not modulated by stimulus valence.

Near Space Encoding Is Supported by Reaction Times and Mu Rhythm Oscillations

In the literature, PPS refers to the facilitated processing of (multi)sensory stimuli when they are located close to the body (for a review, see di Pellegrino & Làdavas, 2015). In line with this, we found faster RTs in both the Tactile task and the Reaching task for objects in near compared with far space, as well as higher response accuracy for objects in near space in the Reaching task. Furthermore, we found bilateral synchronization of mu rhythm over sensorimotor cortex, which, in both tasks, was most profound when visual stimuli were located in far compared with near space. Mu synchronization occurred 500–1000 msec after visual stimulus onset, thus before potential presentation of the Go signal or the tactile stimulus. In this time interval participants presumably were engaged in motor imagery (Reaching task), tactile anticipation (Tactile task), and response preparation (both tasks). Interestingly, in both tasks, objects in near space were associated with mu synchronization that was confined to electrodes over sensorimotor cortex, whereas objects in far space elicited more distributed mu synchronization, including more lateral and more posterior electrodes. Following previous interpretations of similar localization difference between processing of objects in near and far space (e.g., Weiss et al., 2000), this may be interpreted as engagement of the dorsal (motor encoding) and ventral (perceptual encoding) visual processing stream for near and far visual stimuli, respectively. Alternatively, it may indicate that visual attention (alpha oscillations) contributed to the results, particularly in far space (Clayton, Yeung, & Cohen Kadosh, 2018; Jensen & Mazaheri, 2010).

Based on previous literature about mu rhythm, we had expected desynchronization of mu rhythm in near space—rather than reduced synchronization (Coll et al., 2017; Wamain et al., 2016; Llanos et al., 2013; Braadbaart et al., 2013; Hari, 2006; Salmelin & Hari, 1994). The reduced synchronization over sensorimotor cortex observed here could reflect that the sensorimotor cortex is less inhibited when visual stimuli are present in near

compared with far space (following Pfurtscheller et al., 1996). In this study, inhibition rather than activation of sensorimotor cortex may have resulted from the inability to physically interact with objects that are presented as flat images on a computer monitor, as well as the instruction of participants to refrain from actually performing such interactions. Importantly, if mu synchronization reflected inhibition of sensorimotor cortex, our results indicate that sensorimotor cortex is less inhibited when objects are in near space. This change in engagement of the sensorimotor cortex depending on object distance, irrespective of task goals and object valence, is consistent with the PPS characterization postulated by Noel and Serino (2019). Indeed, these authors emphasize the role of distance in defining PPS, claiming that proximity is more important than any other factor sensitive to PPS measures. Our results are also in line with the perspective of Bufacchi and Iannetti (2018), which states that (i) visual objects inside PPS are transformed into representations of potential actions and (ii) different PPS measures lead to different results. Related to (i), the weaker mu rhythm synchronization in far versus near space found in both the Tactile task and the Reaching task could reflect transformation into actions that could respectively be aimed at protecting the body (as investigated in González-Franco et al., 2014) or performing a goal-directed action (as investigated in Wamain et al., 2016). Concerning (ii), the Tactile task revealed different aspects of Defensive space than the two defensive staircases (e.g., touch is an important signal that the body is potentially in danger of being harmed as well as the “comfort” and “retract” questions provide info about cognitive processing related to preventing the body from harm). In the present EEG study, indeed, we compared two regions in space, near and far from the body. In a future study, it would be interesting to vary the analyzed distances parametrically, particularly including distances near the actual reaching distance or PPS boundary, also to see if there is a near-to-far space gradient in space encoding (as suggested regarding PPS by Bufacchi & Iannetti, 2018).

Despite the similar topography and temporal dynamics of mu rhythm synchronization recorded in both spaces, it is worth noting that the Reaching EEG task relies on explicit judgments whereas the Tactile task relies on multisensory processing. Even though multisensory processing and reaching potentialities are not completely detached from each other (Farnè et al., 2005; Maravita et al., 2001), in a future experiment, it would be interesting to add an irrelevant tactile stimulus during the Reaching task (for a similar procedure, see Zanini et al., 2021). This could determine whether the greater desynchronization of beta oscillations found for negative visual stimuli after receiving the tactile input is indeed specific to Defensive space.

