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The anticipatory effect of goal-directed action planning with a lower limb on peri-personal space



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ABSTRACT

Recent studies have demonstrated that the representation of peri-personal space (PPS) can be strongly modulated by the intention to execute a spatially-directed hand-movement. However, the question of whether analogous motor-induced PPS modulations can be observed during the planning and execution of goal-directed lower limbs movements has been scarcely investigated. Here we asked whether changes in the visuo-tactile PPS maps occur during the planning of a goal directed foot-movement. We asked participants to respond to the location of a tactile stimulus delivered to the index finger (top) or the thumb (bottom) of the right hand while ignoring a visual distractor presented at congruent or incongruent elevations, either close to the foot or close to the goal of the foot movement. This version of the cross-modal congruency task was performed under two different experimental conditions, as a baseline (static task, no movement involved) and embedded into a dual-task in which participants also had to plan and execute a goal-directed foot movement (dynamic task). In the static task, comparable cross-modal congruency effects (CCE) were present near the foot and near the movement goal. In the dynamic task, the CCE near the foot shrank considerably, whereas a sizable CCE was present near the movement goal. This anticipatory reweighting of the multisensory representation of near-space demonstrates that PPS is modulated by the intention to perform a goal-directed foot movement, with a weakened representation of the space around the currently occupied foot location when a movement is imminent.

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1. Introduction

The ability to interact with objects or navigate around obstacles is closely dependent upon the ability to consistently register where the body is positioned in space as well as its spatial relations with neighbouring objects. To support this endeavour, the primate brain does not represent the space surrounding the body as a single unitary map. Instead, space is encoded in multiple maps, based not only on the relative spatial proximity between the body and neighbouring objects, but also on the distinct movements the body can perform with different effectors upon those objects (e.g., [Rizzolatti et al., 1983, 1997, 2014](#)). The representation of peripersonal space (PPS) – often defined as the space immediately surrounding the bodies of primates and humans (e.g., [Clery et al., 2015; di Pellegrino & Làdavas, 2015; Serino, 2019](#)) – is considered crucial for the multisensory processing of information which allows body–objects interactions.

Seminal neurophysiological studies with non-human primates provided early evidence that the representation of space around the body is mediated by distinct networks of functionally interconnected neural regions, including the intraparietal sulcus, the premotor cortex and the subcortical putamen, characterized by spatial, multisensory and motor properties ([Duhamel et al., 1998; Graziano & Gross, 1993, 1995; Gross & Graziano, 1995; Rizzolatti et al., 2002](#)). Located within these regions are populations of bimodal visuo-tactile neurons whose receptive fields are in spatial register with each other. While the tactile receptive fields are anchored to a specific body part, the depths of the visual receptive fields are restricted to specifically encompass a limited portion of the space surrounding that body part ([Graziano & Gross, 1993, 1995](#)), ‘as if the cutaneous space extends into the visual space adjacent to it (peripersonal space, PPS)’ ([Rizzolatti et al., 1997](#)). That is, these neurons show strong responses to visual stimuli only when these are presented close to the body part to which their tactile receptive fields are anchored. Physiological work with macaque monkeys has further revealed that the orientations of the visual receptive fields shift in parallel with changes in body position rather than the position (or the movements) of the eyes, thereby ensuring that near-space stimuli are consistently registered within a body-centred reference frame (e.g., [Graziano et al., 1994](#)).

Beyond the primate brain, functional neuroimaging work has established that the PPS representations in humans are grounded in a homologous fronto-parietal network which overlaps substantially with neural regions governing the body schema (e.g., [Bremmer et al., 2001; Brozzoli et al., 2011; Makin et al., 2007; Quinlan & Culham, 2007](#)). These findings imply a close connection between spatial and body representations (e.g., [Cardinali et al., 2009](#)). Importantly, evidence for a PPS representation in humans has been provided by a growing body of behavioural studies investigating patterns of cross-modal interactions, occurring at varying spatial distances from the body as a proxy measure for the multisensory dynamics of PPS. A popular paradigm for this purpose is the crossmodal congruency task (e.g., [Maravita et al., 2003; Spence, Pavani, & Driver, 2004; Spence, Pavani, Maravita, & Holmes, 2004](#)) which typically involves the presentation of a

visual distractor from one of two lights positioned on the top or bottom of a hand-held foam cube and the simultaneous presentation of a tactile target to the index finger or thumb holding the cube. Participants are required to respond to the elevation of the tactile target (top or bottom elevation for stimuli to the index or thumb, respectively) while ignoring the visual distractor. Response times and accuracies are compared across trials in which target and distractor are spatially congruent (e.g., top visual distractor and top tactile target, i.e., to the index finger) or incongruent (e.g., top visual distractor and bottom tactile target, i.e., to the thumb). Typically, worse performance is observed on incongruent compared to congruent trials (the crossmodal congruency effect or CCE) due to the conflicting information between the locations of tactile target and visual distractor. This implies that a visual distractor presented in spatial proximity to a tactually stimulated limb cannot be ignored and significantly influences the speed and accuracy of the tactile localization. Crucially, these crossmodal interactions indexed by the size of the visuo-tactile congruency effects show magnitude reductions when the visual distractor is presented increasingly away from the body (e.g., [Gherri et al., 2022; Holmes, 2012; Làdavas et al., 1998; Holmes & Spence, 2004; Spence, Pavani, Maravita, & Holmes, 2004](#)).

The CCE represents a discrete measure of PPS because crossmodal interactions in space are typically probed at a reduced number of locations, with visual distractors often presented either near the body or far away from it. This discrete PPS measure is likely to have contributed to definitions of PPS as an ‘all-or-nothing’ sensorimotor interface with well-defined spatial boundaries marking the transition from peri-personal to extra-personal space (see [Bufacchi & Iannetti, 2018a, 2018b](#); for an extended discussion on this topic). A similar clear-cut distinction between stimuli within and outside PPS is also often implicit in the commonly used definition of PPS as ‘reaching space’ (but see [Zanini et al., 2020, 2021](#); for recent evidence suggesting systematic differences between these spatial representations). However, more recently, PPS has been conceptualized as a gradient (e.g., [Longo & Lourenco, 2006, 2007](#)) or a field (e.g., [Bufacchi & Iannetti, 2018a, 2018b](#)), whereby the pattern of multisensory interactions decreases gradually as a function of the increasing distance between the body and the external visual (or auditory) stimuli. To map peri-personal space in a more continuous way, a multisensory detection task has been recently developed in a series of behavioural studies (e.g., [Canzoneri et al., 2012; Teneggi et al., 2013; Serino et al., 2015](#)). Participants were asked to detect as quickly as possible a tactile target presented to the hand (or to other body parts) while ignoring a looming or receding auditory distractor. Because the auditory distractor was ‘dynamic’ and presented at different delays from the tactile stimulus, it was possible to analyze participants’ responses to the tactile target as a function of its ‘distance’ from the auditory distractor. Results showed that the detection of the tactile target was faster when the auditory distractor was nearer the tactually stimulated body part compared to when it was presented further away (e.g., [Canzoneri et al., 2012](#)). This suggests that auditory (or visual) stimuli presented closer to the body have a stronger impact on tactile processing compared to those presented

further away from it. The crossmodal patterns illustrated in this body of behavioural evidence support the idea of PPS as a special multisensory interface for body–objects interactions, preferentially encoding stimuli closer to the body.

The question of why stronger multisensory responses are observed for stimuli presented closer than further away from the body has attracted significant interest in the literature. The ‘goal-directed action’ account proposes that the mechanisms underlying PPS representations chiefly subserve voluntary actions and interactions with the environment (e.g., Lādavas & Serino, 2008). According to the ‘avoidance-defensive’ account, the sensorimotor properties of PPS representations exist primarily to facilitate the rapid engagement of defensive responses to stimuli approaching the body (e.g., Bufacchi et al., 2016; Bufacchi & Iannetti, 2018a, 2018b). More recently, the role of PPS as a buffer zone between the body and the environment has been expanded to include also a social function whereby PPS not only contributes to the protection of the body from external threats but also support the organization of social life, determining the space for social interactions (e.g., Coello & Iachini, 2021; see also di Pellegrino & Lādavas, 2015; Serino, 2019, for reviews). While it is likely that PPS representations play a role in all these action-related functions crucial to everyday functioning (de Vignemont & Iannetti, 2015), as this paper is concerned with the planning of goal-directed action, the remaining discussion will be framed within this context.

The neural underpinnings of the space-action relationship is theorised to include a ventral premotor cortex (vPMC) – ventral intraparietal sulcus (vIPS) circuit, wherein the vPMC receives input from the vIPS, a constituent part of the cortical, action-centred dorsal stream and systematically performs sensorimotor transformations on the input to facilitate anticipatory action-centred processing (e.g., Gross & Graziano, 1995; Kakei et al., 2003; Rizzolatti et al., 2002). Encoding of visual stimuli in non-retinocentric reference frames within these regions may indicate that the PPS network is physiologically engineered to provide an effective system for planning and executing movements of body parts in a goal-directed manner.

