COGNITIVE NEUROSCIENCE

Vestibular modulation of peripersonal space boundaries

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Abstract

Human–environment interactions are mediated through the body and occur within the peripersonal space (PPS), the space immediately adjacent to and surrounding the body. The PPS is taken to be a critical interface between the body and the environment, and indeed, body-part specific PPS remapping has been shown to depend on body-part utilization, such as upper limb movements in otherwise static observers. How vestibular signals induced by whole-body movement contribute to PPS representation is less well understood. In a series of experiments, we mapped the spatial extension of the PPS around the head while participants were submitted to passive whole-body rotations inducing vestibular stimulation. Forty-six participants, in three experiments, executed a tactile detection reaction time task while task-irrelevant auditory stimuli approached them. The maximal distance at which the auditory stimulus facilitated tactile reaction time was taken as a proxy for the boundary of peri-head space. The present results indicate two distinct vestibular effects. First, vestibular stimulation speeded tactile detection indicating a vestibular facilitation of somatosensory processing. Second, vestibular stimulation modulated audio-tactile interaction of peri-head space in a rotation direction-specific manner. Congruent but not incongruent audio-vestibular motion stimuli expanded the PPS boundary further away from the body as compared to no rotation. These results show that vestibular inputs dynamically update the multisensory delineation of PPS and far space, which may serve to maintain accurate tracking of objects close to the body and to update spatial self-representations.

Introduction

Most everyday activities involve movement of body parts or the body as a whole, thereby leading to a change in the distance and orientation of the body with respect to environmental objects. As all interactions with such objects take place in the peripersonal space (PPS; Rizzolatti *et al.*, 1981; di Pellegrino *et al.*, 1997; Rizzolatti *et al.*, 1997)—the space immediately adjacent to and surrounding the body—the neural representations of PPS needs to take into account the effects of whole-body displacements (Blanke *et al.*,

2015; Serino *et al.*, 2015). However, the vast majority of previous neurophysiological (e.g., Fogassi *et al.*, 1996; Graziano & Cooke, 2006), neuroimaging (e.g., Makin *et al.*, 2007; Brozzoli *et al.*, 2012), and behavioral studies (e.g., Bassolino *et al.*, 2010; Canzoneri *et al.*, 2012) have mainly characterized the representation of PPS for either static observers or investigated the influence of movements of a single body-part, mostly the arm [(Brozzoli *et al.*, 2012; Clery *et al.*, 2015; Grivaz *et al.*, 2017) for reviews; but see (Noel *et al.*, 2015a) for whole-body movements during walking]. Here, in contrast, we assessed the effects of passive whole-body rotation on PPS representation in humans using a behavioral task for mapping audio-tactile PPS boundaries around the head (Canzoneri *et al.*, 2012; Serino *et al.*, 2015). That is, task-irrelevant sounds approached the participant's body while the participant performed speeded detections of tactile stimuli. The distance where the sounds facilitated tactile response times over and above a no-sound condition was considered the PPS boundary. In doing so, we probe the

contribution of the vestibular system to PPS representation during passive self-motion.

Early electrophysiological studies identified a fronto-parietal cortical network, composed of the ventral intraparietal (VIP) and ventral premotor cortex, encoding PPS by multisensory neurons that respond both to somatosensory stimulation on the hand (Fogassi *et al.*, 1996; Duhamel *et al.*, 1998), face (Fogassi *et al.*, 1996; Duhamel *et al.*, 1998), or trunk (Leinonen & Nyman, 1979; Leinonen *et al.*, 1979) and to auditory or visual stimulation close to but not far from these body parts (Graziano *et al.*, 1997, 1999; Graziano & Cooke, 2006). A key characteristic of these PPS neurons is that their receptive fields remain centered on the body when a limb is displaced (Graziano *et al.*, 1997, 1999; Graziano & Cooke, 2006). Moreover, the auditory or visual receptive fields of these neurons delineate with a sharp spatial boundary the multisensory responses in the space close to the body from unisensory responses for stimuli further away. Accordingly, the maximum distance from the body at which multisensory responses can be observed in these neurons is considered to index the boundary of PPS (Graziano & Cooke, 2006). This boundary is, however, not fixed but varies as a function of body-part (Duhamel *et al.*, 1998), stimulus motion parameters (Fogassi *et al.*, 1996), and prior experience, that is, after tool use the PPS boundary extends as to incorporate the tool tip (Iriki *et al.*, 1996), among other factors.

More recently, neuropsychology (see di Pellegrino & Ladavas, 2015 for a review), neuroimaging (Makin *et al.*, 2007; Brozzoli *et al.*, 2012), and psychophysical studies (Canzoneri *et al.*, 2012; Serino *et al.*, 2015) in humans have confirmed the existence of a similar PPS mechanism in humans (Bremmer *et al.*, 2001). From a behavioral perspective, PPS is reflected in a facilitation of tactile processing when either an auditory or a visual stimulus is presented close to (vs. far from) the body (Canzoneri *et al.*, 2012; Serino *et al.*, 2015). Furthermore, in addition to the above-mentioned factors influencing PPS representation in non-human primates, in humans the spatial extent of PPS has been shown to depend on a host of higher order factors, such as perceived self-location (Noel *et al.*, 2015b, 2017; Salomon *et al.*, 2017), the quality of social interaction (Teneggi *et al.*, 2013), and cognitive or personality factors (Lourenco *et al.*, 2011; Sambo & Iannetti, 2013).

Previous studies established that PPS neurons respond most vigorously to dynamic stimuli (Fogassi *et al.*, 1996) and that proprioceptive inputs contribute to remapping of the peri-hand space upon limb movements (Brozzoli *et al.*, 2009, 2010). Nonetheless, because these studies mainly investigated PPS in static observers, the contribution of vestibular signals—as induced by head or whole-body motion—to human PPS representations remains largely unknown [see (Noel *et al.*, 2015a) and (Galli *et al.*, 2015) for a related idea]. Thus, in this study, we aim at characterizing how physiological vestibular stimulation by passive whole-body rotation alters PPS representation.

We adopt an existing method for mapping the PPS boundaries (Canzoneri *et al.*, 2012; Serino *et al.*, 2015) to the delineation of peri-head space during passive whole-body rotation. First, we quantify the spatial extent of PPS in a static condition without any vestibular stimulation (audio-tactile; Experiment 1). Next, we examine the general contribution of vestibular stimulation to tactile reaction times (RTs, vestibular–tactile; Experiment 2). Finally, in the critical experiment, we test whether vestibular stimulation modulates the multisensory responses to approaching auditory stimulus entering the PPS (vestibular–audio-tactile; Experiment 3). We base this idea on previous evidence from electrophysiological recordings in monkey VIP neurons—pertaining to the network

encoding for PPS—which showed most vigorous responses when dynamic visual, somatosensory, or auditory stimuli were moving in the same (ipsilateral) direction as vestibular motion stimuli (Bremmer *et al.*, 2002; Schlack *et al.*, 2002, 2005). Further, in humans, both sound localization in external space and touch localization on the body depend on the direction of vestibular motion stimuli (Lackner & DiZio, 2005; Van Barneveld & John Van Opstal, 2010; Teramoto *et al.*, 2012), while perceptual thresholds for somatosensory stimuli at a fixed body location are largely independent of the direction of vestibular motion (Ferrè *et al.*, 2014). Based on these previous observations, in the critical experiment here (vestibular–audio-tactile task; Experiment 3), we examined whether the congruency between the direction of vestibular stimulation (whole-body Leftward or Rightward Rotation) and auditory stimuli (Leftward or Rightward looming Sounds) differently modulates peri-head representation. In addition to an audio-tactile space-specific effect (close vs. far), a vestibular–audio-congruency effect would indicate potential contributions of the vestibular system to the encoding of PPS.

Methods

Participants

A total of 46 right-handed subjects (16 females, mean age: 24 years, range: 18–32) participated in this study. Sixteen subjects (six females, mean age: 24 years) participated in Experiment 1. Another group of 16 subjects (five females, mean age: 23 years) participated in Experiment 2, and out of those, 11 subjects (three females, mean age: 22 years) were randomly selected to additionally participate in the sound-distance estimation task of Experiment 3 immediately after having completed Experiment 2. A different group of 14 subjects (five females, mean age: 24 years) exclusively participated in the audio-tactile interaction task of Experiment 3. No subject participated more than once in the same type of task across experiments. All participants reported normal touch, hearing and balance, had normal or corrected-to-normal vision, and no history of neurological or psychiatric disorder. All participants gave their informed consent for participation in the study, which was approved by the local ethical committee—La Commission d'Ethique de la Recherche Clinique de la Faculté et de Medicine de l'Université de Lausanne—and conducted in line with the Declaration of Helsinki.

