Anisotropy of lateral peripersonal space is linked to handedness

Lise Hobeika[1*], Isabelle Viaud-Delmon[1] & Marine Taffou[1,2]

[1]Sorbonne Université, CNRS, IRCAM, Sciences et Technologies de la Musique et du Son, UMR 9912, F-75004 Paris, France
[2]Institut de Recherche Biomédicale des Armées, 91220 Brétigny-sur-Orge, France

*Corresponding author
Email: lise.hobeika@gmail.com

Abstract

The space immediately surrounding our bodies, i.e. peripersonal space (PPS), is a critical area for the interaction with the external world, be it to deal with imminent threat or to attain objects of interest. In the brain, a dedicated system codes PPS in motor terms for the purpose of action. Yet, humans have asymmetric motor abilities: the dominant hand has an advantage in term of movements' precision and reaction time. Furthermore, spatial attention is asymmetric and seems to be linked to a right hemispheric dominance for spatial processing. Here, we tested whether handedness and attentional asymmetries impact the detection of a tactile stimulus when an irrelevant auditory stimulus is looming towards the individual from the right or left hemispace. We examined the distance at which sound started speeding up tactile detection to estimate the morphometry of peri-trunk PPS. Our results show that right-handers' PPS is larger in the left than in the right hemispace whereas left-handers' PPS is symmetric. The expansion of right-handers' PPS on the side of the non-dominant hand is coherent with a protective function of PPS. Left-handers' symmetric PPS can be related to the symmetric request of their motor abilities induced by living in a right-handers' world. These findings reveal that PPS is not uniform and suggest that general mechanisms of spatial processing as well as motor skills could play a role in the representation of peri-trunk PPS.

Keywords: multisensory integration, audio-tactile integration, 3D sound, spatial perception, pseudoneglect, auditory perception

1   Introduction

Proxemics (Hall 1966), i.e. the study of how humans use space, is of particular importance to understand human behavior and interactions with other individuals. The area around the body, called peripersonal space (PPS), is the space through which individuals interact with the external world (Rizzolatti et al. 1997). PPS is opposed to the more distant extra-personal space. Studies on monkeys, healthy and brain-damaged humans brought converging evidence that this PPS is coded in the brain separately from the extra-personal space (e.g. Halligan and Marshall 1991; Graziano and Gross 1993; Cowey et al. 1994; Làdavas and Farnè 2004). A fronto-parietal neural circuit is specialized in coding and integrating both the tactile stimulations on the body and the visual and auditory sensory events occurring near the body (Bremmer et al. 2001; Graziano and Cooke 2006; Serino et al. 2011). At the behavioral level, stronger multisensory interactions can be observed in the space surrounding the body (e.g. Spence et al. 2004a, b; Graziano and Cooke 2006). This multisensory coding dedicated to PPS is thought to contribute to the possibility to act rapidly and precisely around the body, to defend the self (Graziano and Cooke 2006) or to attain objects of interest (Rizzolatti et al. 1997). PPS is coded as a space of action (Iachini et al. 2014; Finisguerra et al. 2015; Serino 2016).

One behavioral method that allows evaluating the location of the boundaries between PPS and the extrapersonal space in humans is based on the multisensory quality of PPS. Research on multisensory perception has shown that when perceiving different sensory stimuli, we automatically integrate them into a unified percept provided that they are close in time and in space (e.g. Bertelson and Aschersleben 1998; Bresciani et al. 2006; see Alais et al. 2010 for a review). Several behavioral studies have examined the spatial determinants of the multisensory interaction between two different sensory events. They observed that a visual or an auditory stimulus interacts more strongly with a tactile stimulus when it is positioned close to the latter i.e. close to the body (e.g. Spence et al. 2004a; Farnè et al. 2007; Serino et al. 2007, 2011; Bassolino et al. 2010; Aspell et al. 2010). Particularly, studies examining tactile detection times in the presence of an irrelevant auditory stimulus report a facilitation of detection when the auditory stimulus is located near – but not far – from the body (Serino et al. 2007, 2011; Bassolino et al. 2010). When presented close to the body, the auditory event is integrated with the tactile stimulus and tactile reaction times are sped up.