In both tasks, the observed mu synchronization was not lateralized. Previous reports of desynchronization of

mu rhythm often report lateralization to the contralateral hemisphere (motor imagery: Nam, Jeon, Kim, Lee, & Park, 2011; McFarland et al., 2000; tactile expectation: van Ede et al., 2010, 2011; response preparation: Deiber et al., 2012), though not under all circumstances (Pfurtscheller & Berghold, 1989; Pfurtscheller & Aranibar, 1979). The lack of lateralization in the present results could be due to the fact that both hands were relevant to the task: the right hand for reaching estimation or tactile anticipation and the left hand for preparing a button press.

Conclusion

Using literature on PPS as a theoretical framework, we here investigated behavioral and neural correlates of Defensive and Reaching spaces by looking at their modulation by visual stimulus valence. The explicit judgments of Defensive space revealed a closer boundary for positively compared with negatively valenced visual stimuli. Furthermore, sensorimotor cortex activation during tactile processing was enhanced when coupled with negatively rather than positively valenced visual stimuli. On the contrary, both the EEG and psychophysical measures of Reaching space did not reveal any modulation by valence. Contrasting their difference regarding valence encoding, we found indications that spatial encoding is similar for Defensive and Reaching spaces. Reaching estimation as well as tactile anticipation were characterized by increased mu synchronization for far compared with near visual stimuli, which could indicate increased inhibition of sensorimotor cortex for far stimuli. In accordance, in both tasks, we found slower RTs for far compared with near stimuli. These findings parallel the Swiss Army knife model of PPS described by de Vignemont and Iannetti (2015) that postulates a single cortical map underlying Reaching PPS and Defensive PPS (contrasting a range of behavioral studies supporting a distinction between the two spaces, e.g., Zanini et al., 2021). Our results are thus compatible with the idea that Reaching and Defensive spaces (and possibly PPS) are processed by the same neural representation that integrates sensory input with encoding of space, whereas task goals and stimulus valence (i.e., contextual information) are implemented in a later processing stage and exert an influence on touch processing and motor output rather than object/space encoding.

Acknowledgments

The authors would like to thank Ermanno Quadrelli for his help with WTools package.

Reprint requests should be sent to Chiara Spaccasassi, Centre for Studies and Research in Cognitive Neuroscience, Department of Psychology, “Alma Mater Studiorum,” Bologna University, via Rasi e Spinelli, 176, 47521, Cesena, Italy, or via e-mail: chiara.spaccasassi2@unibo.it.

Author Contributions

Chiara Spaccasassi: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Software; Validation; Visualization; Writing—Original draft; Writing—Review & editing. Chris H. Dijkerman: Conceptualization; Funding acquisition; Project administration; Resources; Supervision; Writing—Review & editing. Angelo Maravita: Conceptualization. Oscar Ferrante: Formal analysis. Maartje C. de Jong: Conceptualization; Funding acquisition; Methodology; Software; Supervision; Writing—Review & editing.

Funding Information

This research was supported by an NWO Vici grant (453-10-003) awarded to C. H. D., a PhD program grant from the University of Milano-Bicocca awarded to C. S., and an Amsterdam Brain and Cognition Talent grant awarded to M. C. d. J.

Diversity in Citation Practices

A retrospective analysis of the citations in every article published in this journal from 2010 to 2020 has revealed a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience (JoCN)* during this period were $M(\text{an})/M = .408$, $W(\text{oman})/M = .335$, $M/W = .108$, and $W/W = .149$, the comparable proportions for the articles that these authorship teams cited were $M/M = .579$, $W/M = .243$, $M/W = .102$, and $W/W = .076$ (Fulvio et al., *JoCN*, 33:1, pp. 3–7). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