Study design

The aim of this study was to quantify the effects of vestibular stimulation on the location of the PPS boundary in humans. Here, we quantified the PPS boundary by adapting an audio-tactile interaction task initially developed by (Canzoneri *et al.*, 2012) and used in a number of previous studies (Canzoneri *et al.*, 2012; Noel *et al.*, 2015b; Serino *et al.*, 2015). In order to assure that the effects observed in our study were indeed related to an interaction of vestibular, auditory, and tactile processing and not exclusively based on audio-tactile and vestibular–tactile interactions reported in previous studies (e.g., Canzoneri *et al.*, 2012; Ferrè *et al.*, 2014), we conducted three experiments to address this issue. In the first experiment (audio-tactile experiment), we mapped the spatial extend and lateral symmetry of PPS for static listeners, thus distance-dependent audio-tactile interactions in the absence of rotational vestibular stimulation. In the second experiment (vestibular–tactile experiment), before indexing the impact of vestibular cues on PPS representation, we quantified the effects of rotational

vestibular stimulation on tactile detection independent of auditory stimulation. Finally, in the third experiment (vestibular–auditory–tactile experiment), we quantified the effects of rotational vestibular stimulation on audio-tactile interaction in peri-head space. Thus, the first two experiments served to validate our experimental protocol with respect to known bimodal audio-tactile and vestibular–tactile interaction effects based on different experimental manipulations, and the third experiment assessed additional tri-modal vestibular–auditory–tactile interactions. This design further allowed minimizing the number of experimental conditions per experiment and to acquire data from more sampling points (i.e., audio-tactile distances) and more repetitions per condition.

Stimuli and apparatus

Tactile stimuli (Experiments 1–3)

A small vibrating motor (Precision MicroDrives shaftless vibration motors, model 312-101, 3 V, 60 mA, 9000 rpm, 150 Hz, 5 g, weight 113 mm² surface area, maximal rotation speed reached in 50 ms) was attached to the center of participant's forehead and used for presenting vibro-tactile stimulations of 200 ms in duration.

Acoustic stimuli (Experiments 1 and 3)

Participants wore headphones (BOSE QC15 noise-canceling headphones, Sissach, Germany) on which pink-noise stereo sound samples were presented. These sounds mimicked the movement of a sound source in external space along a straight trajectory toward the participant's head. Sound samples were created with custom scripts in MATLAB (MathWorks, Natick, MA, USA) using a spherical head model with 18 cm diameter, a standard head transfer function, and spatial filters for generating interaural level and time differences corresponding to distinct locations of a sound source in external space. Given extensive literature showing that human auditory localization is more accurate along the left–right than the front–back and up–down directions (see Middlebrooks, 2015 for a review), we focused in this study on auditory stimuli presented at different distances along the head-centered binaural axis. Seven head-sound distances were simulated from 0 cm (D1) to 100 cm (D7), both to the left and the right side of the median plane through the body. At stimulus onset, the sound source was static and located at either the left or right side at 100 cm (D7) from the participant for 1 s. Then, the sound moved at 50 cm/s constant velocity toward the participant's head (D6–D2) during 2 s, and finally remained static at 0 cm (D1) for the final second, resulting in 4 s total duration of the sound stimulus (see Fig. 1A and B). The points in space sampled (audio-tactile distances) were given by the temporal offset between sound onset and tactile onset, thus the longer the auditory and tactile onset discrepancy, the closer the sound. It must be noted that because auditory stimuli were presented via headphones the sound source motion was always head-centered and thus independent of head orientation in external space. A similar experimental setup using sounds presented along the front–back axis has been extensively validated by our group (Canzoneri *et al.*, 2012) and has been used for mapping auditory–tactile interaction within PPS in numerous previous studies (Canzoneri *et al.*, 2012; Noel *et al.*, 2015b; Serino *et al.*, 2015).
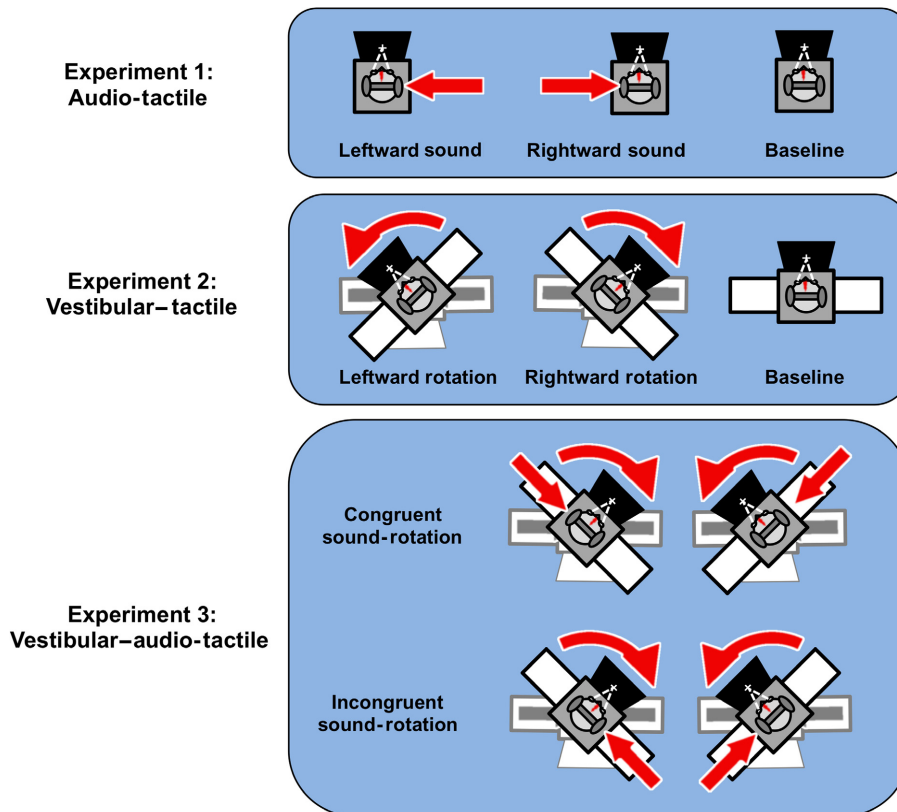

FIG. 1. Overview of experiments. A schematic top view shows the participant's head at center, the rotation platform (Experiments 2 and 3), and a monitor showing the fixation cross. Red flash symbol indicates tactile stimulator placement on the central forehead. Red arrows indicate the direction of sound movement (straight arrows) and the direction of whole-body rotation (curved arrows). [Colour figure can be viewed at wileyonlinelibrary.com].

Vestibular stimuli (Experiments 2 and 3)