On the basis that this multisensory integration boost should be impacted by the distance between the body and the external stimulation, Canzoneri and colleagues developed an audiotactile task to measure the location of PPS boundaries. In this task, participants have to detect a tactile stimulus on their body while a task-irrelevant sound is looming toward them. The tactile stimulus is delivered at different times from sound onset so that the sound source is perceived at different distances from participants' body when they perform the tactile detection. They assume that the distance at which the surrounding auditory stimulus starts to be integrated with the tactile stimulus located on the body reflects the boundaries of PPS (Canzoneri et al. 2012). Thus, they search for the critical distance at which the sound starts to boost tactile reaction times as a proxy of PPS boundaries.

The field of research on PPS is growing and recent studies have shown that PPS boundaries are flexible and can be modulated by changes in motor abilities. The size of PPS has already been demonstrated as being impacted by participants' body schema (Maravita and Iriki 2004), by the size of the arms (Longo and Lourenco 2007), and also by the integration of a tool in the body schema (Longo and Lourenco 2006; Farnè et al. 2007; Bassolino et al. 2010; Canzoneri et al. 2013b). Moreover, obstructing movement also modulates PPS. It has been evidenced that wrist weight (Lourenco and Longo 2009), immobilization of the arm (Bassolino et al. 2014) as well as mild immobilization of the body with chin-rest (Vagnoni et al. 2017) reduce PPS size.

Beyond physical body structure and physical constraint, another factor that influences motor abilities is handedness. Human motor abilities are inherently asymmetric. The vast majority of the population has a preference in hand use (Annett 1970; Nicholls et al. 2013) and using the dominant hand is advantageous in terms of rapidity (Kerr et al. 1963) and precision (Flowers 1975) of movement in space. To date, even though most of previous studies examined the size and the plasticity of PPS around the hand (Farnè et al. 2005; Makin et al. 2007; Brozzoli et al. 2011; Gentile et al. 2011; Serino 2016), the question of the possible link between hand use preference and PPS implementation has not been raised. Bassolino and colleagues (2014) studied specifically limb overuse induced by temporarily immobilizing one of the limbs. Their findings suggest that PPS is not modified around the free and overused limb and that PPS representation is shaped as a function of the dimension of the acting space (Bassolino et al. 2014). Therefore, it seems that the preferential use of one hand linked to handedness should not impact PPS, at least after development is complete. However, Le Bigot and Grosjean have shown that visual processing in peri-hand space seems to be determined by the different ways in which left- and right-handers use their hands (Le Bigot and Grosjean 2012). According to their functional hypothesis, sensory detection could be enhanced where action is more likely to occur, i.e., on the side of the dominant hand.

Furthermore, the spatial constraints on multisensory integration might not be solely linked to the distance between the body and the source of the sensory stimulation. Multisensory interactions could be modulated by the hemispace in which the auditory stimulus is presented. Several brain imaging studies suggest that the left and right auditory hemispaces are coded asymmetrically, with a rightward attentional bias linked to a right-hemisphere dominance for spatial processing (see Krumbholz et al. 2005, 2007; Dietz et al. 2014). This bias is influenced by handedness: right-handed subjects are more biased towards the right hemispace (Savel 2009; Railo et al. 2011).

The aim of the present study is to investigate the implementation of PPS, taking into account the general asymmetries of human spatial processing linked to handedness and to the dominance of the right cerebral hemisphere in deploying spatial attention (Heilman and Van Den Abell 1979; Reuter-Lorenz et al. 1990). Specifically, we studied whether handedness and hemispatial processing impact the lateral boundaries of PPS around the trunk.