REFERENCES

- Babiloni, C., Capotosto, P., Brancucci, A., Del Percio, C., Petrini, L., Buttiglione, M., et al. (2008). Cortical alpha rhythms are related to the anticipation of sensorimotor interaction between painful stimuli and movements: A high-resolution EEG study. *Journal of Pain*, 9, 902–911. <https://doi.org/10.1016/j.jpain.2008.05.007>, PubMed: 18619907
- Babiloni, C., Capotosto, P., Del Percio, C., Babiloni, F., Petrini, L., Buttiglione, M., et al. (2010). Sensorimotor interaction between somatosensory painful stimuli and motor sequences affects both anticipatory alpha rhythms and behavior as a function of the event side. *Brain Research Bulletin*, 81, 398–405. <https://doi.org/10.1016/j.brainresbull.2009.11.009>, PubMed: 19932156
- Babiloni, C., Carducci, F., Cincotti, F., Rossini, P. M., Neuper, C., Pfurtscheller, G., et al. (1999). Human movement-related potentials vs desynchronization of EEG alpha rhythm: A high-resolution EEG study. *NeuroImage*, 10, 658–665. <https://doi.org/10.1006/nimg.1999.0504>, PubMed: 10600411
- Balcetis, E., & Dunning, D. (2010). Wishful seeing: More desired objects are seen as closer. *Psychological Science*, 21, 147–152. <https://doi.org/10.1177/0956797609356283>, PubMed: 20424036
- Behmer, L. P., Jr., & Jantzen, K. J. (2011). Reading sheet music facilitates sensorimotor mu-desynchronization in musicians. *Clinical Neurophysiology*, 122, 1342–1347. <https://doi.org/10.1016/j.clinph.2010.12.035>, PubMed: 21216663
- Bernasconi, F., Noel, J. P., Park, H. D., Faivre, N., Seeck, M., Spinelli, L., et al. (2018). Audio-tactile and peripersonal space processing around the trunk in human parietal and temporal cortex: An intracranial EEG study. *Cerebral Cortex*, 28, 3385–3397. <https://doi.org/10.1093/cercor/bhy156>, PubMed: 30010843
- 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, 99–105. <https://doi.org/10.1016/j.ijpsycho.2013.05.019>, PubMed: 23756148
- Brozzoli, C., Cardinali, L., Pavani, F., & Farné, A. (2010). Action-specific remapping of peripersonal space. *Neuropsychologia*, 48, 796–802. <https://doi.org/10.1016/j.neuropsychologia.2009.10.009>, PubMed: 19837102
- Bufacchi, R. J., & Iannetti, G. D. (2018). An action field theory of peripersonal space. *Trends in Cognitive Sciences*, 22, 1076–1090. <https://doi.org/10.1016/j.tics.2018.09.004>, PubMed: 30337061
- 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, 25–42. <https://doi.org/10.1007/s00221-013-3532-2>, PubMed: 23640106
- Cartaud, A., Ott, L., Iachini, T., Honoré, J., & Coello, Y. (2020). The influence of facial expression at perceptual threshold on electrodermal activity and social comfort distance. *Psychophysiology*, 57, e13600. <https://doi.org/10.1111/psyp.13600>, PubMed: 32437046
- Cartaud, A., Ruggiero, G., Ott, L., Iachini, T., & Coello, Y. (2018). Physiological response to facial expressions in peripersonal space determines interpersonal distance in a social interaction context. *Frontiers in Psychology*, 9, 657. <https://doi.org/10.3389/fpsyg.2018.00657>, PubMed: 29867639
- Chaumon, M., Bishop, D. V., & Busch, N. A. (2015). A practical guide to the selection of independent components of the electroencephalogram for artifact correction. *Journal of Neuroscience Methods*, 250, 47–63. <https://doi.org/10.1016/j.jneumeth.2015.02.025>, PubMed: 25791012
- Cheyne, D., Gaetz, W., Garnero, L., Lachaux, J. P., Ducorps, A., Schwartz, D., et al. (2003). Neuromagnetic imaging of cortical oscillations accompanying tactile stimulation. *Cognitive Brain Research*, 17, 599–611. [https://doi.org/10.1016/S0926-6410\(03\)00173-3](https://doi.org/10.1016/S0926-6410(03)00173-3), PubMed: 14561448
- Christensen, K. R. (2009). Negative and affirmative sentences increase activation in different areas in the brain. *Journal of Neurolinguistics*, 22, 1–17. <https://doi.org/10.1016/j.jneuroling.2008.05.001>
- Clayton, M. S., Yeung, N., & Cohen Kadosh, R. (2018). The many characters of visual alpha oscillations. *European Journal of Neuroscience*, 48, 2498–2508. <https://doi.org/10.1111/ejn.13747>, PubMed: 29044823
- Codispoti, M., Bradley, M. M., & Lang, P. J. (2001). Affective reactions to briefly presented pictures. *Psychophysiology*, 38, 474–478. <https://doi.org/10.1111/1469-8986.3830474>, PubMed: 11352135
- Coll, M. P., Press, C., Hobson, H., Catmur, C., & Bird, G. (2017). Crossmodal classification of mu rhythm activity during action observation and execution suggests specificity to somatosensory features of actions. *Journal of Neuroscience*,