In an acoustically and light-shielded room, a motion platform was installed that consisted of an electrical engine (PCI-7352 servo control) on which a beam platform (200 cm diameter) and a racing car seat were fixated. Angular platform motions were controlled with LAB-VIEW software (version 8.6, National Instruments, Austin, TX, USA) with a precision of 0.1 angular degrees at 100 Hz sampling rate. Participants were seated upright with their head centered above their trunk, and their trunk centered above the axis of rotation. A forehead and chin rest gently restrained the head at approximately 30° pitch-down angle with respect to an earth-horizontal plane. As anatomical landmarks, the experimenter used a transversal plane through the inion and both ear holes of the participant (Reid's plane). This procedure served to align the semicircular canals of the inner ear with the rotation plane to allow for selective stimulation of the horizontal semicircular canals (Fernandez & Goldberg, 1971; Goldberg & Fernandez, 1971). Participants passively received whole-body yaw rotations in clockwise (Rightward Rotation) or counterclockwise (Leftward Rotation) direction about a head-centered earth-vertical axis. This experimental setup has been used previously in several studies (Prsa et al., 2012; van Elk & Blanke, 2013; Ferrè et al., 2014; Gale et al., 2016; Kaliuzhna et al., 2016; Pfeiffer et al., 2016). At the beginning of an experimental trial, the platform accelerated in clockwise or counterclockwise direction from 0 °/s to 140 °/s maximum velocity following a cosine-smoothed acceleration profile (i.e., Gaussian shape, 70 °/s² maximum acceleration reached at 2 s after onset) during 4 s. This acceleration profile was chosen because the semicircular canals are maximally tuned to such cosine-smoothed accelerations resembling natural voluntary head movements (Bertolini et al., 2011; Prsa et al., 2012). Presentation of experimental tactile and acoustic stimuli was restricted to this 4-s platform acceleration period. Immediately after 140 °/s maximum velocity were reached the platform decelerated to a full stop (0 °/s velocity) during 1 s (i.e., no experimental stimuli were presented). This was followed by a resting period (i.e., no platform motion and no experimental stimulation) of 2.5- to 3.5-s random duration (i.e., sampled in steps of 100 ms from a uniform distribution) to avoid anticipation effects regarding the onset of the next rotation (Prsa et al., 2012; van Elk & Blanke, 2013). During all times, participants were instructed to fixate at a central cross presented on a computer screen (Samsung Syncmaster 2233RZ, Seoul, Korea; 120 Hz refresh rate; 22-inch diameter) that was firmly attached to the rotation platform and positioned in front of the participant (29 cm eye-to-screen distance; 56° vertical and 80° horizontal visual angles). This precaution was taken to suppress vestibular nystagmus (Raphan et al., 1979; Cohen et al., 1981). A low-volume acoustic noise floor was present during experiments involving the rotating chair. This was related to a pneumatic system reducing friction of the motion platform with the ground floor (active during rotation and rest) and minor engine noises during chair rotations. The noise-canceling headphones worn by participants largely attenuated the noise floor. To reduce somatosensory cues from chair rotations, the racing car seat was padded with foam and had a tight ergonomic fit.

Experimental design and procedure

Experiment 1: audio-tactile interaction

The first experiment served to map the spatial extend and lateral symmetry of auditory–tactile interactions in peri-head space in static listeners. The experimental protocol was adapted from (Canzoneri et al., 2012) and consisted of two tasks.

The audio-tactile interaction task served to identify the maximum distance at which sounds facilitate tactile responses, which is considered a proxy of the boundary of PPS (Canzoneri et al., 2012; Serino et al., 2015). This task consisted of a 3 (Sound: Leftward Sound, Rightward Sound, Baseline) × 7 (Distance: D1–D7) experimental design (i.e., 21 trial repetitions per onset delay). For each trial, a single vibro-tactile stimulus was presented at a random onset delay from 500 ms (D7) to 3500 ms (D1) in steps of 500 ms from trial onset. In addition to the experimental trials (Leftward and Rightward Sounds) Baseline trials were intermixed in the design. These Baseline trials consisted of unimodal tactile stimulation (in absence of sound stimulation) presented at the same temporal offsets as used for bimodal audio-tactile trials and served as a control condition for bimodal audio-tactile trials for assessing sound-distance-dependent facilitation of tactile responses (Serino et al., 2015; Kandula et al., 2017). For consistency across conditions, the sampling points (i.e., temporal offsets) for tactile stimuli are labeled D1–D7 both in Baseline and in bimodal audio-tactile trials. Audio-tactile trials (i.e., Leftward Sound, Rightward Sound) consisted of tactile stimulation at distinct temporal delays from sound onset, and thus corresponding to sounds being perceived at different Distances (D7–D1) from the body. Bimodal audio-tactile trials allowed for quantifying the farthest distance from the body at which sounds significantly promoted tactile processing as reflected in audio-tactile RTs becoming significantly faster than responses to tactile stimuli alone. Such distance is taken to index the boundary of PPS representation (Serino et al., 2015). Finally, 42 catch trials were presented (9% of total trials) for which no tactile stimuli were presented and participants were to withhold from responding. Catch trials were included to avoid entrainment of automatic motor responses and to assure that participants were attentive to the task [see (Kandula et al., 2017), for a recent formal analysis of the impact of temporal expectation on PPS mapping]. Before the experiment, participants were informed that during they experiment they would be repeatedly presented with tactile stimuli and approaching sounds, which they were told were task-irrelevant. Participants were instructed to respond as accurately and rapidly as possible to tactile vibration by pressing with their right index finger a button on a serial keyboard positioned centrally in front of the participant. Participants were also informed that in some trials (Baseline) tactile stimuli would be administered in the absence of auditory stimulation, and in another type of trials (Catch trials) no tactile stimuli would be presented, for which they were to withhold from button response. Each participant completed at least 10 practice trials before the experiment for which no data were recorded.

After having completed the audio-tactile interaction task, each participant took part in the sound-distance estimation task, which served to assess subjective estimates of sound-distance along the head-centered binaural axis. A 2 (Sound: Leftward Sound, Rightward Sound) × 7 (Distance: D1–D7) experimental design was used that consisted of the same bimodal audio-tactile stimuli used for the Leftward Sound and Rightward Sound conditions of the audio-tactile interaction task. No unimodal tactile trials and no catch trials were presented, and each experimental audio-tactile condition was presented 10 times in a random order. Participants were instructed that they would receive the same tactile and auditory stimuli previously used during the audio-tactile interaction task. They were instructed to estimate the head-centered distance along the binaural axis of the sound source at the moment they felt the vibration onset. Immediately after stimulus presentation was completed, participants were shown a visual display to indicate their sound-distance estimate. The visual display consisted of a horizontal analogue scale

ranging from −100 cm (left side) to 0 cm (screen center) to +100 cm (right side), showing intermediate values in steps of 20 cm. Participants were instructed to place a cursor using a computer mouse at any position along the visual scale (i.e., continuous values in steps of 1 cm were recorded) and to confirm their judgment with a mouse click. There were no temporal limits for making this judgment.

Experiment 2: vestibular–tactile interaction

The second experiment quantified the effects of rotational vestibular stimulation on tactile detection independent of auditory stimulation. This experiment was motivated by previous studies providing evidence for vestibular–somatosensory interaction at the neural level in animals (Fredrickson *et al.*, 1966; Schwarz & Fredrickson, 1971; Odkvist *et al.*, 1974; Grüsser *et al.*, 1990) and humans (Bottini *et al.*, 2001; Bremmer *et al.*, 2001; Fasold *et al.*, 2008; Ferrè *et al.*, 2012; Mazzola *et al.*, 2014; Pfeiffer *et al.*, 2016) as well as for vestibular effects on human somatosensory perception (Bottini *et al.*, 2005; Ferrè *et al.*, 2011a). Because the majority of these studies used artificial vestibular stimulation, here we aimed to assess how physiological vestibular stimulation by passive whole-body rotation would affect processing of tactile stimuli used in the PPS mapping experiments. Further, we aimed to identify whether Leftward and Rightward Rotations would differentially affect tactile detection performance. Tactile stimulus onset delays from initiation of the trial and vestibular stimulation will be labeled with respect to the time from trial onset as T1 (i.e., first onset delay, 500 ms) to T7 (i.e., last onset delay, 3500 ms). Thus, a 3 (Rotation: Leftward Rotation, Rightward Rotation, Baseline) × 7 (Time: T1–T7) experimental design was used. The Baseline condition was identical to the unimodal tactile stimulations used for Experiment 1 and served here to assess vestibular effects on tactile detection at different temporal offsets from rotation onset. For consistency with the vestibular–tactile condition, sampling points of the Baseline condition are labeled: T1 (0.5 s from trial onset), T2 (1 s), T3 (1.5 s), T4 (2 s), T5 (2.5 s), T6 (3 s), and T7 (3.5 s). The experimental procedure was identical to Experiment 1 except that no sounds, but vestibular stimuli were presented. Each experimental condition was repeated 10 times to prevent participant's discomfort due to too many rotation stimuli.