The presence of such PPS-action links has been well established in the literature. For instance, functional neuroimaging work has implicated premotor neurons in the initial formulation of motor responses to stimuli exclusively within PPS boundaries (Bonini et al., 2014; Bremmer et al., 2001). Furthermore, transcranial magnetic stimulation (TMS) applied to the PMC modulates corticospinal activity in response to stimuli presented within but not outside PPS boundaries, hundreds of milliseconds before motor cortex or muscle activity and under conditions where no action is required, reflecting the anticipatory sensorimotor transformations that facilitate controlled and precise action-execution (e.g., Avenanti et al., 2012; Townsend et al., 2011; Umiltà et al., 2007). Dovetailing nicely with these findings, a recent electrophysiological investigation (Wamain et al., 2016) has revealed event-related desynchronization of the μ rhythm, a pattern of neural activity underlying motor imagery, motor planning and the processing of object manipulability, for objects specifically within PPS. This effect occurred approximately 300 msec post-stimulus presentation, once

again implying that sensorimotor transformations are automatically primed by contexts potentiating action or object-interaction.

Behavioural investigations in humans demonstrated that, from the onset of hand-centred action-execution, visuo-tactile interactions between the hand and a target object located within PPS are continuously reweighted (Brozzoli et al., 2009; 2010). More specifically, this hand-specific PPS reweighting occurred when reaching to grasp, but not when reaching to point. This implies that the differences observed between visuo-tactile interactions across different actions cannot be simply attributable to the decreasing spatial distance between the visual and tactile signals during action-execution and that the sensorimotor architecture of PPS is remarkably fine-tuned to the specific goals of each movement (Brozzoli et al., 2009; 2010). More recently, a similar remapping of hand PPS was observed also during the planning of a reach to grasp movement, demonstrating that changes to the weights of visuo-tactile interactions in space start already before the onset of the hand movement (Patanè et al., 2019).

While the research described above strongly supports (one of) the function(s) of PPS as action-centric, it is important to acknowledge that the hands and their goal-directed movements were the main focus of these empirical investigations. Because the hands have a well-defined functional importance, the question remains as to whether the findings of hand-centred studies can be extrapolated to other limb-centred representations. Indeed, initial evidence suggests the existence of independent PPS representations centred on distinct body parts such as the trunk, the hand, and the face (e.g., Cléry et al., 2015; Serino et al., 2015). Therefore, a relatively unexplored question concerns the spatial and functional properties of PPS representations centred on body parts other than the hands.

Few studies to date have attempted to probe the PPS representation around the lower limbs and their dynamics (Pozeg et al., 2015; Scandola et al., 2016; Schicke et al., 2009; Stone et al., 2018; van Elk et al., 2013). The first studies to report the existence of PPS representations around the lower limbs used a modified versions of the classic visuo-tactile cross-modal congruency task and observed the presence of reliable visuo-tactile CCEs when tactile targets and visual distractors were presented to/next to the foot (Schicke et al., 2009; van Elk et al., 2013). More recently, two behavioural studies assessed the multisensory spatial properties of the lower-limbs PPS. Stone et al. (2018) presented tactile targets directly to the feet, under static conditions (in the absence of real or induced feet movement) and observed faster responses only when the target was presented with an approaching visual distractor, not a receding one. They reported that PPS boundaries around the feet were located at approximately 70 cm from the feet. Interestingly, when the spatial properties of hand and feet PPS were directly contrasted, different strengths of the integration of visuo-tactile information were observed around the upper and the lower limbs (Gherri et al., 2022). Specifically, while PPS around the upper limbs was maximal next to the hand and decreased as visual distractors were presented 40 cm away from it as indexed by a decreasing pattern of CCEs, visuo-tactile interactions around the lower limbs were stronger when the visual distractor was presented 40 cm from the foot compared to when it was just above the lower limb (i.e.,

increasing pattern of CCEs; [Gherri et al., 2022](#)). Together, these findings demonstrate the existence of PPS representations around the lower limbs characterized by idiosyncratic spatial features, different from those observed for the upper limbs.

Because the studies reviewed above involved static situations, they did not address questions related to the functional role of PPS representations around the lower limbs. Initial evidence suggests that the space around the body is dynamically remapped during walking (e.g., [Noel et al., 2015](#)). Specifically, PPS boundaries extended while walking as compared to a still condition in a task in which audio–tactile interactions were used as a proxy for the PPS boundary ([Noel et al., 2015](#)). Evidence for a similar remapping of PPS was also reported when a walking movement sensation was induced through the presentation of a walking-sound vibration under the soles of participants feet, in the absence of actual walking movements ([Amemiya et al., 2019](#)). Thus, active or even illusory movements linked to locomotion of the lower limbs can dynamically induce a remapping of the space around the body. Furthermore, passive movements of the feet restored a degraded lower-limb PPS representation in patients with paraplegia ([Scandola et al., 2016](#)). The fact that the PPS representation was influenced even by relatively minor and artificial movement in the absence of motor feedback effectively implies that the motor-centric properties of PPS are present across different movement-oriented effectors, with the lower-limb PPS particularly sensitive to motion-inspired postural adjustments.

However, it remains unclear whether a remapping of PPS can also be found when goal-directed lower limb movements are planned and performed. Because one of PPS functions appears to be the facilitation of sensorimotor transformation subserving hand actions towards reachable objects ([Bremmer et al., 2001](#); [Brozzoli et al., 2010](#); [Làdavas & Serino, 2008](#); [van Elk & Blanke, 2011](#)), it is conceivable that PPS may also support the planning and execution of goal directed foot movements. Indeed, the feet have the potential to subserve body–objects interactions despite their reduced prehensile qualities, as suggested by studies and observations of upper-limb aplasics and amputees (e.g., [Friedmann, 1988](#); [Gazzola et al., 2007](#)). For example, infants born without upper-limbs will spontaneously utilise their feet to explore the surrounding environment, implying that an action-centred spatial representation should not be exclusive to the hands (e.g., [Friedmann, 1988](#); [Gazzola et al., 2007](#)).

The present study investigated whether planning a goal-directed foot movement induces a remapping of PPS. To investigate the effect of foot action-planning on PPS representations, we followed Brozzoli et al.'s approach ([2009](#); [2010](#); [Patanè et al., 2019](#)) in which visuo-tactile crossmodal interactions were compared under static (no movement required) and dynamic conditions (during the planning/execution phases of a goal-directed foot movement). In both Static and Dynamic tasks of the present study, we asked participants to localize a tactile target presented to their right hand while ignoring an irrelevant visual distractor was presented next to or near their right foot. To better understand if and how PPS visuo-tactile interactions remap as a consequence of foot action-planning, visual distractors were positioned across different spatial locations in depth: next to or near the resting position of the foot or adjacent to or near the

goal of the foot movement, thus encapsulating the entire outward span of reachable foot space. It is worth noting that the measurement of foot-specific PPS would have implied the presentation of both tactile stimuli and visual distractors to/near the foot (for example, see [Gherri et al., 2022](#); [Van Helk et al., 2013](#), for a direct comparison between hand- and foot-specific PPS under static conditions). However, delivering tactile stimuli directly to the foot was not possible in the dynamic task, due to the physical constraints imposed by the tactile stimulators (which were wired to a controller box). Hence, to avoid the risk of losing or dislodging the stimulators during the foot movement (which occurred on the majority of trials), we adopted a 'hybrid' crossmodal congruency task. In this task, first developed by [Schicke et al. \(2009\)](#) and more recently used by [Scandola et al. \(2016\)](#), the visual distractor was presented in close proximity to the feet, but the tactile target was delivered to the hands. Evidence has shown that visual distractors presented to/near the foot were able to interfere with the tactile judgements carried out on the hands, resulting in sizable CCEs ([Schicke et al., 2009](#); [Scandola et al., 2016](#)). These findings suggest that PPS representations centered on distinct body parts are interconnected and can interact under these experimental circumstances (c.f. [Schicke et al., 2009](#)), making the hybrid crossmodal congruency task an appropriate tool to investigate the remapping of PPS during foot movement planning. Henceforth, we will refer more broadly to PPS to indicate the visuo-tactile map deriving from the hybrid task of the present study, i.e., the integration of visual information presented within different sectors of the space occupied by the foot (i.e., next to the foot or further away from it) and the tactile processing of stimuli to the hand, whereas we will use the terms hand-specific or foot-specific PPS to refer to results of studies measuring visuo-tactile integration of stimuli presented to/close the same limb.

Importantly, in the present study we were interested in PPS remapping driven by foot movement planning. Given that in both the static and dynamic tasks the tactile stimuli were delivered to the hand, CCE differences between tasks could be reasonably attributed to changes in the remapping of the visual space around the foot probed by the visual distractors during the planning of the foot movement. If visuo-tactile interactions do remap to anticipate and update the relationship between the body and the space targeted by the foot action, one would expect stronger CCEs for the visual distractors located adjacent to the movement goal during action-planning than for the distractors presented next to the initial resting position of the foot during the covert planning of the foot movement (i.e., in the dynamic task).