- 37, 5936–5947. <https://doi.org/10.1523/JNEUROSCI.3393-16.2017>, PubMed: 28559380
- Conroy, M. A., & Polich, J. (2007). Affective valence and P300 when stimulus arousal level is controlled. *Cognition and Emotion*, *21*, 891–901. <https://doi.org/10.1080/02699930600926752>
- Cooke, D. F., & Graziano, M. S. (2004). Sensorimotor integration in the precentral gyrus: Polysensory neurons and defensive movements. *Journal of Neurophysiology*, *91*, 1648–1660. <https://doi.org/10.1152/jn.00955.2003>, PubMed: 14586035
- Cornish, E. R., & Wason, P. C. (1970). The recall of affirmative and negative sentences in an incidental learning task. *Quarterly Journal of Experimental Psychology*, *22*, 109–114. <https://doi.org/10.1080/0033557043000032>
- Cornsweet, T. N. (1962). The staircase-method in psychophysics. *American Journal of Psychology*, *75*, 485–491. <https://doi.org/10.2307/1419876>, PubMed: 13881416
- D'Angelo, M., di Pellegrino, G., & Frassinetti, F. (2019). The illusion of having a tall or short body differently modulates interpersonal and peripersonal space. *Behavioural Brain Research*, *375*, 112146. <https://doi.org/10.1016/j.bbr.2019.112146>, PubMed: 31401144
- de Haan, A. M., Smit, M., Van der Stigchel, S., & Dijkerman, H. C. (2016). Approaching threat modulates visuotactile interactions in peripersonal space. *Experimental Brain Research*, *234*, 1875–1884. <https://doi.org/10.1007/s00221-016-4571-2>, PubMed: 26894891
- de Jong, M. C., & Dijkerman, H. C. (2019). The influence of joint attention and partner trustworthiness on cross-modal sensory cueing. *Cortex*, *119*, 1–11. <https://doi.org/10.1016/j.cortex.2019.04.005>, PubMed: 31059978
- 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. <https://doi.org/10.1016/j.neuropsychologia.2014.01.016>, PubMed: 24486423
- de Vignemont, F., & Iannetti, G. D. (2015). How many peripersonal spaces? *Neuropsychologia*, *70*, 327–334. <https://doi.org/10.1016/j.neuropsychologia.2014.11.018>, PubMed: 25448854
- di Pellegrino, G., & Làdavas, E. (2015). Peripersonal space in the brain. *Neuropsychologia*, *66*, 126–133. <https://doi.org/10.1016/j.neuropsychologia.2014.11.011>, PubMed: 25448862
- Deiber, M. P., Sallard, E., Ludwig, C., Ghezzi, C., Barral, J., & Ibañez, V. (2012). EEG alpha activity reflects motor preparation rather than the mode of action selection. *Frontiers in Integrative Neuroscience*, *6*, 59. <https://doi.org/10.3389/fnint.2012.00059>, PubMed: 22912607
- DeLaRosa, B. L., Spence, J. S., Shakal, S. K., Motes, M. A., Calley, C. S., Calley, V. I., et al. (2014). Electrophysiological spatiotemporal dynamics during implicit visual threat processing. *Brain and Cognition*, *91*, 54–61. <https://doi.org/10.1016/j.bandc.2014.08.003>, PubMed: 25222294
- 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*, 9–21. <https://doi.org/10.1016/j.jneumeth.2003.10.009>, PubMed: 15102499
- Delorme, A., Sejnowski, T., & Makeig, S. (2007). Enhanced detection of artifacts in EEG data using higher-order statistics and independent component analysis. *Neuroimage*, *34*, 1443–1449. <https://doi.org/10.1016/j.neuroimage.2006.11.004>, PubMed: 17188898
- Dijkerman, H. C., & Medendorp, W. P. (2021). Visuotactile predictive mechanisms of peripersonal space. In F. de Vignemont, H. Y. Wong, A. Farne, & A. Serino (Eds.), *The world at our fingertips: A multidisciplinary exploration of peripersonal space*. Oxford, United Kingdom: Oxford University Press. <https://doi.org/10.1093/oso/9780198851738.003.0005>