Experiment 3: vestibular–audio-tactile interaction

The third experiment quantified the effects of vestibular stimulation on audio-tactile interaction in peri-head space. Based on previous evidence for direction-specific PPS expansion during limb movements (e.g., Brozzoli *et al.*, 2010) and whole-body walking (e.g., Noel *et al.*, 2015a), as well as direction-dependent encoding of visual, auditory, and somatosensory motion stimuli in monkey VIP neurons (Bremmer *et al.*, 2002, 2013; Schlack *et al.*, 2005; Chen *et al.*, 2013), we hypothesized that vestibular stimulation would induce remapping of peri-head space boundaries that depended on the directions of the presented motion stimuli. We tested this prediction in Experiment 3 by combining whole-body Leftward or Rightward Rotation with Leftward or Rightward looming Sound stimulation, collapsed into Congruent trials (i.e., Leftward Rotation and Leftward Sound, Rightward Rotation and Rightward Sound) and Incongruent trials (i.e., Leftward Rotation and Rightward Sound, Rightward Rotation and Leftward Sound, Fig. 1). Thus, a 2 (Congruency: Congruent, Incongruent) × 7 (Distance: D1–D7) experimental design was used. These experimental trials were trimodal (i.e., vestibular–auditory–tactile) in that according to the relative

directions of vestibular and auditory stimuli were defined as Congruent (i.e., Leftward Rotation—Leftward Sound trials, Rightward Rotation—Rightward Sound trials) or Incongruent trials (i.e., Leftward Rotation—Rightward Sound trials, Rightward Rotation—Leftward Sound trials). The experimental procedure and number of repetitions per onset delay were identical to Experiment 2.

The sound-distance estimation task of Experiment 3 had a similar procedure and number of trial repetitions as used in Experiment 1, except for the following differences. A 2 (Congruency: Congruent, Incongruent) × 7 (Distance: D1–D7) experimental design was used, where all trials consisted of concurrent presentation of vestibular (Leftward or Rightward Rotation), auditory (Leftward or Rightward Sound) and tactile stimulation (D1–D7)—same stimuli as used in the audio-tactile interaction task. After stimulus presentation a polar plot was shown consisting of five circles of different diameters centered on a visual representation of a head in top view. Each circle had labels ranging from −100 cm (left and bottom) to +100 cm (top and right) with intermediate labels in steps of 20 cm. Participants were told this display represented a top view of their head and circles represent spatial distances in a transversal plane—that is, top, bottom, left, and right side of the screen corresponded, respectively, to front, back, left, and right space relative to the participant's head. Participants were instructed to move a cursor, initially presented at the center of the display, using the arrow keys of a keyboard to a location within this two-dimensional plane that corresponded to the perceived sound location when they felt the vibro-tactile stimulus. Participants were trained before the experiment to perform their judgments within 4 s, and during the experiment, the position of the cursor after 4 s was taken as the final judgment of the participant. Note that different groups of participants performed the audio-tactile interaction task and the sound-distance estimation task of Experiment 3 (see Participants section). This was a precaution intended to reduce participants' discomfort and risk of inducing nausea by limiting the number of rotation stimuli presented to each participants.

Data analysis

Statistical analyses were performed with JASP software (version 0.8.4, https://jasp-stats.org) and MATLAB (2015b version, The MathWorks) Statistics toolbox, Measures of Effect Size toolbox (version 1.3, authors: H. Hentschke and C. Stüttgen, 2013, https://ch.mathworks.com/matlabcentral/fileexchange/32398-hhentschke-measures-of-effectsize-toolbox?s_tid=srchtitle), and custom scripts. Outlier removal was based on removing all RTs exceeding ±2.5 SD about the individual mean (less than 10% removed for each subject). Condition averages were calculated and subjected to repeated-measures ANOVA with two within-subjects factors (factor labels and levels depended on the specific experimental design, see above). Violation of sphericity (i.e., inequal variances across pairwise differences between conditions) was assessed with Maulchy's test. If violations were detected (i.e., $P < 0.05$), we applied Greenhouse–Geisser correction of degrees of freedom used in the ANOVA. For consistency, we report Greenhouse–Geisser ε coefficients both for corrected and uncorrected results. Note that this correction did not affect statistical significance (alpha threshold of 0.05) as compared to no correction for all effects of this study. Based on statistically significant effects in the main analysis, we performed multiple comparisons using paired-samples *t*-tests (Bonferroni correction for multiple comparisons). We complemented these frequency-based analyses with Bayesian *t*-tests (i.e., implemented in JASP, using Cauchy's probability distribution with 0 center and 0.707 width) to assess whether there was evidence in favor of one over the other hypothesis. In this

context, we computed Bayes factors (BFs; i.e., Bayesian equivalent to a frequentist P-value) proving information about strong (BF > 10) or moderate (BF = 3–10) evidence for the alternative hypothesis (i.e., difference between experimental conditions) over the null hypothesis (i.e., no difference between conditions) and strong (BF < 0.10) or moderate (BF = 0.10–0.33) evidence for the null hypothesis over the alternative hypothesis (Jeffreys, 1963). We estimated the boundary of PPS in audio-tactile (Experiment 1) and vestibular–audio-tactile (Experiment 3) conditions by determining the farthest distance from the body at which Bonferroni-corrected multiple comparisons and BF between subsequent sound-distances showed a significant facilitation of tactile RTs as compared to unimodal Baseline RTs [see (Canzoneri et al., 2012; Serino et al., 2015) for similar approach].

Results

Overall task performance in the audio-tactile interaction task was high across all experiments. There were less than 5% errors (i.e., false alarm) in catch trials and less than 5% omissions (i.e., miss) and early responses in experimental trials for each subject. Thus, extensive analysis is performed on the RT data alone as done previously (Canzoneri et al., 2012; Teneggi et al., 2013; Galli et al., 2015; Noel et al., 2015b; Serino et al., 2015, 2017; Salomon et al., 2017).

Experiment 1: audio-tactile interaction

Analysis of RTs showed a main effect of Distance ($F_{2.30,34.54} = 37.22$, $P < 0.001$, partial $\eta^2 = 0.71$, Greenhouse–Geisser $\varepsilon = 0.38$, Fig. 2) reflected in a decrease of RTs with decreasing sound-distance from D7 ($M = 320$ ms, SD = 51 ms) to D1 ($M = 288$ ms, SD = 49 ms). There was no effect of Sound ($F_{1.18,17.68} = 1.40$, $P = 0.26$, partial $\eta^2 = 0.09$, Greenhouse–Geisser $\varepsilon = 0.59$), thus no differences in average RTs for Leftward Sound ($M = 302$ ms, SD = 47 ms), Rightward Sound ($M = 301$ ms, SD = 46 ms) and Baseline conditions ($M = 306$ ms, SD = 55 ms).

Importantly, however, the Sound × Distance interaction was highly significant ($F_{5.83,87.38} = 8.79$, $P < 0.001$, partial $\eta^2 = 0.37$, Greenhouse–Geisser $\varepsilon = 0.49$). Bonferroni-corrected multiple comparisons showed that tactile RTs were significantly faster when Leftward or Rightward Sounds were close to the body (i.e., at D1 and D2), as compared to the no-sound Baseline (i.e., Rightward Sound vs. Baseline at D2: $t_{15} = -4.08$, $P < 0.05$, corrected, Hedges' $g = -0.34$; Rightward Sound vs. Baseline at D1: $t_{15} = -3.90$, $P < 0.05$, corrected, Hedges' $g = -0.39$; Leftward Sound vs. Baseline at D2: $t_{15} = -3.81$, $P < 0.05$, corrected, Hedges' $g = -0.37$; Leftward Sound vs. Baseline at D1: $t_{15} = -2.71$, $P = 0.016$, uncorrected, Hedges' $g = -0.31$). Tactile RTs did, however, not differ between Sound and Baseline conditions when sounds were further away from the body (i.e., at D3–D7: all P-values > 0.20, uncorrected). Bayesian t-tests showed evidence for a RT difference (as compared to no difference) between Sound and Baseline conditions when sounds were close to the body (i.e., Rightward Sound vs. Baseline at D2: BF = 81.40, i.e., strong evidence; Rightward Sound vs. Baseline at D1: BF = 54.02, i.e., strong evidence; Leftward Sound vs. Baseline at D2: BF = 44.47, i.e., strong evidence; Leftward Sound vs. Baseline at D1: BF = 4.71, i.e., moderate evidence). No evidence for a RT difference as opposed to no difference (and vice versa) was found for sounds further away from the body (i.e., at D3–D7; all BFs = 0.34–0.55). We estimated the boundary of PPS (dashed line in Fig. 2) for the Leftward Sound and Rightward Sound condition by determining the farthest distance from the body at which Bonferroni-corrected multiple comparisons between subsequent sound-distances showed a significant facilitation of tactile RTs as compared to unimodal Baseline RTs [see (Canzoneri et al., 2012; Serino et al., 2015) for similar approach]. This analysis showed RT facilitation up until D2 and a transition from RT difference to no difference between D2 and D3 for both the Rightward Sound (i.e., Rightward Sound minus Baseline RT difference at D2: $M = -20$ ms, SD = 19 ms; at D3: $M = -7$ ms, SD = 24 ms; paired-samples t-test: $t_{15} = 5.17$, $P < 0.05$, corrected, Hedges' $g = 0.58$; Bayesian