2. Method

2.1. Participants

An a-priori power analysis was conducted for sample size estimation, based on data from our previous study ([Gherri et al., 2022](#)), in which we measured PPS around the lower limbs with a similar crossmodal congruency task. In that study ($N = 50$), CCEs of 75 msec ($C = 690$ msec and $I = 766$ msec) for near visual distractors and 86 msec ($C = 691$ msec and

$I = 776$ msec) for far visual distractors. Power analyses were performed using the *simr* package in R (Green & MacLeod, 2016), simulating and then modelling 1000 independent experiments with an increasing number of participants. The results showed that with a sample size of $N = 30$ the power reached 91.80% (CIs: 89.92, 93.43) of the effect size reported. Thus, the obtained sample size of $N = 24$ is more than adequate to reach a power $>80\%$ with a significance criterion of $\alpha = .05$.

Thirty participants were originally sampled but six were removed due to problems with the recording equipment. Thus, twenty-four neurologically ‘typical’ participants (15 females, mean age = 24 yrs ± 3.3) took part in the present study. All participants had normal or corrected-to-normal vision and normal tactile sensitivity, and all recognised their right hand and foot as dominant by self-report. This study was granted ethical approval by the PPLS Research Ethics Committee at the University of Edinburgh and carried out in compliance with the Declaration of Helsinki (World Medical Association, 2013). Written informed consent was provided prior to the commencement of the study, and participants were reimbursed £10 for their time.

2.2. Materials and apparatus

Throughout the experiment, participants were seated in a chair raised ~46 cm from the ground. A purpose-built, black wooden board placed on the floor (length = 45 cm; width = 90 cm) was used to house the pad used for the resting position of the foot, the two response pedals (left and right movement goals), and the visual distractors (see Fig. 1). The

board slanted backwards at an angle of approximately 45° in order to facilitate the pressing of the pedals without the need for corresponding shifts in the overall body position. The foot-pedals (8 cm $\times$ 4 cm) were positioned 22 cm apart and approximately 45 cm anterior to the resting position of the foot on the raised edge of the board. When stationary, the foot rested on a black, rubber support.

Four light-emitting diodes (LEDs) were placed along the midline of the wooden board and were used to present the visual distractors. These were presented across four spatial locations. Two were placed near the resting position of the foot (5 cm and 10.5 cm, distant from the resting foot position, ‘bottom’ locations), while the remaining two were located near the movement goal, ‘top’ locations (30.5 cm and 36 cm distant from the resting foot position), thus encapsulating the entire outwards space of PPS. The two top and the two bottom LEDs were 5.5 cm apart and the two pairs of LEDs were approximately 20 cm distant (see Fig. 1).

The hand, in a pinch-grip position, held a cuboid (5.5 $\times$ 4 $\times$ 4 cm) which was attached to a purpose-built, black wooden frame (width = 68.5 cm; height = 71.5 cm) placed in front of each participant’s trunk. Importantly, while the hand was raised from the floor (at a height that allowed participants to rest their hand on the raised wooden frame comfortably while seated), the hand holding the cuboid was visually equidistant from the two top and the two bottom visual distractors (approximately 9 cm distant from either), see Fig. 1.

Tactile targets were presented via one of two miniature solenoids tappers (Miniature Solenoid Tapper Controller Mk3, model MSTC3-4) attached to the index finger or to the thumb of the right hand with velcro. These 12 V solenoids propelled a

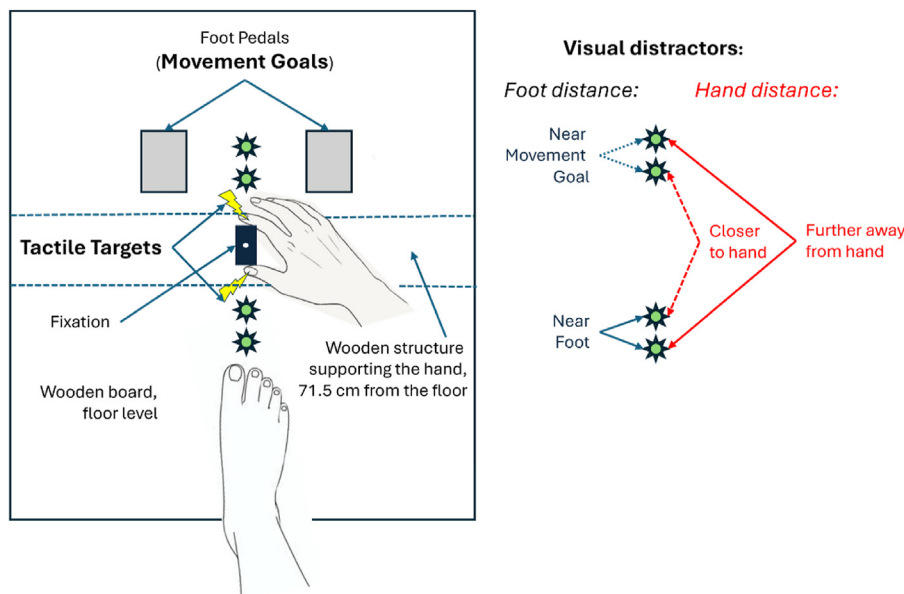


Fig. 1 – Schematic representation of the experimental set-up as seen by participants during the Experiment. A purpose-built, wooden board was used to house the foot in its resting position as well as the visual distractors and the response pedals serving as movement goals. The right hand holding a foam cube was resting on an elevated wooden structure/table (10 cm deep) and visually located exactly in between top and bottom visual distractors. Tactile tappers were attached to the index and thumb of the right hand and delivered top and bottom tactile targets, respectively. The four visual distractor locations were coded relative to the foot (near the foot versus near the movement goal) and relative to the hand (closer to the hand versus further away from the hand).

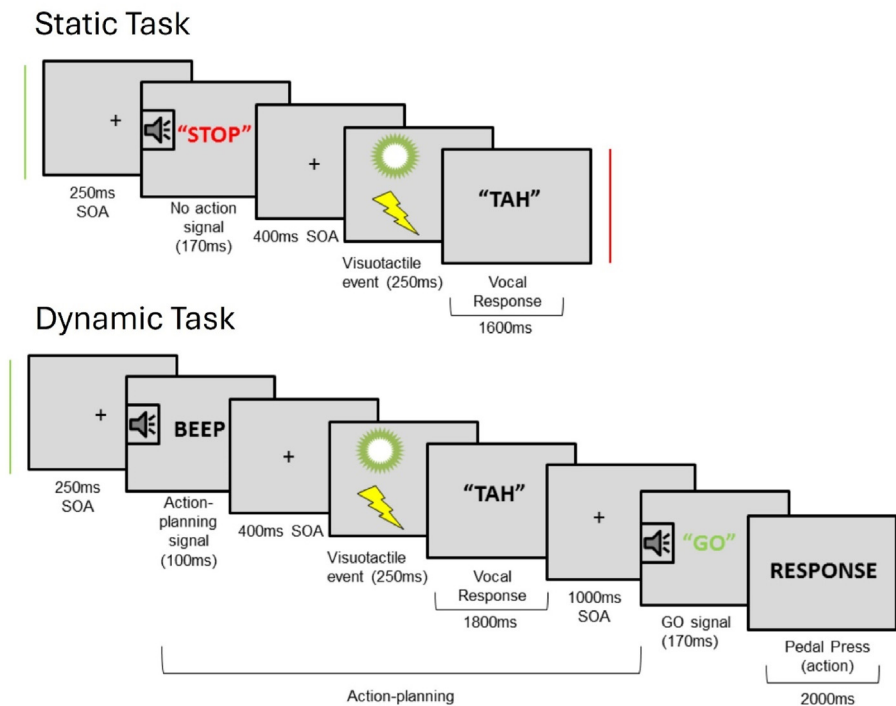


Fig. 2 – Schematic representation of the trial events in both the Static and the Dynamic tasks.

blunt conical rod (surface area 28.27 mm²) onto the skin when current passed through them, producing suprathreshold tactile stimuli.

The visual distractor consisted of three consecutive bursts of green light (50 msec each in duration) delivered from one of the four LEDs, separated by two 50 msec long offset periods. The tactile target involved the delivery of three suprathreshold vibrations (50 msec each in duration), in rapid succession. Similar to the procedures used by Brozzoli et al. (2009; 2010; Patanè et al., 2019), Gherri et al. (2022), Scandola et al. (2016) and Schicke et al. (2009), the onset and offset of the visual and tactile pulses were simultaneous. Overall, the duration of the visuo-tactile stimulation was 250 msec long. All participants were tested before the experiment to ensure adequate perception of these vibrations.

White noise was played in the testing environment throughout the experiment by 2 speakers (Zalman 2M5300) to mask any residual noise of the tappers which might have served as auditory cues for tactile localisation.