- Duhamel, J. R., Bremmer, F., Hamed, S. B., & Graf, W. (1997). Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature*, *389*, 845–848. <https://doi.org/10.1038/39865>, PubMed: 9349815
- Ellena, G., Starita, F., Haggard, P., & Làdavas, E. (2020). The spatial logic of fear. *Cognition*, *203*, 104336. <https://doi.org/10.1016/j.cognition.2020.104336>, PubMed: 32516582
- Farnè, A., Iriki, A., & Làdavas, E. (2005). Shaping multisensory action–space with tools: Evidence from patients with cross-modal extinction. *Neuropsychologia*, *43*, 238–248. <https://doi.org/10.1016/j.neuropsychologia.2004.11.010>, PubMed: 15707908
- Faul, F., Erdfelder, E., Buchner, A., & Lang, A. G. (2009). Statistical power analyses using G* Power 3.1: Tests for correlation and regression analyses. *Behavior Research Methods*, *41*, 1149–1160. <https://doi.org/10.3758/BRM.41.4.1149>, PubMed: 19897823
- 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. <https://doi.org/10.1016/j.neuropsychologia.2015.03.001>, PubMed: 25744869
- 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*, 141–157. <https://doi.org/10.1152/jn.1996.76.1.141>, PubMed: 8836215
- Gaetz, W., & Cheyne, D. (2006). Localization of sensorimotor cortical rhythms induced by tactile stimulation using spatially filtered MEG. *Neuroimage*, *30*, 899–908. <https://doi.org/10.1016/j.neuroimage.2005.10.009>, PubMed: 16326116
- Genna, C., Oddo, C. M., Fanciullacci, C., Chisari, C., Jörmte, H., Artoni, F., et al. (2017). Spatiotemporal dynamics of the cortical responses induced by a prolonged tactile stimulation of the human fingertips. *Brain Topography*, *30*, 473–485. <https://doi.org/10.1007/s10548-017-0569-8>, PubMed: 28497235
- 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*, 875–887. <https://doi.org/10.1007/s00221-013-3800-1>, PubMed: 24337257
- Graziano, M. S., & Cooke, D. F. (2006). Parieto-frontal interactions, personal space, and defensive behavior. *Neuropsychologia*, *44*, 845–859. <https://doi.org/10.1016/j.neuropsychologia.2005.09.009>, PubMed: 16277998
- Graziano, M. S., Reiss, L. A., & Gross, C. G. (1999). A neuronal representation of the location of nearby sounds. *Nature*, *397*, 428–430. <https://doi.org/10.1038/17115>, PubMed: 9989407
- Güntekin, B., & Başar, E. (2010). Event-related beta oscillations are affected by emotional eliciting stimuli. *Neuroscience Letters*, *483*, 173–178. <https://doi.org/10.1016/j.neulet.2010.08.002>, PubMed: 20692324
- Hari, R. (2006). Action–perception connection and the cortical mu rhythm. *Progress in Brain Research*, *159*, 253–260. [https://doi.org/10.1016/S0079-6123\(06\)59017-X](https://doi.org/10.1016/S0079-6123(06)59017-X)
- Hu, L., Peng, W., Valentini, E., Zhang, Z., & Hu, Y. (2013). Functional features of nociceptive-induced suppression of alpha band electroencephalographic oscillations. *Journal of Pain*, *14*, 89–99. <https://doi.org/10.1016/j.jpain.2012.10.008>, PubMed: 23273836
- Jensen, O., & Mazaheri, A. (2010). Shaping functional architecture by oscillatory alpha activity: Gating by inhibition. *Frontiers in Human Neuroscience*, *4*, 186. <https://doi.org/10.3389/fnhum.2010.00186>, PubMed: 21119777