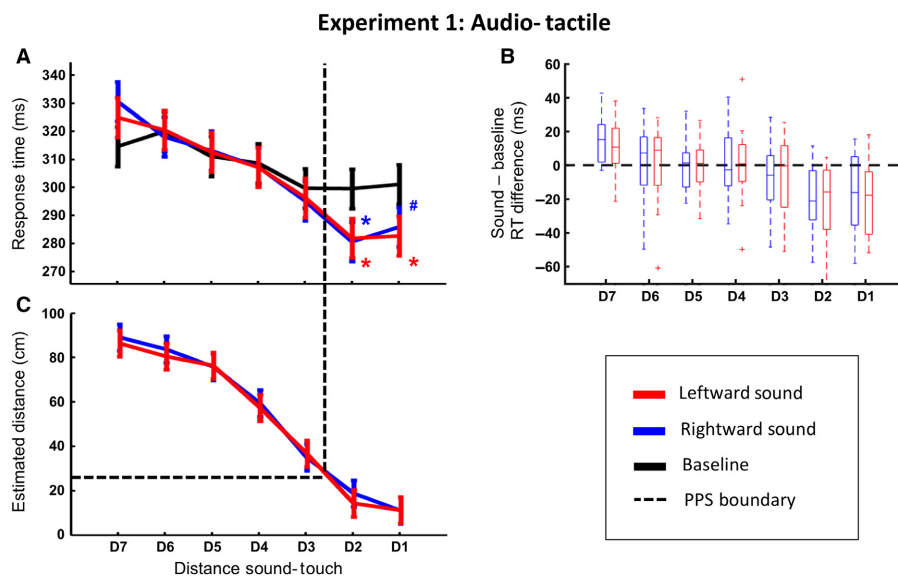
Experiment 1: Audio- tactile

FIG. 2. Results of the audio-tactile experiment (Experiment 1). (A) Group-average ($N = 16$) tactile response times (RTs) as a function of sound-distance (x-axis) and experimental condition. (B) Distance-wise Sound minus Baseline RT differences across subjects for the Leftward (in red) and Rightward (in blue) Sound condition. (C) Group-average sound-distance estimates from the sound-distance estimation task. The dashed line indicates our estimate of the boundary of audio-tactile peripersonal space (PPS) as identified in the audio-tactile interaction task, corresponding to a subjective distance of 25 cm from the head. Stars (*) represent Bonferroni-corrected and hashtag (#) uncorrected ($P < 0.05$) differences between Sound and Baseline condition. Error bars represent 95% confidence intervals from the within-subject variance. [Colour figure can be viewed at wileyonlinelibrary.com].

t-test: BF = 1137.30, i.e., strong evidence for a differences as compared to no difference) and the Leftward Sound condition (i.e., Leftward Sound minus Baseline RT difference at D2: $M = -21$ ms, SD = 22 ms; at D3: $M = -7$ ms, SD = 22 ms; paired-samples *t*-test: $t_{15} = 4.51$, $P < 0.05$, corrected, Hedges' $g = 0.61$; Bayesian *t*-test: BF = 227.79, i.e., strong evidence for a difference as compared to no difference). No significant differences were found for the no-sound Baseline (paired-samples *t*-test between D2 and D3: $t_{15} = 0.85$, $P = 0.41$, uncorrected, Hedges' $g = 0.03$; Bayesian *t*-test: BF = 0.44, i.e., no evidence for a differences as compared to no difference). Thus, we estimated the PPS boundary at a location between D2 and D3.

Next, we analyzed results of the sound-distance estimation task (Fig. 2 lower panel). Statistical analysis using repeated-measures ANOVA revealed a main effect of Distance ($F_{6,90} = 135.13$, $P < 0.001$, partial $\eta^2 = 0.90$), reflecting a time-wise decrease of sound-distance estimates for approaching sounds (e.g., from D7: $M = 88$ cm, SD = 11 cm to D1: $M = 10$ cm, SD = 13 cm). The analysis revealed neither a main effect of Sound ($F_{1,15} = 0.79$, $P = 0.39$, partial $\eta^2 = 0.05$) nor a Sound × Distance interaction ($F_{6,90} = 0.62$, $P = 0.71$, partial $\eta^2 = 0.04$) indicating that subjective sound-distance estimates were highly similar for Leftward looming and Rightward looming Sounds. These findings suggest that our auditory setup was able to induce a clear perception of sounds approaching the body from a distance. Taking into account the results from the sound-distance estimation task, the boundary of PPS, which was estimated between D2–D3 sound-distances based on audio-tactile task results, corresponds to the sound-distance estimate average (i.e., across D2 and D3 estimates) of 25 cm (SD = 13 cm; Fig. 2 lower panel).

Experiment 2: vestibular–tactile interaction

In the second experiment, we assessed the effects of vestibular stimulation on tactile responses in the absence of auditory stimulation. Participants performed timed tactile responses during vestibular stimulation (Leftward Rotation and Rightward Rotation conditions) and a no-rotation condition. Analysis of the tactile detection RTs showed a Time main effect ($F_{6,90} = 18.52$, $P < 0.001$, partial $\eta^2 = 0.55$, Greenhouse–Geisser $\varepsilon = 0.57$) reflecting a decrease of RTs over time (i.e., from T1: $M = 344$ ms, SD = 73 ms; to T7:

$M = 315$ ms, SD = 67 ms). Next, a main effect of Rotation was found ($F_{1.15,17.26} = 11.08$, $P = 0.003$, partial $\eta^2 = 0.43$, Greenhouse–Geisser $\varepsilon = 0.58$), reflecting faster tactile responses during rotation (i.e., Leftward Rotation: $M = 320$ ms, SD = 73 ms; Rightward Rotation: $M = 317$ ms, SD = 71 ms) than during the no-rotation condition (i.e., $M = 334$ ms, SD = 73 ms; Rightward Rotation vs. Baseline, paired-samples *t*-test: $t_{15} = -3.69$, $P < 0.05$, corrected, Hedges' $g = -0.23$; Bayesian *t*-test: BF = 34.05, i.e., strong evidence for a difference as compared to no difference; Leftward Rotation vs. Baseline, paired-samples *t*-test: $t_{15} = -3.06$, $P < 0.05$, corrected, Hedges' $g = -0.19$; Bayesian *t*-test: BF = 9.22, i.e., moderate evidence for a difference as compared to no difference; Fig. 3). There were no differences in tactile RTs between Leftward and Rightward Rotation conditions (paired-samples *t*-test: $t_{15} = 1.80$, $P = 0.09$, uncorrected, Hedges' $g = 0.04$; Bayesian *t*-test: BF = 1.13, i.e., no evidence for a difference as compared to no difference).These results suggest that vestibular stimulation facilitated tactile responses independent of the direction of rotation. Importantly, the analysis revealed no Rotation × Time interaction ($F_{5.10,76.55} = 1.70$, $P = 0.15$, partial $\eta^2 = 0.10$, Greenhouse–Geisser $\varepsilon = 0.43$), suggesting that though vestibular simulation speeded tactile RTs (see above), this effect did not significantly change throughout the duration of the rotational acceleration period.