In the dynamic task (involving action-planning and execution), an auditory stimulus (100 msec duration), formatted on Goldwave (v6.23, 2016), informed the participants of which pedal they would have to move towards (single beep = left; double beep = right) and when (GO signal; vocal "GO"; 170 msec). These were relayed over headphones (Sony MDR-V150) at a comfortable volume. In the Static task, a NO-GO signal (vocal "STOP"; 170 msec) was included at the beginning of each trial to prevent movement.

Tactile, visual and auditory stimulus presentation as well as the recording of responses during both the static and dynamic tasks were controlled by a Desktop Dell OptiPlex 745 computer (Dell Inc., Round Rock, TX) running an E-

Prime 2.0 (Psychology Software Tools Inc., Sharpsburg, PA) script.

2.3. Design and procedure

A 2 (crossmodal congruency effect) x 2 (visual distractor foot distance) x 2 (visual distractor hand distance) x 2 (task) within-subjects design was used to investigate whether the cross-modal congruency effect (CCE) measured near the resting position of the foot and near the movement goal was impacted by the simultaneous planning of a goal directed foot movement. As shown in Fig. 1, the variable *crossmodal congruency effect* coded the spatial relationship (congruent versus incongruent) between the elevation of the tactile target to the hand (top, index or bottom, thumb) and the irrelevant visual distractor (top or bottom). The variable *visual distractor foot distance* (near the foot versus near the movement goal) indicated the distance of the visual distractor from the foot. The variable *visual distractor hand distance* indicated the spatial separation between the visual distractor and the hand (closer to the hand versus further away from the hand). The variable *task* indicated whether the crossmodal congruency task was performed under single-task (static task) or under dual-task conditions, embedded in the motor task (dynamic task), see Fig. 2.

The experiment took place at the Crossmodal Lab at the University of Edinburgh in a dimly lit environment. Participants were positioned so that their right foot was centred with respect to the wooden board and equidistant from the left and right foot pedals, while the left foot was positioned beneath the chair so as not to be visible. Prior to the start of the study, all participants were explicitly instructed to maintain the

same body posture throughout and to visually fixate on a small white point (.3 cm in diameter) in the middle of the cuboid they were holding. A camera, positioned to the right of the board, was used to monitor fixation in real time. All participants were positioned so that they could reach both pedals with their right foot and perceive all of the LEDs on the board as well as the position of their foot at resting position. Practice blocks were conducted for each participant in both tasks. In the dynamic task, due to the complexity of the timing of the events, a minimum accuracy of 70% was required in order to take part in the main experiment. The order of the static versus dynamic tasks was counterbalanced across participants so that, for half of the participants, the static task preceded the dynamic task and for the other half the opposite order was followed.

In the static task (Fig. 2, top panel) participants performed the crossmodal congruency task only under static conditions, no movement was required. Each trial started with an empty interval of 250 msec, after which the NO-GO signal was played to remind participants not to plan/execute any action. This was followed by an SOA of 400 msec. The synchronous visual and tactile stimuli were subsequently presented for 250 msec. Participants were asked to ignore the visual distractor and respond vocally to the elevation of the tactile target as rapidly and accurately as possible while indicating their elevations on the hand (“TAH” for index finger – top, “TOH” for thumb – bottom). They were also reminded to keep their eyes on the central fixation throughout the task. The timing of these responses was recorded by a microphone while vocal accuracy was manually recorded with a keyboard press by the experimenter. If no vocal response was provided within 1600 msec from stimulus offset, the trial was terminated.

The static task consisted of 4 blocks (64 trials per block), with each tactile target location (thumb versus index) x visual distractor foot distance (near the foot versus near the foot movement goal) x visual distractor hand distance (closer to the hand versus further away from the hand) randomly repeated 8 times within each block, yielding a total of 256 trials and lasting approximately 15 min.

The dynamic task was dual-task in nature (Fig. 2, bottom panel). Participants were asked to complete the same cross-modal congruency task performed in the static task, while they completed a motor task in which they covertly planned and executed a goal-directed foot movement. Brozzoli et al. (2010) included a rotating cylinder in their task as the target object to encourage hand action-planning on a trial-by-trial basis. In a similar way, we utilised two possible target objects (a left and a right foot-pedal), one of which was randomly cued as the movement goal on a trial-by-trial basis, for the same purpose. The location of the foot movement goal (left versus right movement goal, see Fig. 1), was specific to the motor task but was not expected to influence the results as the foot was positioned along the midline of the board, equidistant from both target pedals. For this reason, it was not included in the analyses. On each trial, after a delay of 250 msec, one of the two beep tones (100 msec duration) was presented to cue the goal of the movement (high pitch indicated the left foot pedal while low pitch cued the right foot pedal). Following a SOA of 400 msec, the tactile and visual stimuli were simultaneously presented for 250 msec. After

1000 msec the auditory GO or NO-GO signal was presented. A vocal response was required to indicate the elevation of the tactile target within 1800 msec from visuo-tactile stimulus offset to be correctly registered. The GO signal, which informed participants to execute the previously cued foot movement, maintained precise timing of the onset of the action. If no pedal press was recorded within 2000 msec of the GO signal, the trial was terminated.

In the dynamic task, participants were instructed to start planning the foot movement upon cue presentation, but to refrain from executing it until the GO/NOGO signal was presented. To measure visuo-tactile remapping during the covert preparation of the foot movements, participants were also instructed to vocally respond as quickly and as accurately as possible to the elevation of the tactile target while ignoring visual distractors. They were also reminded to keep their eyes on the central fixation throughout the task.

All possible combinations of tactile target location (thumb versus index) x visual distractor foot distance (near the foot versus near the movement goal) x visual distractor hand distance (closer to the hand versus further away from the hand) x movement goal (left versus right) were presented randomly, but with equal frequency (x8), for 4 blocks, yielding a total of 512 trials. To make sure that participants waited for the imperative stimulus before executing the planned foot movement, NO-GO trials were included once per condition, resulting in 16 additional trials for each of the 4 blocks. In total, the dynamic task consisted of 576 trials and lasted approximately 45 min. To control for fatigue, all participants were allowed to rest in between blocks if necessary.

2.4. Data analysis

Data analyses were performed with R 4.4.2 (R Core Team, 2024). First, all no-go trials were removed from the Dynamic task dataset (14%). Afterward, anticipatory responses were removed from the dataset (<100 msec; 15 datapoints, .11%). Only correct response RTs were transformed to logarithm following a Box–Cox (Box & Cox, 1964; Klein Entink et al., 2009) iterative procedure indicating a lambda value = 0. Outliers were later identified as $\text{Log}(\text{RTs}) > 3 \text{ SD}$, calculated for each participant and excluded from further analyses. RTs trimming produced a loss of 119 trials (.85%).

RTs were analysed following the mixed-model approach which allows to predict participant-by-participant and stimulus-by-stimulus variation in the model parameters (random effects) and to discount these differences to compute within-participant and within-stimulus confidence intervals around estimates of fixed effects. Furthermore, it allows to compare conditions directly using confidence intervals around estimated effects, as suggested by current recommendations in psychology and behavioural neuroscience (see Cumming, 2014; Kline, 2004). For the RT analysis, data and confidence interval limits reported in the manuscript were transformed back to ms by computing the inverse of the transformation.

Participants' errors were submitted to a logistic mixed regression.

Both errors and RTs models included the fixed effects crossmodal congruency effect (2 levels: congruent and incongruent), visual distractor foot distance (2 levels: near the

resting foot and near the movement goal); visual distractor hand distance (2 levels: closer to the hand and further away from the hand), and Task (2 levels: static task and dynamic task), as well as all their interactions. Participants was set as random effect, including random slopes of each fixed effect for errors and RTs (Barr et al., 2013).

In both RT and error analyses, we were interested in the three-way interaction *crossmodal congruency effect* $\times$ *visual distractor foot distance* $\times$ *Task*. Confidence intervals around the estimates for the CCE fixed effect calculated separately for congruent and incongruent conditions revealed the presence (or lack of) of statistically reliable CCE at different locations and tasks. To explore further this interaction, we ran planned comparisons using t-tests between the CCE (difference between the mean RTs observed on incongruent – congruent trials) measured at different visual distractor foot distances (near the foot versus near the movement goal) across tasks (Static and Dynamic tasks).

3. Results

3.1. Error rates

Participants responded incorrectly on 3.04% of all trials in the Static Task and on 4.84% of all trials in the Dynamic tasks.

Participants' errors were submitted to a logistic mixed regression that did not show any reliable effect (all z s < 1.6 , all p s $> .13$).

3.2. Reaction time

Log(RTs) model revealed a reliable effect of task ($\beta_{\text{std}} = .44$, $t(23) = |11.52|$, $p < .001$). Unsurprisingly, participants were faster in the Static task ($M = 516.9 \text{ msec} \pm 108.2$) than in the Dynamic task ($M = 590.3 \text{ msec} \pm 127.4$), due to the dual task nature of the latter. A significant main effect was also observed for CCE ($\beta_{\text{std}} = .09$, $t(23) = |2.73|$, $p = .006$), with slower RTs on incongruent ($572.5 \text{ msec} \pm 114.6$) than congruent

($546.3 \text{ msec} \pm 107.2$) trials, confirming the overall presence of the crossmodal congruency effect ($\sim 26 \text{ msec}$) and indicating that participants coded the visual distractors above the hand as 'top' and the visual distractor below the hand as 'bottom'. The main effects of VD foot distance and VD hand distance were not statistically significant (both $t(23) < |1.4|$, both p s $> .19$).