We adapted Canzoneri and colleagues' audiotactile task (Canzoneri et al. 2012) in order to estimate right-handers' and left-handers' peri-trunk PPS size in the left and in the right hemispace. Participants performed a speeded tactile detection task while irrelevant sounds were looming toward them from the frontal hemifield, either from the left or the right hemispace. Participants received tactile stimuli on their hand. Previous experiments have shown that when the hand is placed on the midline and near the trunk, the peri-hand PPS is encapsulated in the peri-trunk PPS so that the former is indistinguishable from the latter (Serino et al. 2015). Thus, in order to measure peri-trunk PPS boundaries (and not peri-hand PPS boundaries), we instructed our participants to keep their hands aligned with their mid-sagittal plane and in contact with their trunk. Tactile stimuli were delivered at different delays from sound onset. Hence, participants perceived the sound at different distances from their body when they processed the tactile stimulus. As the delay increased, the looming sound was perceived as closer. As a proxy of the lateral boundaries of peri-trunk PPS, we pinpointed in the left and in the right hemispaces the distance from participants' body at which the sound started to boost tactile detection.

2   Materials and Methods

2.1   Participants

Fifty-six healthy individuals (29 females; age: $M \pm SD = 26.63 \pm 4.41$, range 18-37) with normal audition and touch participated in the study. Twenty-eight individuals were right-handed (RH) and composed the RH group (12 females; age: $M \pm SD = 23.57 \pm 4.22$, range 18-34), the other 28 individuals were left-handed (LH) and composed the LH group (17 females; age: $M \pm SD = 25.68 \pm 4.41$, range 19-37). Samples sizes were decided a priori based on previous work examining PPS boundaries with the same audiotactile paradigm (Canzoneri et al. 2012; Taffou and Viaud-Delmon 2014; Serino et al. 2015). Participants' handedness was verified with a questionnaire measuring skilled hand preference. The scores on this questionnaire, called the Flinders Handedness survey (FLANDERS) (Nicholls et al. 2013), range from -10 for strong left-handed individuals to +10 for strong right-handed individuals. Five participants were excluded from the analysis due to missing data on the FLANDERS questionnaire. Two participants were excluded from the analysis as they scored as mixed-handed in the FLANDERS questionnaire (+1 and +4). The analysis were performed on the remaining 49 participants (21 RH and 28 LH). The FLANDERS scores of the 21 remaining participants of the RH group ranged from 6 to 10 ($M \pm SD = 9.4 \pm 1.1$, the scores of five RH participants were missing). The FLANDERS scores of the 28 participants in the LH group ranged from -10 to -6 ($M \pm SD = -9.2 \pm 1.2$). All participants provided a written informed consent prior to the experiment, which was approved by the Institutional Review Board of INSERM (IRB00003888). The experiment was performed in accordance with the committee's guidelines. Participants received a financial compensation of 10€/hour for their participation.

2.2   Materials

We used a modified version of Canzoneri et al.'s audiotactile interaction task (Canzoneri et al. 2012). Participants sat on a chair with their hands palms-down on a table. Both of their hands were aligned with their mid-sagittal plane and in contact with their trunk. Participants were instructed to fix a visual target located at 65cm in front of them.

Auditory stimuli were presented through Beyer Dynamic DT770 headphones. The auditory stimulus was a sound of bubbling water (32 bits, 44100 Hz digitization), processed through binaural rendering using non-individual head related transfer functions (HRTF) of the LISTEN HRTF database (http://recherche.ircam.fr/equipes/salles/listen/). With this procedure, the virtual sound source location can be manipulated by rendering accurate auditory cues such as frequency spectrum, intensity, and inter-aural differences.

The tactile stimulus was a vibratory stimulus delivered by means of a small loudspeaker on the palmar surface of the non-dominant hand index finger of participants (left for RH, right for LH). A sinusoid signal was displayed for 20ms at 250 Hz. With these parameters, the vibration of the loudspeaker was perceivable, but the sound was inaudible. A PC running Presentation® software was used to control the presentation of the stimuli and to record the responses.