- Kandula, M., Hofman, D., & Dijkerman, H. C. (2015). Visuo-tactile interactions are dependent on the predictive value of the visual stimulus. *Neuropsychologia*, *70*, 358–366. <https://doi.org/10.1016/j.neuropsychologia.2014.12.008>, PubMed: 25498404
- Làdavas, E., Pellegrino, G. D., Farnè, A., & Zeloni, G. (1998). Neuropsychological evidence of an integrated visuotactile representation of peripersonal space in humans. *Journal of Cognitive Neuroscience*, *10*, 581–589. <https://doi.org/10.1162/089892998562988>, PubMed: 9802991
- 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*, 1019–1026. <https://doi.org/10.1016/j.neuropsychologia.2013.02.008>, PubMed: 23462240
- 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*, 11841–11851. <https://doi.org/10.1523/JNEUROSCI.2955-09.2009>, PubMed: 19776270
- Mancini, F., Longo, M. R., Canzoneri, E., Vallar, G., & Haggard, P. (2013). Changes in cortical oscillations linked to multisensory modulation of nociception. *European Journal of Neuroscience*, *37*, 768–776. <https://doi.org/10.1111/ejn.12080>, PubMed: 23216684
- 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*, 580–585. [https://doi.org/10.1016/S0028-3932\(00\)00150-0](https://doi.org/10.1016/S0028-3932(00)00150-0), PubMed: 11257283
- Mathôt, S., Schreij, D., & Theeuwes, J. (2012). OpenSesame: An open-source, graphical experiment builder for the social sciences. *Behavior Research Methods*, *44*, 314–324. <https://doi.org/10.3758/s13428-011-0168-7>, PubMed: 22083660
- McFarland, D. J., Miner, L. A., Vaughan, T. M., & Wolpaw, J. R. (2000). Mu and beta rhythm topographies during motor imagery and actual movements. *Brain topography*, *12*, 177–186. <https://doi.org/10.1023/A:1023437823106>, PubMed: 10791681
- Michail, G., Dresel, C., Witkovský, V., Stankewitz, A., & Schulz, E. (2016). Neuronal oscillations in various frequency bands differ between pain and touch. *Frontiers in Human Neuroscience*, *10*, 182. <https://doi.org/10.3389/fnhum.2016.00182>, PubMed: 27199705
- Muthukumaraswamy, S. D., & Johnson, B. W. (2004). Changes in rolandic mu rhythm during observation of a precision grip. *Psychophysiology*, *41*, 152–156. <https://doi.org/10.1046/j.1469-8986.2003.00129.x>, PubMed: 14693010
- Nam, C. S., Jeon, Y., Kim, Y. J., Lee, I., & Park, K. (2011). Movement imagery-related lateralization of event-related (de)synchronization (ERD/ERS): Motor-imagery duration effects. *Clinical Neurophysiology*, *122*, 567–577. <https://doi.org/10.1016/j.clinph.2010.08.002>, PubMed: 20800538
- Naro, A., Calabrò, R. S., La Rosa, G., Andronaco, V. A., Billeri, L., Lauria, P., et al. (2019). Toward understanding the neurophysiological basis of peripersonal space: An EEG study on healthy individuals. *PLoS One*, *14*, e0218675. <https://doi.org/10.1371/journal.pone.0218675>, PubMed: 31233542
- 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*, 668–677. <https://doi.org/10.1016/j.cogbrainres.2005.08.014>, PubMed: 16236487
- Noel, J. P., & Serino, A. (2019). High action values occur near our body. *Trends in Cognitive Sciences*, *23*, 269–270. <https://doi.org/10.1016/j.tics.2019.01.001>, PubMed: 30824226
- Noel, J. P., Serino, A., & Wallace, M. T. (2019). Increased neural strength and reliability to audiovisual stimuli at the boundary of peripersonal space. *Journal of Cognitive Neuroscience*, *31*, 1155–1172. https://doi.org/10.1162/jocn_a_01334, PubMed: 30188779