The two-way interactions CCE $\times$ task ($\beta_{\text{std}} = .15$, $t(23) = |2.98|$, $p = .003$), VD foot distance $\times$ VD hand distance ($\beta_{\text{std}} = .11$, $t(23) = |3.39|$, $p = .017$) and CCE $\times$ VD hand distance were statistically significant ($\beta_{\text{std}} = .09$, $t(23) = |1.97|$, $p = .049$). No reliable interaction was observed for CCE $\times$ VD foot distance, task $\times$ VD foot distance and task $\times$ VD hand distance (all t s $< |1.5|$, all p s $> .14$).

Results revealed a significant three-way interaction between CCE, VD foot distance and VD hand distance ($\beta_{\text{std}} = .23$, $t(23) = |3.88|$, $p < .001$). When the visual distractor was closer to the hand, reliable CCEs were observed for both the VD near the foot and the one near the movement goal (28 msec and 21 msec). By contrast, when the VD was further away from the hand, a reliable CCE emerged close to the movement goal (43 msec), but not close to the foot (12 msec).

Importantly for the aim of this study, the three-way interaction between CCE, VD foot distance and task emerged to be significant ($\beta_{\text{std}} = .16$, $t(23) = |2.41|$, $p = .016$), see Fig. 3. This interaction revealed that the pattern of CCE observed near the foot or the movement goal varied as a function of task. In the static task, results revealed the presence of significant CCEs for visual distractors near the foot as well as for those near the movement goal (both p s $< .001$; 35 msec and 25 msec, respectively). By contrast, in the dynamic task a significant CCE was present near the movement goal ($p < .001$; 36 msec) but not near the foot ($p = .13$; 9 msec). Planned comparisons revealed that the CCE did not differ across visual distractor foot distances (near the foot versus near the movement goal) in the Static task ($p = .18$), while in the dynamic task the CCE near the movement goal was significantly larger than that observed near the foot ($p = .04$). When CCEs observed at homologous VD foot distances (near the foot versus near the foot movement

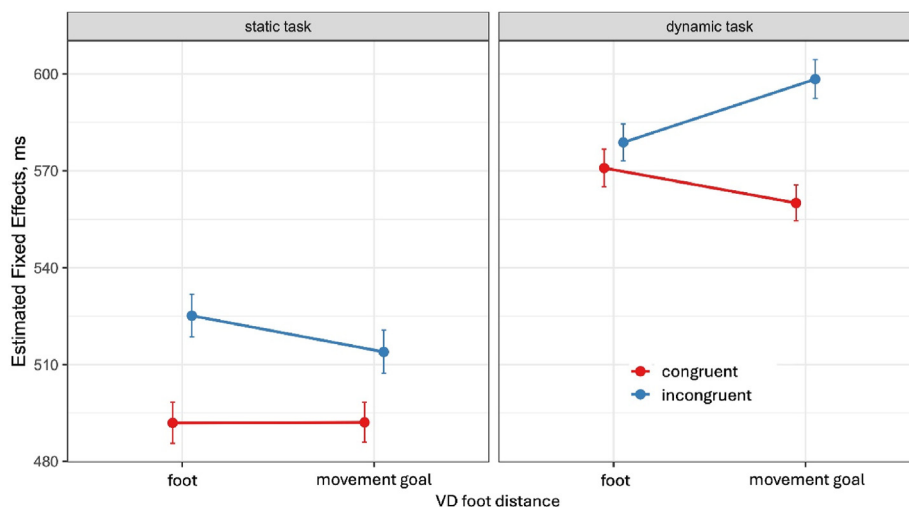


Fig. 3 – Log(RTs) estimated effects, transformed back to ms, shown as a function of CCE, VD foot distance and task. Error bars represent 95% CIs, discounting participant-by-participant variation.

goal) were compared between tasks, no task difference was observed between the CCE measured near the movement goal ($p = .23$), while the CCE near the foot was significantly larger in the static than in the dynamic task ($p = .007$) (see Fig. 3).

No other three-way or four-way interactions emerged to be significant (all t s $< |1.5|$, all p s $> .14$).

4. Discussion

The present study investigated whether the multisensory representation of near-space is influenced by the planning of a goal-directed movement with the dominant foot. Participants performed a visuo-tactile crossmodal congruency task in which a tactile target was delivered to the right hand while a simultaneous visual distractor appeared near the foot or near the movement goal. The presence and size of the crossmodal congruency effects (CCE) observed when the visual distractor was near the foot and near the movement goal were compared across tasks as a function of movement planning. Results revealed systematic differences between visuo-tactile interactions across space in the Static task, in the absence of movement planning, and in the Dynamic task, during the covert preparation of a goal-directed foot movement.

In the Static task, comparable CCEs were observed for distractors close to the foot and close to the movement goal, suggesting that variations of the visual distractor locations did not influence visuo-tactile interactions. Visual distractors presented within hand PPS are known to elicit strong and reliable crossmodal interference effects when tactile targets are delivered to the hands, which tend to decrease as the distance between the tactile target (hand) and the visual distractor increases (e.g., Gherri et al., 2022; Holmes, 2012; Holmes & Spence, 2004; Lådavas et al., 1998; Spence, Pavani, Maravita, & Holmes, 2004). Notably, recent evidence has highlighted a different pattern of results when foot PPS was directly mapped across different portions of space (Gherri et al., 2022). When the tactile target was delivered to the foot and the visual distractor was presented either above it or 40 cm from the foot, larger CCEs were reported further away than right above the foot, revealing an increasing pattern of visuo-tactile interactions (Gherri et al., 2022). It was suggested that the differences between hand and foot PPS are driven by the distinct functional use of upper and lower limbs. While relevant hand–objects interactions tend to occur closer to the hand in near PPS, foot–objects interactions (e.g., kicking a ball) are more likely to take place further away from the body for optimal execution (Stettler & Thomas, 2017). In the present study, tactile targets were delivered to the participants' hand, while visual distractors were presented within the space near the foot, following a task already established in the literature (e.g., Scandola et al., 2016; Schicke et al., 2009; van Elk et al., 2013). This 'hybrid' crossmodal congruency task does not map visuo-tactile integration exclusively related to hand or foot PPS but is likely to measure a contribution of both. Indeed, results of the present study confirmed that under these experimental circumstances both hand and foot PPS contributed to determine the strength of visuo-tactile interactions in the static task with their decreasing and increasing CCE

patterns across space, respectively, (c.f. Gherri et al., 2022), resulting in no overall differences between CCEs measured when visual distractors were near the foot or further away from it (i.e., near the movement goal).

Importantly, the distribution of the CCE across space in the static task served as a baseline to map the strength of visuo-tactile interactions. The crucial question was whether this multisensory map was affected by the covert planning of a goal-directed foot movement. Results of the dynamic task showed a relevant remapping of visuo-tactile interactions within PPS. Specifically, visuo-tactile interactions in the dynamic task weakened when the visual distractor was presented next to the foot, as shown by the absence of a statistically reliable CCE. By contrast, visuo-tactile interactions in the space closer (to) and around the movement goal were still referenced back to the body, as evidenced by the reliable CCE observed with visual distractors at that location. This confirms that visual distractors close to the goal of the foot movement were consistently integrated with the tactile stimuli to the hand during foot action-planning (Duhamel et al., 1998; Gross & Graziano, 1995; Rizzolatti et al., 2002). As the visuo-tactile discriminations in the Static and Dynamic tasks were virtually identical, other than the addition of the action-planning motor task, these results suggest that the weaker representation of the space proximal to the foot is attributable to the influence of anticipatory reweighting of PPS occurring during a goal directed foot movement.

The spatial relations between the action-oriented effector and the movement goal are known to be updated on-line during action-planning (e.g., Glover, 2004; Karok & Newport, 2010). In our study, the remapping of PPS during the planning of a goal directed foot movement was particularly evident within the portion of space closer to the movement effector with decreased visuo-tactile interactions compared to the portion of space closer to the movement goal. It is conceivable that this type of goal-directed foot movement (reach and press of a pedal) requires sensorimotor transformations concerning the forward space into which the foot is about to move (movement goal) rather than the starting location of the effector. This remapping facilitates the control of the action and the avoidance of potential threats or obstacles, which are the purported, interlinked functions of the sensorimotor PPS (Bufacchi et al., 2016; de Vignemont & Iannetti, 2015; Graziano & Cooke, 2006; Iachini et al., 2014; Lådavas & Serino, 2008; Quinlan & Culham, 2007). Importantly, neuroimaging and neurophysiological evidence has shown the selectivity of ventral premotor neuronal populations to the processing of target location, rather than limb use, during the preparatory stages of action, which may offer a possible neurophysiological basis for the observed weakening of the representation of the effector space but simultaneous maintenance of the target space during action-planning (Boussaoud & Wise, 1993; Hoshi & Tanji, 2002, 2006; Kakei et al., 2003; Mushiake et al., 1997). It is therefore possible that the representations of the surrounding spaces are not equally maintained as the planning of the foot movement is finalized over time and that the representation of the space towards which the lower limb is about to move (movement goal location) is preferentially maintained over the one related

to the current location of the effector, because it is the most relevant in terms of behavioural goals.