Experiment 3: vestibular–audio-tactile interaction

We observed in Experiment 1 an auditory facilitation of tactile responses that was independent of the direction of sound movement (Leftward Sound, Rightward Sound) and in Experiment 2 a vestibular facilitation of tactile responses independent of the rotation direction. In Experiment 3, we investigated whether the combination of auditory and vestibular stimulations would induce a congruency-dependent modulation of tactile responses beyond what was found in Experiments 1 and 2. The analysis of audio-tactile interaction task data during rotation showed a main effect of Distance ($F_{1.93,25.06} = 21.12$, $P < 0.001$, partial $\eta^2 = 0.62$, Greenhouse–Geisser $\varepsilon = 0.32$), reflecting an overall decrease of RTs to tactile stimuli as audio-tactile distance decreases. There was no main effect of Congruency ($F_{1,13} = 0.26$, $P = 0.62$, partial $\eta^2 = 0.02$, Greenhouse–Geisser $\varepsilon = 1$), indicating no difference in average RTs between vestibular–auditory Congruent ($M = 362$ ms, SD = 63 ms) and Incongruent
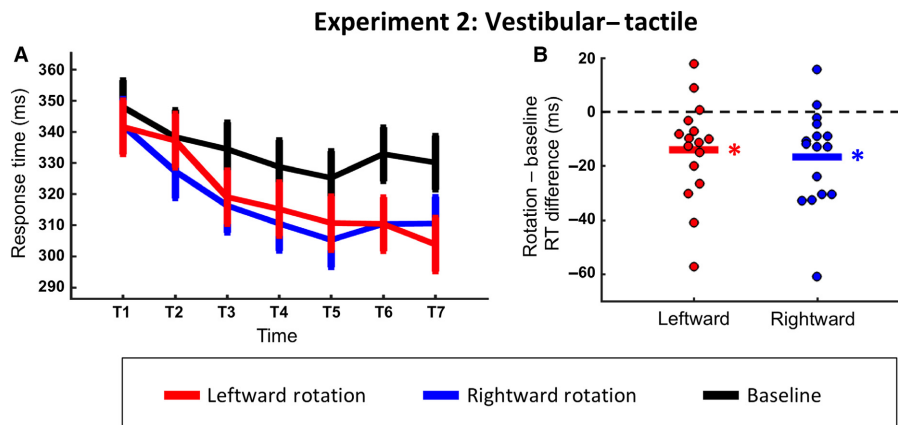
Experiment 2: Vestibular–tactile

FIG. 3. Results of the vestibular–tactile experiment (Experiment 2). (A) Tactile response times (RTs) as a function of time after rotation onset (*x*-axis) and experimental condition. No time-wise *post hoc* comparisons were run (see Results section). Error bars represent 95% confidence intervals from within-subject variance. (B) Rotation – Baseline RT differences for the Leftward Rotation (in red) and Rightward Rotation (in blue) condition. Individual values (circles) and group averages ($N = 16$; solid lines) are shown. The dashed line represents the Baseline level. Stars (*) represent a significant difference at group level ($P < 0.05$, Bonferroni-corrected). [Colour figure can be viewed at wileyonlinelibrary.com].

conditions (M = 363 ms, SD = 58 ms; paired-samples t-test: t_{13} = −0.51, P = 0.62, Hedges' g = 0.02; Bayesian t-test: BF = 0.39, i.e., no evidence for a difference as compared to no difference). Critically, however, a Congruency × Distance interaction was observed ($F_{6,78}$ = 3.10, P = 0.009, partial η^2 = 0.19, Greenhouse–Geisser ε = 0.75). Bonferroni-corrected multiple comparisons showed at D3 significantly faster RTs for the Congruent (M = 345 ms, SD = 61 ms) than the Incongruent condition (M = 358 ms, SD = 64 ms, post hoc paired-samples t-test: t_{13} = 3.23, P < 0.05, corrected, Hedges' g = 0.20; Bayesian t-test: BF = 11.87, i.e., strong evidence for a difference as compared to no difference)—thus at the boundary of PPS as identified in Experiment 1. RT comparisons between Congruent an Incongruent conditions at any other Distance (D1, D2, D4–D7) showed no differences (paired-samples t-tests: all P-values > 0.20, uncorrected, Hedges' g < 0.07; Bayesian t-tests: all BFs = 0.35–0.63, i.e., no evidence for a differences as compared to no difference). To further investigate whether this effect was driven by a specific rotation direction, we conducted separate analysis of the data from Leftward and Rightward Rotations. For each rotation direction, a Congruency × Distance interaction and a post hoc difference between Congruent and Incongruent condition at D3 (P < 0.05, Fig. 4A) were found, similar to the analysis of the data collapsed across Leftward and Rightward Rotation trials. Next, we estimated the boundary of PPS for each condition by performing post hoc

comparison of consecutive sound-distances (i.e., same approach as for Experiment 1). This analysis revealed the farthest distance from the body where tactile RTs significantly differed between subsequent sound-distances was for Congruent trials between D3 (M = 345 ms, SD = 61 ms) and D4 sound-distance (M = 362 ms, 69 ms; paired-samples t-test: t_{13} = 3.04, P < 0.05, corrected, Hedges' g = 0.25; Bayesian t-test: BF = 8.25, i.e., moderate evidence for a difference as compared to no difference) and for Incongruent trials between D2 (M = 343 ms, SD = 67 ms) and D3 (M = 358 ms, SD = 64 ms; paired-samples t-test: t_{13} = 2.78, P < 0.05, corrected, Hedges' g = 0.22; Bayesian t-test: BF = 5.13, i.e., moderate evidence for a difference as compared to no difference). Thus, the boundary of PPS for Congruent trials was located farther away from the body (i.e., D3–D4 Distance) than for Incongruent trials (i.e., D2–D3 Distance). For the sake of maximizing the number of trials, this analysis was based on collapsed data across Leftward–Rightward Rotations and Leftward–Rightward looming Sounds. Thus, to further explore whether this effect was specific to one of the rotation directions, we separately analyzed the data from Leftward Rotations and Rightward Rotations. The results of both analyses were highly similar to the main analysis of the collapsed data (i.e., main effect of Direction and Direction × Congruency interaction; for illustration see Fig. 4A). We also note that the facilitation of tactile RTs (i.e., the proxy of the PPS boundary) for the Incongruent condition was found at the same Distance (i.e., between
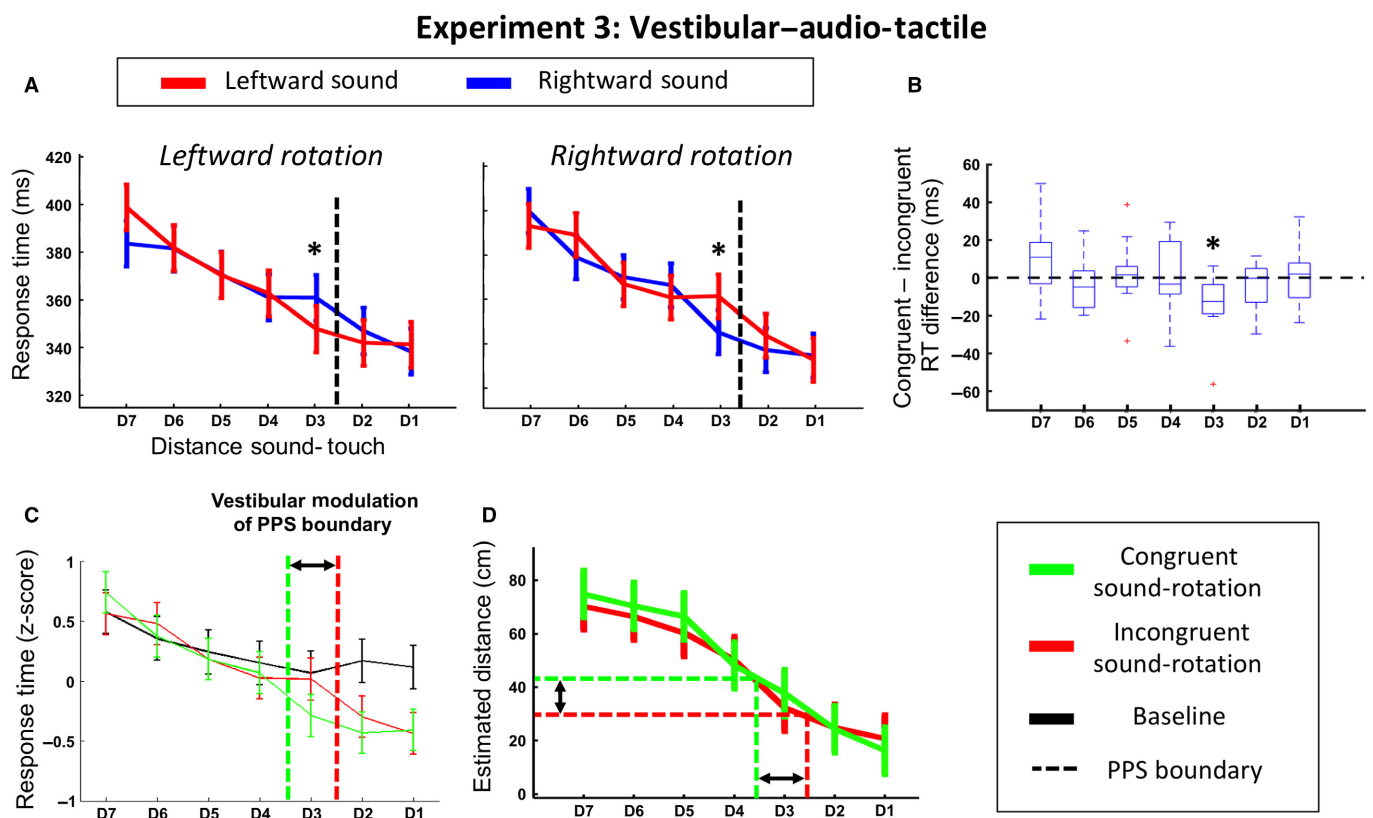
Experiment 3: Vestibular–audio-tactile