- Nyström, P., Ljunghammar, T., Rosander, K., & von Hofsten, C. (2011). Using mu rhythm desynchronization to measure mirror neuron activity in infants. *Developmental Science*, *14*, 327–335. <https://doi.org/10.1111/j.1467-7687.2010.00979.x>, PubMed: 22213903
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, *2011*, 156869. <https://doi.org/10.1155/2011/156869>, PubMed: 21253357
- Parise, E., & Csibra, G. (2013). Neural responses to multimodal ostensive signals in 5-month-old infants. *PLoS One*, *8*, e72360. <https://doi.org/10.1371/journal.pone.0072360>, PubMed: 23977289
- Patané, I., Farnè, A., & Frassinetti, F. (2017). Cooperative tool-use reveals peripersonal and interpersonal spaces are dissociable. *Cognition*, *166*, 13–22. <https://doi.org/10.1016/j.cognition.2017.04.013>, PubMed: 28554081
- 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. <https://doi.org/10.1016/j.brainres.2009.05.059>, PubMed: 19500557
- Perry, A., Stein, L., & Bentin, S. (2011). Motor and attentional mechanisms involved in social interaction—Evidence from mu and alpha EEG suppression. *Neuroimage*, *58*, 895–904. <https://doi.org/10.1016/j.neuroimage.2011.06.060>, PubMed: 21742042
- Pfurtscheller, G. (1981). Central beta rhythm during sensorimotor activities in man. *Electroencephalography and Clinical Neurophysiology*, *51*, 253–264. [https://doi.org/10.1016/0013-4694\(81\)90139-5](https://doi.org/10.1016/0013-4694(81)90139-5), PubMed: 6163614
- Pfurtscheller, G. (1986). Rolandic mu rhythms and assessment of cerebral functions. *American Journal of EEG Technology*, *26*, 19–32. <https://doi.org/10.1080/00029238.1986.11080187>
- Pfurtscheller, G., & Aranibar, A. (1979). Evaluation of event-related desynchronization (ERD) preceding and following voluntary self-paced movement. *Electroencephalography and Clinical Neurophysiology*, *46*, 138–146. [https://doi.org/10.1016/0013-4694\(79\)90063-4](https://doi.org/10.1016/0013-4694(79)90063-4), PubMed: 86421
- Pfurtscheller, G., & Berghold, A. (1989). Patterns of cortical activation during planning of voluntary movement. *Electroencephalography and Clinical Neurophysiology*, *72*, 250–258. [https://doi.org/10.1016/0013-4694\(89\)90250-2](https://doi.org/10.1016/0013-4694(89)90250-2)
- 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*, 153–159. <https://doi.org/10.1016/j.neuroimage.2005.12.003>
- Pfurtscheller, G., & Da Silva, F. L. (1999). Event-related EEG/MEG synchronization and desynchronization: Basic principles. *Clinical Neurophysiology*, *110*, 1842–1857. [https://doi.org/10.1016/S1388-2457\(99\)00141-8](https://doi.org/10.1016/S1388-2457(99)00141-8), PubMed: 10576479
- Pfurtscheller, G., Stancak, A., Jr., & Neuper, C. (1996). Event-related synchronization (ERS) in the alpha band—An electrophysiological correlate of cortical idling: A review. *International Journal of Psychophysiology*, *24*, 39–46. [https://doi.org/10.1016/S0167-8760\(96\)00066-9](https://doi.org/10.1016/S0167-8760(96)00066-9), PubMed: 8978434
- Pineda, J. A. (2005). The functional significance of mu rhythms: Translating “seeing” and “hearing” into “doing.” *Brain Research Reviews*, *50*, 57–68. <https://doi.org/10.1016/j.brainresrev.2005.04.005>, PubMed: 15925412