Intriguingly, recent behavioural evidence has suggested that foot related movements are preferentially afforded by environmental scenes depicting objects at a larger distance and eccentricity from the observer compared to scene in which objects were closer to the observer (Di Marco et al., 2019). In this priming study participants performed a go/no-go task in which they had to execute a footstep ahead in response to the presentation of pictures of environmental layouts with objects presented at different distances (far versus near) (Di Marco et al., 2019). Results showed response facilitation when the participants were shown pictures of more distant objects in space, compared to near ones. This suggests that during the planning and execution of foot movements the space that is preferentially encoded is distal PPS as opposed to near PPS.

However, if the forward space is the most relevant to the current goals of the action, one might expect not only the maintenance of that spatial region but also a significant increase in its representation (consistent with Brozzoli et al., 2009; 2010; Patanè et al., 2019), of which there was no statistical evidence in the present study. While the space close to the effector appears to weaken in anticipation of movement onset, it may be the case that the significant reweighting of the movement goal space is contingent upon the actual initiation of motor responses projected towards that space, that is at a later stage. This possibility is consistent with Brozzoli et al.'s results (2009; 2010) and future studies should investigate whether – similarly to what observed with goal-directed hand movements – planning a movement with the foot results in increased visuo-tactile integration closer to the movement goal *after* the movement onset.

Results of the present study demonstrate for the first time that PPS is modulated by the intention to execute a goal-directed foot movement, already before the onset of the movement. In other words, we observed *anticipatory* changes to the visuo-tactile representation of near space driven by the covert planning of a foot movement. These findings demonstrate that the goal-directed function of PPS, already demonstrated for hand actions (Brozzoli et al., 2009; 2010; Patanè et al., 2019), can be extended to include also goal-directed actions executed with the lower limbs. To confirm and expand these results, future studies should investigate the impact of goal-directed foot movement on foot-specific PPS, that is, with tasks presenting both tactile and visual stimuli directly to/near the foot. So far, existing evidence has primarily linked the function of lower limbs PPS to the monitoring of space for the detection and avoidance of obstacles ('avoidance-defensive' function). Specifically, the processing of forward space is particularly relevant in the context of walking because it allows to monitor potential obstacles or threats during navigation (e.g., Hollands et al., 2002; Krell & Patla, 2002; Patla & Vickers, 1997, 2003). Because the distance between stationary obstacles and the body is constantly changing during locomotion, it is particularly relevant to monitor (visual) information about potential obstacles located in far PPS and/or extrapersonal space so as to guarantee sufficient time to change the movement plan to avoid such obstacles (for a recent review see Higuchi et al., 2006).

Importantly, not only visual information but also proprioceptive and kinematic information play a key role in the modulation of far PPS, as demonstrated by the expansion of PPS observed when participants walked on a treadmill (e.g., Noel et al., 2015). This 'avoidance-defensive' function of lower limbs PPS is likely aimed at facilitating the rapid amendment of motor plans to avoid stimuli approaching the body. Future studies should explore further the nature of the mechanisms that are responsible for the remapping of PPS during self-motion/locomotion and goal-directed foot planning. Specifically, whether these *anticipatory* and *reactive* changes to multisensory PPS observed during foot movement and self-motion, respectively, are mediated by different mechanisms or whether the same circuits are responsible for the encoding of space around the lower limbs, regardless of the specific movement planned (self-motion/locomotion versus goal-directed movement; see for instance De Vigemont and Iannetti (2015), for a discussion on the shared versus independent nature of action versus defensive PPS representations). Finally, future studies should also address the question of whether lower limbs PPS can be modulated by social factors, hence contributing to the debate related to the dissociation between the social function of PPS and the representation of interpersonal space (Iachini et al., 2014; 2015; Patanè et al., 2016, 2017).

One final consideration concerns the role of spatial attention in the remapping of PPS observed during movement planning. As discussed above the on-line planning and execution of goal-directed hand movements induce a remapping of PPS (Brozzoli et al., 2009; 2010; Patanè et al., 2019). Importantly, a growing body of evidence has demonstrated that movement planning and execution are linked to changes in the perceptual processing of stimuli presented within action-relevant regions of space, suggesting changes in the distribution of attention across space driven by action planning (e.g., Baldauf & Deubel, 2010; Deubel & Schneider, 2004; Eimer et al., 2007; Gherri & Eimer, 2008, 2010; Gherri et al., 2007; Gherri & Forster, 2012a, 2012b; Juravle et al., 2010; Mason et al., 2015). Hence, one important question concerns the extent to which the remapping of multisensory space ascribed to changes in PPS is instead the consequence of a different distribution of attention in space, driven by movement planning and execution. The role of spatial attention in PPS plasticity and remapping is a long-standing issue and there is some evidence suggesting that a differential distribution of attention contributes to the changes in PPS reported in some studies (see Holmes, 2012, for a discussion of PPS remapping induced by tool use). Indeed, irrelevant information presented at the locus of spatial attention is harder to ignore and typically results in stronger interference effects (e.g., Spence et al., 2000). While there is no reason to believe that the planning of a foot movement does NOT result in shifts of attention towards the movement goal, to the best of our knowledge no study to date has mapped the perceptual/attentional consequences of planning a goal-directed foot movement. If foot movement planning results in shifts of attention to the goal, visual distractors presented at that location should interfere more strongly with the tactile discrimination at the hand. If this were the case, the size of the CCE should increase in the dynamic compared to the static

tasks for visual distractors delivered near the movement goal. The pattern of results observed in the present study is not fully consistent with this hypothesis, as the stronger difference between the static and dynamic tasks was observed for visual distractors close to the resting location of the foot rather than near the movement goal. While the reduced CCE observed near the foot in the dynamic compared to the static task cannot be explained by a shift of attention to the goal driven by movement planning, future studies should further investigate the perceptual/attentional consequences of foot movement planning and the role of attention in PPS remapping observed during action planning.

In conclusion, the present study provides the first observations suggesting that PPS representations are sensitive to the influence of goal-directed actions of the lower limbs. PPS representation appears to weaken near the foot as a reach and press action is covertly planned with this effector. This PPS reduction possibly reflects the updating of the PPS map in anticipation of a foot movement directed towards the forward space. Results demonstrate that similarly to what observed for the hand, PPS is a sensorimotor interface, attuned also to voluntary actions of the foot and subserving not only defensive-avoidance purposes but also goal-directed ones.

CRediT authorship contribution statement

Elena Gherri: Writing – review & editing, Supervision, Project administration, Methodology, Conceptualization. Gioacchino Garofalo: Writing – review & editing, Visualization, Software, Resources, Formal analysis, Data curation. Alan O'Dowd: Writing – original draft, Methodology, Investigation, Data curation. Aurora Cudia: Conceptualization, Investigation, Software.

Consent to participate

All participants gave written informed consent to participate in the study after the nature of the study had been explained to them.

Availability of data and material

The datasets generated and analysed during the current study are publicly available on the figshare repository https://figshare.com/articles/dataset/Data_generate_for_The_anticipatory_effect_of_goal-directed_action_planning_with_the_lower_limb_on_peri-personal_space/27331467?file=50079564.

Code availability

Commercial software applications were used to present the stimuli during the experiment and analyse the data. These are listed in the manuscript.

Ethics approval

The study was approved by the PPLS Research Ethics Committee of the University of Edinburgh and was carried out in accordance with the ethical standards as laid down in the 2013 Declaration of Helsinki and its later amendments.

Consent for publication

All participants gave written informed consent for the publication of their anonymised data in public research repositories and in scientific journals.

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Conflict of interest

The authors have no relevant financial or non-financial interests to disclose.

REFERENCES

- Amemiya, T., Ikei, Y., & Kitazaki, M. (2019). Remapping peripersonal space by using foot-sole vibrations without any body movement. *Psychological Science*, 30(10), 1522–1532.
- Avenanti, A., Annala, L., & Serino, A. (2012). Suppression of premotor cortex disrupts motor coding of peripersonal space. *Neuroimage*, 63(1), 281–288.
- Baldauf, D., & Deubel, H. (2010). Attentional landscapes in reaching and grasping. *Vision Research*, 50(11), 999–1013.
- Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, 68(3), 255–278.
- Bonini, L., Maranesi, M., Livi, A., Fogassi, L., & Rizzolatti, G. (2014). Space-dependent representation of objects and other's action in monkey ventral premotor grasping neurons. *Journal of Neuroscience*, 34(11), 4108–4119.
- Boussaoud, D., & Wise, S. P. (1993). Primate frontal cortex: Effects of stimulus and movement. *Experimental Brain Research*, 95(1), 28–40.
- Box, G. E., & Cox, D. R. (1964). An analysis of transformations. *Journal of the Royal Statistical Society Series B: Statistical Methodology*, 26(2), 211–243.
- Bremmer, F., Schlack, A., Shah, N. J., Zafiris, O., Kubischik, M., Hoffmann, K. P., ... Fink, G. R. (2001). Polymodal motion processing in posterior parietal and premotor cortex: A human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron*, 29(1), 287–296.
- Brozzoli, C., Cardinali, L., Pavani, F., & Farnè, A. (2010). Action-specific remapping of peripersonal space. *Neuropsychologia*, 48(3), 796–802.
- Brozzoli, C., Gentile, G., Petkova, V. I., & Ehrsson, H. H. (2011). fMRI adaptation reveals a cortical mechanism for the coding of space near the hand. *The Journal of Neuroscience*, 31(24), 9023–9031.