FIG. 4. Results of the vestibular–audio-tactile experiment (Experiment 3). (A) Group-average (N = 14) tactile RTs. Results are presented separately for Leftward Rotation condition (left panel) and Rightward Rotation condition (right panel) as a function of sound-distance and sound-direction conditions. The dashed lines represent the sound-distance condition where the PPS boundary was identified in Experiment 1. Note that rotation directions modulated tactile RTs at farther sound distance from the PPS boundary. (B) Distance-wise Congruent minus Incongruent RT differences across subjects. (C) Illustration showing z-normalized RTs from Congruent and Incongruent condition of Experiment 3 superimposed with z-normalized average of the Baseline conditions from Experiment 1 and 2. This figure shows the vestibular facilitation of audio-tactile interaction at farther distance from the body by congruent vestibular–auditory movement directions. (D) Results of sound-distance estimations of Experiment 3. Dashed lines represent the estimated PPS boundaries for the Congruent (green) and Incongruent (red) vestibular–auditory condition. Results show extension of the PPS boundary from 29 to 42 cm. Error bars represent 95% confidence intervals from within-subject variance. Stars (*) represent a significant difference at group level (P < 0.05, Bonferroni-corrected). [Colour figure can be viewed at wileyonlinelibrary.com].

D2 and D3) as for auditory-only stimulation in Experiment 1 (compare Fig. 2 with Fig. 4).

Lastly, we assessed whether combined vestibular–auditory stimulation affected the distance estimates of sounds at tactile stimulus onset in order to clarify whether the PPS boundary modulation from the audio-tactile interaction task was related to a change of the perceived sound distance. Results from the sound-distance estimation task showed that along the lateral axis sound-distance estimates showed a main effect of Distance ($F_{6,60} = 28.78$, $P < 0.001$, partial $\eta^2 = 0.74$), reflecting a decrease of the average sound-distance estimates from D7 ($M = 73$ cm, SD = 18 cm) to D1 ($M = 19$ cm, SD = 15 cm) for looming sounds. No main effect of Congruency ($F_{1,10} = 0.99$, $P = 0.34$, partial $\eta^2 = 0.09$) and no Congruency × Distance interaction were observed ($F_{6,60} = 0.94$, $P = 0.47$, partial $\eta^2 = 0.09$), indicating that sound-distance perception was similar in both vestibular–auditory Congruent and Incongruent conditions. Statistical analysis of the same sound-distance estimates along the front–back axis showed no main effects of Congruency, no main effect of Distance, and no Congruency × Distance interaction (all *F*-values < 1). Thus, whole-body rotation in the present experiments did not systematically alter sound localization along the front–back axis. These results suggest that changes in the location of the PPS boundary were not due to changes of perceived sound-distance [see (Salomon *et al.*, 2017), for a similar argument]. Based on the results from the audio-tactile interaction task, we estimated the boundary of PPS for vestibular–auditory Congruent condition at 42 cm (SD = 15 cm; i.e., average at D3–D4 Distance) and at 29 cm (SD = 14 cm; i.e., average at D2–D3 Distance) for the Incongruent condition. Thus, vestibular stimulation congruent with auditory stimulation (e.g., in the same direction) extended the PPS boundary by about 12 cm.

Discussion

We studied how the vestibular system contributes to the encoding of audio-tactile peri-head space in humans. Extending previous work in static observers, here we quantified multisensory interactions both under static and dynamic whole-body motion conditions and provide evidence for direction-specific remapping of audio-tactile peri-head space by naturalistic vestibular stimulation. In the first experiment, we mapped PPS in static participants along a head-centered binaural axis using a well-established audio-tactile interaction task (Canzoneri *et al.*, 2012; Teneggi *et al.*, 2013; Galli *et al.*, 2015; Noel *et al.*, 2015b; Serino *et al.*, 2015, 2017; Salomon *et al.*, 2017). Results show that the PPS around the head was left–right symmetric and its boundary was situated at a subjective distance of about 25 cm. The second experiment tested for direct effects of vestibular stimulation on tactile detections used for PPS mapping in Experiments 1 and 3. Based on previous studies that demonstrated improved perception of near-threshold somatosensory stimuli at the hands by artificial or natural vestibular stimulation (Bottini *et al.*, 2005; Ferrè *et al.*, 2011a, 2014; Kaliuzhna *et al.*, 2016), we here assessed how above-threshold tactile stimulus detection at the face is affected by whole-body rotation. We found faster tactile responses during vestibular stimulation, in contrast to a resting condition, independent of whether the participant was rotated in a Leftward or Rightward direction and independent of the timing of tactile stimulation with respect to ongoing vestibular stimulation, compatible with previous work (Ferrè *et al.*, 2011b, 2014). Lastly, in the critical experiment (Experiment 3), we assessed the effect of congruent vs. incongruent vestibular–auditory stimulation on the location of the PPS boundary and found an audio-tactile space-dependent congruency effect (i.e., a

trimodal interaction effect). That is, congruent directions of vestibular and auditory stimuli expanded the PPS boundary (as based on a tactile detection task) from approximately 29 cm (with incongruent rotation) to approximately 42 cm (with congruent rotation). Importantly, vestibular stimulation did not affect subjective sound localization of dynamically looming sounds. In the following, we will discuss each effect separately and with respect to previous literature.

Lateral symmetry of peri-head space

The spatial extent of PPS laterally around the head for static participants (Experiment 1) is in line with both early neurophysiological investigations and recent psychophysical studies. More precisely, single cell recordings from neurons encoding for the peri-head space indicated that these neurons have depth restricted receptive fields that extended in space within the range of 10 cm up to 150 cm (Graziano *et al.*, 1994). Using an audio-tactile task similar to the present study, a recent psychophysical study reported the dimension of the peri-head space between 37 and 69 cm (Serino *et al.*, 2015). However, previous behavioral studies delineating the extent of the peri-head space via a multisensory interaction task have done so in the sagittal plane, and hence to the best of our knowledge the present is the first human study to delineate the extension of peri-head space laterally via a multisensory interaction task and to suggest that peri-head space is left–right symmetrical. Indeed Bufacchi *et al.* (2016) did map the representation of the peri-head in three dimensions; however, these authors utilized a hand-eye blink reflex paradigm which did not allow characterization of the multisensory nature of PPS. We note that these authors reported a left–right symmetry in eye blink responses to tactile stimulation at the hand when positioned at various distances from the face (Bufacchi *et al.*, 2016). In addition to left–right symmetry, peri-head space was elongated in an upward vertical direction for upright participants (Bufacchi & Iannetti, 2016; Bufacchi *et al.*, 2016) and this elongation remained oriented in the upward vertical direction even if the participant's head was tilted to one side (Bufacchi & Iannetti, 2016), indicating potential contributions of static vestibular (i.e., otolithic) signals to peri-head space at rest. Thus, the present data show that in static, upright individuals the audio-tactile boundary of peri-head space is left–right symmetric.