- Proverbio, A. M. (2012). Tool perception suppresses 10–12 Hz μ rhythm of EEG over the somatosensory area. *Biological Psychology*, *91*, 1–7. <https://doi.org/10.1016/j.biopsycho.2012.04.003>, PubMed: 22543070
- Rizzolatti, G., Fadiga, L., Fogassi, L., & Gallese, V. (1997). The space around us. *Science*, *277*, 190–191. <https://doi.org/10.1126/science.277.5323.190>, PubMed: 9235632
- Rizzolatti, G., Scandolaro, C., Gentilucci, M., & Camarda, R. (1981). Response properties and behavioral modulation of ‘mouth’ neurons of the postarcuate cortex (area 6) in macaque monkeys. *Brain Research*, *225*, 421–424. [https://doi.org/10.1016/0006-8993\(81\)90847-7](https://doi.org/10.1016/0006-8993(81)90847-7), PubMed: 7306798
- 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. <https://doi.org/10.1016/j.neuropsychologia.2015.01.019>, PubMed: 25595342
- Ruggiero, G., Frassinetti, F., Coello, Y., Rapuano, M., Di Cola, A. S., & Iachini, T. (2017). The effect of facial expressions on peripersonal and interpersonal spaces. *Psychological Research*, *81*, 1232–1240. <https://doi.org/10.1007/s00426-016-0806-x>, PubMed: 27785567
- Salenius, S., Schnitzler, A., Salmelin, R., Jousmäki, V., & Hari, R. (1997). Modulation of human cortical rolandic rhythms during natural sensorimotor tasks. *Neuroimage*, *5*, 221–228. <https://doi.org/10.1006/nimg.1997.0261>, PubMed: 9345551
- Salmelin, R., & Hari, R. (1994). Characterization of spontaneous MEG rhythms in healthy adults. *Electroencephalography and Clinical Neurophysiology*, *91*, 237–248. [https://doi.org/10.1016/0013-4694\(94\)90187-2](https://doi.org/10.1016/0013-4694(94)90187-2), PubMed: 7523073
- Sambo, C. F., Liang, M., Cruccu, G., & Iannetti, G. D. (2012). Defensive peripersonal space: The blink reflex evoked by hand stimulation is increased when the hand is near the face. *Journal of Neurophysiology*, *107*, 880–889. <https://doi.org/10.1152/jn.00731.2011>, PubMed: 22090460
- Saraiva, A. C., Schüür, F., & Bestmann, S. (2013). Emotional valence and contextual affordances flexibly shape approach-avoidance movements. *Frontiers in Psychology*, *4*, 933. <https://doi.org/10.3389/fpsyg.2013.00933>, PubMed: 24379794
- 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*, 189. <https://doi.org/10.1037/1528-3542.4.2.189>, PubMed: 15222855
- Serino, A. (2019). Peripersonal space (PPS) as a multisensory interface between the individual and the environment, defining the space of the self. *Neuroscience & Biobehavioral Reviews*, *99*, 138–159. <https://doi.org/10.1016/j.neubiorev.2019.01.016>, PubMed: 30685486
- Serino, A., Noel, J. P., Galli, G., Canzoneri, E., Marmaroli, P., Lissek, H., et al. (2015). Body part-centered and full body-centered peripersonal space representations. *Scientific Reports*, *5*, 18603. <https://doi.org/10.1038/srep18603>, PubMed: 26690698
- Singh, H., Bauer, M., Chowanski, W., Sui, Y., Atkinson, D., Baurley, S., et al. (2014). The brain’s response to pleasant touch: An EEG investigation of tactile caressing. *Frontiers in Human Neuroscience*, *8*, 893. <https://doi.org/10.3389/fnhum.2014.00893>, PubMed: 25426047
- Spaccasassi, C., Frigione, I., & Maravita, A. (2021). Bliss in and out of the body: The (extra)corporeal space is impervious to social pleasant touch. *Brain Sciences*, *11*, 225. <https://doi.org/10.3390/brainsci11020225>, PubMed: 33673297
- Spaccasassi, C., & Maravita, A. (2020). Peripersonal space is diversely sensitive to a temporary vs permanent state of anxiety. *Cognition*, *195*, 104133. <https://doi.org/10.1016/j.cognition.2019.104133>, PubMed: 31734548
- 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*, *192*, 42–51. <https://doi.org/10.1016/j.actpsy.2018.10.013>, PubMed: 30412839
- Taffou, M., & Viaud-Delmon, I. (2014). Cynophobic fear adaptively extends peri-personal space. *Frontiers in Psychiatry*, *5*, 122. <https://doi.org/10.3389/fpsyg.2014.00122>, PubMed: 25232342
- Teneggi, C., Canzoneri, E., di Pellegrino, G., & Serino, A. (2013). Social modulation of peripersonal space boundaries. *Current Biology*, *23*, 406–411. <https://doi.org/10.1016/j.cub.2013.01.043>, PubMed: 23394831
- 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*, e49162. <https://doi.org/10.1371/journal.pone.0049162>, PubMed: 23185304
- 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. <https://doi.org/10.1016/j.neuropsychologia.2014.04.009>, PubMed: 24747210
- Valentini, E., Liang, M., Aglioti, S. M., & Iannetti, G. D. (2012). Seeing touch and pain in a stranger modulates the cortical responses elicited by somatosensory but not auditory stimulation. *Human Brain Mapping*, *33*, 2873–2884. <https://doi.org/10.1002/hbm.21408>, PubMed: 22234936
- 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*, 2016–2024. <https://doi.org/10.1523/JNEUROSCI.5630-10.2011>, PubMed: 21307240
- van Ede, F., Jensen, O., & Maris, E. (2010). Tactile expectation modulates pre-stimulus β -band oscillations in human sensorimotor cortex. *Neuroimage*, *51*, 867–876. <https://doi.org/10.1016/j.neuroimage.2010.02.053>, PubMed: 20188186
- Vieira, J. B., Pierzchajlo, S. R., & Mitchell, D. G. (2020). Neural correlates of social and non-social personal space intrusions: Role of defensive and peripersonal space systems in interpersonal distance regulation. *Social Neuroscience*, *15*, 36–51. <https://doi.org/10.1080/17470919.2019.1626763>, PubMed: 31151372
- 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. <https://doi.org/10.1016/j.cortex.2015.10.006>, PubMed: 26606301
- Weiss, P. H., Marshall, J. C., Wunderlich, G., Tellman, L., Halligan, P. W., Freund, H. J., et al. (2000). Neural consequences of acting in near versus far space: A physiological basis for clinical dissociations. *Brain*, *123*, 2531–2541. <https://doi.org/10.1093/brain/123.12.2531>, PubMed: 11099454
- Zanini, A., Patané, I., Blini, E., Salemme, R., Koun, E., Farnè, A., et al. (2021). Peripersonal and reaching space differ: Evidence from their spatial extent and multisensory facilitation pattern. *Psychonomic Bulletin & Review*, 1–12.