- Brozzoli, C., Pavani, F., Urquizar, C., Cardinali, L., & Farnè, A. (2009b). Grasping actions remap peripersonal space. *Neuroreport*, 20(10), 913–917.
- Brozzoli, C., Pavani, F., Urquizar, C., Cardinali, L., & Farnè, A. (2009a). Grasping actions remap peripersonal space. *Neuroreport*, 20(10), 913–917.
- Bufacchi, R. J., & Iannetti, G. D. (2018a). An action field theory of peripersonal space. *Trends in Cognitive Sciences*, 22(12), 1076–1090.
- Bufacchi, R. J., & Iannetti, G. D. (2018b). An action field theory of peripersonal space. *Trends in Cognitive Sciences*, 22(12), 1076–1090.
- Bufacchi, R. J., Liang, M., Griffin, L. D., & Iannetti, G. D. (2016). A geometric model of defensive peripersonal space. *Journal of Neurophysiology*, 115(1), 218–225.
- Canzoneri, E., Magosso, E., & Serino, A. (2012). Dynamic sounds capture the boundaries of peripersonal space representation in humans. *Plos One*, 7(9), Article e44306.
- Cardinali, L., Brozzoli, C., & Farnè, A. (2009). Peripersonal space and body schema: Two labels for the same concept? *Brain Topography*, 21(3–4), 252–260.
- Cléry, J., Guipponi, O., Wardak, C., & Hamed, S. B. (2015). Neuronal bases of peripersonal and extrapersonal spaces, their plasticity and their dynamics: Knowns and unknowns. *Neuropsychologia*, 70, 313–326.
- Coello, Y., & Iachini, T. (2021). The social dimension of peripersonal space. In F. de Vignemont, A. Serino, H. Y. Wong, & A. Farnè (Eds.), *The world at our fingertips: A multidisciplinary exploration of peripersonal space* (pp. 267–284). Oxford University Press. <https://doi.org/10.1093/oso/9780198851738.003.0015>.
- Cumming, G. (2014). The new statistics: Why and how. *Psychological Science*, 25(1), 7–29.
- de Vignemont, F., & Iannetti, G. D. (2015). How many peripersonal spaces? *Neuropsychologia*, 70, 327–334.
- Deubel, H., & Schneider, W. X. (2004). Attentional selection in sequential manual movements, movements around an obstacle and in grasping. In *Attention in action* (pp. 85–108). Psychology Press.
- Di Marco, S., Tosoni, A., Altomare, E. C., Ferretti, G., Perrucci, M. G., & Committeri, G. (2019). Walking-related locomotion is facilitated by the perception of distant targets in the extrapersonal space. *Scientific Reports*, 9(1), 9884.
- 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>. Epub 2014 Nov 13. PMID: 25448862.
- Duhamel, J. R., Colby, C. L., & Goldberg, M. E. (1998). Ventral intraparietal area of the macaque: Congruent visual and somatic response properties. *Journal of Neurophysiology*, 79(1), 126–136.
- Eimer, M., Van Velzen, J., Gherri, E., & Press, C. (2007). ERP correlates of shared control mechanisms involved in saccade preparation and in covert attention. *Brain Research*, 1135, 154–166.
- Friedmann, L. (1988). Functional skills in multiple limb anomalies. In *Comprehensive management of the upper-limb amputee* (pp. 150–164). New York, NY: Springer New York.
- Gazzola, V., van der Worp, H., Mulder, T., Wicker, B., Rizzolatti, G., & Keysers, C. (2007). Aphasics born without hands mirror the goal of hand actions with their feet. *Current Biology*, 17(14), 1235–1240.
- Gherri, E., & Eimer, M. (2008). Links between eye movement preparation and the attentional processing of tactile events: An event-related brain potential study. *Clinical Neurophysiology*, 119(11), 2587–2597.
- Gherri, E., & Eimer, M. (2010). Manual response preparation disrupts spatial attention: An electrophysiological investigation of links between action and attention. *Neuropsychologia*, 48(4), 961–969.
- Gherri, E., & Forster, B. (2012a). Crossing the hands disrupts tactile spatial attention but not motor attention: Evidence from event-related potentials. *Neuropsychologia*, 50(9), 2303–2316.
- Gherri, E., & Forster, B. (2012b). The orienting of attention during eye and hand movements: ERP evidence for similar frame of reference but different spatially specific modulations of tactile processing. *Biological Psychology*, 91(2), 172–184.
- Gherri, E., Van Velzen, J., & Eimer, M. (2007). Dissociating effector and movement direction selection during the preparation of manual reaching movements: Evidence from lateralized ERP components. *Clinical Neurophysiology*, 118(9), 2031–2049.
- Gherri, E., Xu, A., Ambron, E., & Sedda, A. (2022). Peripersonal space around the upper and the lower limbs. *Experimental Brain Research*, 240, 2039–2050.
- Glover, S. (2004). Separate visual representations in the planning and control of action. *Behavioural and Brain Sciences*, 27(1), 3–24.
- Graziano, M. S., & Cooke, D. F. (2006). Parieto-frontal interactions, personal space, and defensive behavior. *Neuropsychologia*, 44(6), 845–859.
- Graziano, M. S., & Gross, C. G. (1993). A bimodal map of space: Somatosensory receptive fields in the macaque putamen with corresponding visual receptive fields. *Experimental Brain Research*, 97(1), 96–109.
- Graziano, M. S. A., & Gross, C. G. (1995). The representation of extrapersonal space: A possible role for bimodal, visual-tactile neurons. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 1021–1034). The MIT Press.
- Graziano, M. S., Yap, G. S., & Gross, C. G. (1994). Coding of visual space by premotor neurons. *Science*, 266, 1054–1056.
- Green, P., & MacLeod, C. J. (2016). Simr: An R package for power analysis of generalized linear mixed models by simulation. *Methods in Ecology and Evolution*, 7(4), 493–498.
- Gross, C. G., & Graziano, M. S. A. (1995). Multiple representations of space in the brain. *The Neuroscientist: a Review Journal Bringing Neurobiology, Neurology and Psychiatry*, 1(1), 43–50.
- Higuchi, T., Imanaka, K., & Patla, A. E. (2006). Action-oriented representation of peripersonal and extrapersonal space: Insights from manual and locomotor actions. *Japanese Psychological Research*, 48(3), 126–140.
- Hollands, M. A., Patla, A. E., & Vickers, J. N. (2002). “Look where you’re going!”: Gaze behaviour associated with maintaining and changing the direction of locomotion. *Experimental Brain Research*, 143(2), 221–230.
- Holmes, N. P. (2012). Does tool use extend peripersonal space? A review and re-analysis. *Experimental Brain Research*, 218(2), 273–282.
- Holmes, N. P., & Spence, C. (2004). The body schema and multisensory representation(s) of peripersonal space. *Cognitive Processing*, 5(2), 94–105.
- Hoshi, E., & Tanji, J. (2002). Contrasting neuronal activity in the dorsal and ventral premotor areas during preparation to reach. *Journal of Neurophysiology*, 87(2), 1123–1128.
- Hoshi, E., & Tanji, J. (2006). Differential involvement of neurons in the dorsal and ventral premotor cortex during processing of visual signals for action planning. *Journal of Neurophysiology*, 95(6), 3596–3616.
- Iachini, T., Coello, Y., Frassinetti, F., & Ruggiero, G. (2014a). Body space in social interactions: A comparison of reaching and comfort distance in immersive virtual reality. *Plos One*, 9(11), Article e111511.
- Iachini, T., Pagliaro, S., & Ruggiero, G. (2015). Near or far? It depends on my impression: Moral information and spatial behavior in virtual interactions. *Acta Psychologica*, 161, 131–136.
- Iachini, T., Ruggiero, G., Ruotolo, F., & Vinciguerra, M. (2014b). Motor resources in peripersonal space are intrinsic to spatial