General vestibular facilitation of tactile detection

Previous electrophysiological (Fredrickson *et al.*, 1966; Schwarz & Fredrickson, 1971), neuroimaging (Fasold *et al.*, 2002; Ferrè *et al.*, 2012; Mazzola *et al.*, 2014; Pfeiffer *et al.*, 2016), and psychophysical (Vallar *et al.*, 1990; Bottini *et al.*, 1995, 2005; Ferrè *et al.*, 2011a, 2013, 2014; Kaliuzhna *et al.*, 2016) studies provided compelling evidence for direct vestibular–somatosensory interaction in animals and humans. However, in these studies mostly artificial vestibular stimulation (e.g., caloric or galvanic vestibular stimulation) and near-threshold somatosensory stimulation at the hands were used. Here, we tested whether a similar effect occurs for above-threshold stimuli applied to the face during natural vestibular stimulation, probing the dependence of vestibular–somatosensory interaction on stimulus type. In addition, we tested for confounding effects imposed by potential differences in vestibular–somatosensory interaction across rotation directions and sampling points of tactile stimulation in our experimental design, before indexing the audio-tactile–vestibular trimodal interaction in Experiment 3. Thus in Experiment 2, we assessed how passive whole-body rotation affected speeded tactile detections on the forehead. We observed

generally faster tactile RTs during vestibular stimulation than during static periods, suggesting that our paradigm indeed induced vestibular facilitation of somatosensory detection. With respect to previous psychophysical studies mentioned above, our results suggest that vestibular stimulation generally facilitates tactile processing, independent of the specific stimulus type and experimental task chosen. Most importantly for the purpose of the present study, the vestibular facilitation effect observed in Experiment 2 was independent of the direction of the rotation—similar to (Ferrè *et al.*, 2014) who used near-threshold stimulation at the left or right fingertip—and crucially did not change over the duration of the rotation stimulus until tactile stimulus onset (i.e., absence of a Rotation × Time interaction). Given previous evidence from electrophysiological studies in animals about direct thalamo-cortical vestibular projections to somatosensory cortex (Buttner & Buettner, 1978; Akbarian *et al.*, 1994) and evidence from human EEG studies about early vestibular effects on somatosensory evoked potentials in the 30–70 ms post-stimulus range (Ferrè *et al.*, 2012; Pfeiffer *et al.*, 2016), the rotation direction-unspecific facilitation effect in the present study may reflect a general vestibular modulation of neural excitability of early somatosensory cortical regions independent of vestibular stimulus type and duration—which are important factors in Experiment 3.

Vestibular-mediated enlargement of audio-tactile peri-head space

In the critical Experiment 3, we found a rotation direction-dependent modulation of the peri-head boundary that extended beyond the boundary of PPS as measured in the audio-tactile Baseline conditions (25 cm in Experiment 1). Thus, incongruence of vestibular and auditory motion direction resulted in a PPS boundary estimate (29 cm) that was very similar to the resting condition (25 cm in Experiment 1), whereas congruent vestibular–auditory stimulations induced an enlargement of the PPS boundary to approximately 42 cm. This effect cannot be explained auditory–tactile (Experiment 1) or vestibular–tactile bimodal interactions (Experiment 2) that were highly similar for Leftward and Rightward stimuli, but instead seems to reflect a trimodal interaction of dynamic vestibular and auditory stimuli and static somatosensory stimulus presentation (Bremmer *et al.*, 2001; Ferrè *et al.*, 2014; Kaliuzhna *et al.*, 2016). The present results are unlikely related to vestibular changes in perceived sound location, as documented in previous work for static sounds (Lewald & Karnath, 2001), because in our study sound location estimates for Leftward or Rightward dynamic sounds did not differ between congruent and incongruent vestibular–auditory motion directions. Moreover, the results we observed were not reflected in a general facilitation of tactile RTs, but were specific to the D2–D4 sound-distance range, where the boundary of PPS was identified in Experiment 1. Indeed, PPS boundary changes that depend on the direction of constant gravitational vestibular input have been observed before by (Bufacchi & Iannetti, 2016). Here we extend these results by demonstrating the contribution of rotational vestibular signals to dynamic remapping of PPS. Importantly, we also demonstrate a distance- and direction-specific trimodal interaction, evidencing that the vestibular system does not only play an important role in spatial orientation and self-motion processing, but, via interaction with exteroceptive sensory signals (e.g., auditory, somatosensory), also contributes to an updated delineation of the external space into near or far from the body. Key neurophysiological findings are compatible with these vestibular–multisensory effects. Indeed, the core brain regions of PPS—area VIP and ventral premotor cortex (Graziano *et al.*, 1994; di Pellegrino *et al.*, 1997)—

receive prominent vestibular, somatosensory, auditory, and visual inputs (Bremmer *et al.*, 2001; Schlack *et al.*, 2005; Chen *et al.*, 2013). Furthermore, direction-dependent tuning of multimodal neurons has been demonstrated in VIP neurons (Bremmer *et al.*, 2002, 2013; Schlack *et al.*, 2002), as dynamic visual and somatosensory stimuli at or close to the head induced the strongest neuronal response when monkeys are rotated in the same direction as the stimulus motion (Bremmer *et al.*, 2002). We suggest that the neurophysiological substrate for our reported behavioral effects are rooted within homologues areas of such PPS network in humans, and in particular the VIP region (Guipponi *et al.*, 2013).

Functional role of vestibular-mediated remapping of space

The PPS has been demonstrated to remap—most notoriously enlarge—as a function of an array of different factors in the context of goal-directed actions. For example, this has been demonstrated for hand PPS as a function of movement (Graziano & Cooke, 2006; Noel *et al.*, 2015a) or tool use (Iriki *et al.*, 1996; Maravita & Iriki, 2004). Recent psychophysical work has suggested a similar effect in humans and as a consequence of arm utilization (Makin *et al.*, 2009; Brozzoli *et al.*, 2010; Canzoneri *et al.*, 2013). Interestingly, Noel *et al.* (2015a) showed that PPS may be remapped as a consequence of whole-body movement, as in the case of walking. Thus, while it may be argued that motor and/or proprioceptive signals may be critical information for the remapping of PPS in case of arm movement, the present data show that vestibular signals may play an important role for a general and whole-body remapping of PPS.

Beyond its contribution to whole-body actions, vestibular remapping of PPS is in line with recent proposals (Blanke, 2012; Pfeiffer *et al.*, 2014b; Blanke *et al.*, 2015) and empirical findings (Noel *et al.*, 2015b; Salomon *et al.*, 2017) suggesting that PPS representation may be important for ego-centric processing and self-consciousness. Indeed, PPS appears to index the experienced position of the bodily self, as compared to the actual position of a person's body (Noel *et al.*, 2015b; Salomon *et al.*, 2017). Self-location, as indexed via PPS or other measures (e.g., Pfeiffer *et al.*, 2013, 2014a), is one important component of bodily self-consciousness (Blanke & Metzinger, 2009). Another cornerstone of bodily self-consciousness is the first-person perspective, that is, a conscious experience of facing the world from a given, embodied location and with a give direction, which is thought to depend on multisensory-vestibular information [(Ionta *et al.*, 2011; Pfeiffer *et al.*, 2013, 2014a), see (Pfeiffer *et al.*, 2014b) for a review]. Hence, the demonstration that PPS representation, the space of the bodily self (Noel *et al.*, 2015b) is molded by an array of sensory modalities including the vestibular system, may represent an important avenue of confluence between the study of self-location and first-person perspective (Blanke, 2012; Pfeiffer *et al.*, 2014b; Blanke *et al.*, 2015; Pfeiffer, 2015).

Limitations and outlook

It should be noted that the rotational vestibular and linear auditory stimuli used here did not correspond in terms of the movement axis (i.e., rotation vs. translation). Thus, the PPS boundary modulation observed here cannot be directly interpreted as rotation, translation, or expansion, but may be the result of a combination of these. We also note that our results were based on vestibular stimulation induced by passive movements known to be processed differently by the brain (already at the level of the vestibular nuclei) than vestibular input resulting from active movements (see Cullen & Roy, 2004 for a review). In addition, active head movements are

often accompanied by additional multisensory cues (i.e., proprioceptive, tactile, visual) that were absent or largely attenuated in our experimental setup. These considerations limit the interpretability of our results in terms of vestibular signals and PPS under ecologically valid conditions frequently resulting from body movements, calling for future vestibular PPS studies under more naturalistic conditions.

Conflict of interest

We declare no conflicts of interest.

Data accessibility

The data are available on request by the authors.

Author contributions

CP, JPN, AS, and OB designed the study and wrote the manuscript. CP developed the experimental protocol, recorded, and analyzed the data.

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