- encoding: Evidence from motor interference. *Acta Psychologica*, 153, 20–27.
- Juravle, G., Deubel, H., Tan, H. Z., & Spence, C. (2010). Changes in tactile sensitivity over the time-course of a goal-directed movement. *Behavioural Brain Research*, 208(2), 391–401.
- Takei, S., Hoffman, D. S., & Strick, P. L. (2003). Sensorimotor transformations in cortical motor areas. *Neuroscience research*, 46(1), 1–10.
- Karok, S., & Newport, R. (2010). The continuous updating of grasp in response to dynamic changes in object size, hand size and distractor proximity. *Neuropsychologia*, 48(13), 3891–3900.
- Klein Entink, R., van Der Linden, W. J., & Fox, J. P. (2009). A Box–Cox normal model for response times. *British Journal of Mathematical and Statistical Psychology*, 62(3), 621–640.
- Kline, R. B. (2004). Beyond significance testing: Reforming data analysis methods in behavioral research. In *American psychological association*. Washington, DC: American Psychological Association.
- Krell, J., & Patla, A. E. (2002). The influence of multiple obstacles in the travel path on avoidance strategy. *Gait & Posture*, 16(1), 15–19.
- Làdavas, E., Di Pellegrino, G., Farnè, A., & Zeloni, G. (1998). Neuropsychological evidence of an integrated visuotactile representation of peripersonal space in humans. *Journal of Cognitive Neuroscience*, 10(5), 581–589.
- Làdavas, E., & Serino, A. (2008). Action-dependent plasticity in peripersonal space representations. *Cognitive Neuropsychology*, 25(7–8), 1099–1113.
- Longo, M. R., & Lourenco, S. F. (2006). On the nature of near space: Effects of tool use and the transition to far space. *Neuropsychologia*, 44(6), 977–981.
- Longo, M. R., & Lourenco, S. F. (2007). Spatial attention and the mental number line: Evidence for characteristic biases and compression. *Neuropsychologia*, 45(7), 1400–1407.
- Makin, T. R., Holmes, N. P., & Zohary, E. (2007). Is that near my hand? Multisensory representation of peripersonal space in human intraparietal sulcus. *The Journal of Neuroscience*, 27(4), 731–740.
- Maravita, A., Spence, C., & Driver, J. (2003). Multisensory integration and the body schema: Close to hand and within reach. *Current Biology*, 13(13), 531–539.
- Mason, L., Linnell, K. J., Davis, R., & Van Velzen, J. (2015). Visual processing at goal and effector locations is dynamically enhanced during motor preparation. *Neuroimage*, 117, 243–249.
- Mushiake, H., Tanatsugu, Y., & Tanji, J. (1997). Neuronal activity in the ventral part of premotor cortex during target-reach movement is modulated by direction of gaze. *Journal of Neurophysiology*, 78(1), 567–571.
- Noel, J. P., Grivaz, P., Marmaroli, P., Lissek, H., Blanke, O., & Serino, A. (2015). Full body action remapping of peripersonal space: The case of walking. *Neuropsychologia*, 70, 375–384.
- Patané, I., Cardinali, L., Salemme, R., Pavani, F., Farnè, A., & Brozzoli, C. (2019). Action planning modulates peripersonal space. *Journal of Cognitive Neuroscience*, 31(8), 1141–1154.
- Patané, I., Farnè, A., & Frassinetti, F. (2017). Cooperative tool-use reveals peripersonal and interpersonal spaces are dissociable. *Cognition*, 166, 13–22.
- Patané, I., Iachini, T., Farnè, A., & Frassinetti, F. (2016). Disentangling action from social space: Tool-use differently shapes the space around us. *Plos One*, 11(5), Article e0154247.
- Patla, A. E., & Vickers, J. N. (1997). Where and when do we look as we approach and step over an obstacle in the travel path? *Neuroreport*, 8(17), 3661–3665.
- Patla, A. E., & Vickers, J. N. (2003). How far ahead do we look when required to step on specific locations in the travel path during locomotion? *Experimental Brain Research*, 148(1), 133–138.
- Pozeg, P., Galli, G., & Blanke, O. (2015). Those are your legs: The effect of visuo-spatial viewpoint on visuo-tactile integration and body ownership. *Frontiers in Psychology*, 6, 1749.
- Quinlan, D. J., & Culham, J. C. (2007). fMRI reveals a preference for near viewing in the human parieto-occipital cortex. *Neuroimage*, 36(1), 167–187.
- R Core Team. (2024). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Rizzolatti, G., Cattaneo, L., Fabbri-Destro, M., & Rozzi, S. (2014). Cortical mechanisms underlying the organization of goal-directed actions and mirror neuron-based action understanding. *Physiological Reviews*, 94(2), 655–706.
- Rizzolatti, G., Fadiga, L., Fogassi, L., & Gallese, V. (1997). The space around us. *Science*, 277(5323), 190–191.
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2002). Motor and cognitive functions of the ventral premotor cortex. *Current Opinion in Neurobiology*, 12(2), 149–154.
- Rizzolatti, G., Matelli, M., & Pavesi, G. (1983). Deficits in attention and movement following the removal of postarcuate (area 6) and prearcuate (area 8) cortex in macaque monkeys. *Brain: a Journal of Neurology*, 106(3), 655–673.
- Scandola, M., Aglioti, S. M., Bonente, C., Avesani, R., & Moro, V. (2016). Spinal cord lesions shrink peripersonal space around the feet, passive mobilization of paraplegic limbs restores it. *Scientific Reports*, 6(1), Article 24126.
- Schicke, T., Bauer, F., & Röder, B. (2009). Interactions of different body parts in peripersonal space: How vision of the foot influences tactile perception at the hand. *Experimental Brain Research*, 192(4), 703–715.
- Serino, A. (2019). Peripersonal space (PPS) as a multisensory interface between the individual and the environment, defining the space of the self. *Neuroscience and Biobehavioral Reviews*, 99, 138–159.
- Serino, A., Noel, J. P., Galli, G., Canzoneri, E., Marmaroli, P., Lissek, H., & Blanke, O. (2015a). Body part-centered and full body-centered peripersonal space representations. *Scientific Reports*, 5(1), Article 18603.
- Serino, A., Noel, J. P., Galli, G., Canzoneri, E., Marmaroli, P., Lissek, H., & Blanke, O. (2015b). Body part-centered and full body-centered peripersonal space representations. *Scientific Reports*, 5, 1–14.
- Spence, C., Pavani, F., & Driver, J. (2004a). Spatial constraints on visual-tactile cross-modal distractor congruency effects. *Cognitive, Affective, & Behavioral Neuroscience*, 4(2), 148–169.
- Spence, C., Pavani, F., Maravita, A., & Holmes, N. (2004b). Multisensory contributions to the 3-D representation of visuotactile peripersonal space in humans: Evidence from the crossmodal congruency task. *Journal of Physiology*, 98(1), 171–189.
- Spence, C., Ranson, J., & Driver, J. (2000). Cross-modal selective attention: On the difficulty of ignoring sounds at the locus of visual attention. *Perception & Psychophysics*, 62, 410–424.
- Stettler, B. A., & Thomas, L. E. (2017). Visual processing is biased in peripersonal foot space. *Attention, Perception, & Psychophysics*, 79, 298–305.
- Stone, K. D., Kandula, M., Keizer, A., & Dijkerman, H. C. (2018). Peripersonal space boundaries around the lower limbs. *Experimental Brain Research*, 236, 161–173.
- Teneggi, C., Canzoneri, E., di Pellegrino, G., & Serino, A. (2013). Social modulation of peripersonal space boundaries. *Current Biology*, 23(5), 406–411.
- Townsend, B. R., Subasi, E., & Scherberger, H. (2011). Grasp movement decoding from premotor and parietal cortex. *The Journal of Neuroscience*, 31(40), 14386–14398.
- Umiltà, M. A., Brochier, T., Spinks, R. L., & Lemon, R. N. (2007). Simultaneous recording of macaque premotor and primary motor cortex neuronal populations reveals different

- functional contributions to visuomotor grasp. *Journal of Neurophysiology*, 98(1), 488–501.
- van Elk, M., & Blanke, O. (2011). Manipulable objects facilitate cross-modal integration in peripersonal space. *Plos One*, 6(9), 1–7.
- van Elk, M., Forget, J., & Blanke, O. (2013). The effect of limb crossing and limb congruency on multisensory integration in peripersonal space for the upper and lower extremities. *Consciousness and Cognition*, 22(2), 545–555.
- 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; a Journal Devoted To the Study of the Nervous System and Behavior*, 74, 20–30.
- World Medical Association. (2013). World Medical Association Declaration of Helsinki: Ethical principles for medical research involving human subjects. *Journal of the American Medical Association*, 310(20), 2191–2194.
- Zanini, A., Patané, I., Blini, E., Salemme, R., Koun, E., Farnè, A., & Brozzoli, C. (2020). Patterns of multisensory facilitation distinguish peripersonal from reaching space. *BioRxiv*, 2020–06.
- Zanini, A., Patané, I., Blini, E., Salemme, R., Koun, E., Farnè, A., & Brozzoli, C. (2021). Peripersonal and reaching space differ: Evidence from their spatial extent and multisensory facilitation pattern. *Psychonomic Bulletin & Review*, 28(6), 1894–1905.