2.3   Design and procedure

Participants were asked to place the index finger of their non-dominant hand (left for RH, right for LH) on the vibrator and to press a button with their other index finger each time a tactile stimulus was detected. A black fabric hid participants' hands. An auditory stimulus was presented for 3000ms for each trial. The sound source approached from the front hemi-field, either from the right (-60°) or from the left hemispace (60°), with a spatial location varying
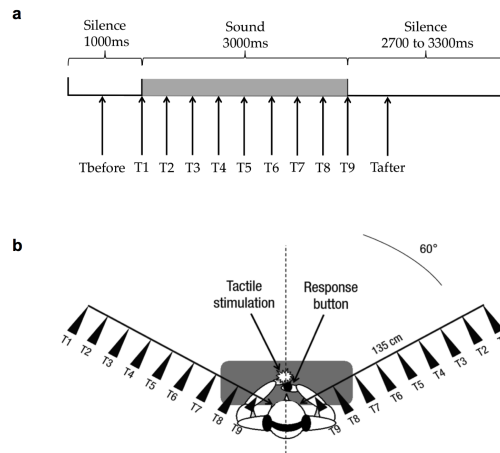
Fig. 1 Experimental paradigm. (a) Description of a trial. **(b)** The figure depicts a right-handed participant in the experimental setup. Participants responded with their dominant hand to a tactile stimulus delivered on their other hand while task-irrelevant sounds approached them from the frontal hemi-field, either in the left or in the right hemispace. On each trial, tactile stimulation was delivered at one among eleven possible delays from sound onset (Tbefore, T1, T2, T3, T4, T5, T6, T7, T8, T9, Tafter). Depending on the temporal condition, the looming sound source was positioned at different distances from the participants' body when the tactile stimulation was processed (from the farthest distance at T1 to the closest distance at T9). The looming sound directions are indicated with black arrows and the sound source location at the different delays are indicated with black triangles.

from 135 to 20 cm from the center of the participant's head. The sound velocity was 38.33 cm.s^{-1}. The auditory stimulus was preceded by 1000ms of silence. A period of silence, with a duration varying between 2700 and 3300ms, also occurred after the offset of the sound.

In 91.7% of the trials, a tactile stimulus was presented along with the auditory stimuli. The remaining 8.3% trials were catch trials with auditory stimulation only. Participants were instructed to ignore the auditory stimuli and to press a button with the index of their dominant hand (right for RH, left for LH) as quickly as possible each time a tactile stimulus was detected. They were asked to emphasize speed, but to refrain from anticipating. Reaction times (RTs) were measured.

Vibratory tactile stimuli were delivered at different delays from sound onset. With this procedure, the tactile stimuli were processed when the sound source was perceived at varying distances from participants' bodies. Given that a looming auditory stimulus speeds up the processing of a tactile stimulus as long as it is perceived near the body, i.e. within PPS (Canzoneri et al. 2012), we considered the distance at which sounds started to boost tactile RTs as a proxy of PPS boundaries.

Temporal delays for the tactile stimulus were set as follows: T1 was a tactile stimulation administered simultaneously with the sound onset; T2 at 375 ms from sound onset; T3 at 750 ms from sound onset; T4 at 1125 ms from sound onset; T5 at 1500 ms from sound onset, T6 at 1875 ms from sound onset; T7 at 2250 ms from sound onset; T8 at 2625 ms from sound onset and T9 at 3000 ms from sound onset. Thus, tactile stimulation occurred when the sound source was perceived at different locations with respect to the body, i.e. far from the body at low temporal delays and close to the body at high temporal delays (see Fig. 1). Moreover, in order to measure RTs in the unimodal tactile condition (without any sound), tactile stimulation was also delivered during the silent periods, preceding or following sound administration, namely at −650ms (Tbefore) and at 3650ms (Tafter) from sound onset.

After a small training block aiming at acquainting participants with the task, we checked, by asking participants, that they actually perceived the changes in sound source distance and not just loudness changes before starting the experimental blocks. The total experimental test consisted of a random combination of ten target stimuli in each of the 22 conditions. The factors were: DELAY (eleven levels: Tbefore, T1, T2, T3, T4, T5, T6, T7, T8, T9 and Tafter), HEMISPACE (two levels: left/right). There were a total of 220 trials with a tactile target, randomly intermingled with 20 catch trials. Trials were equally divided in 5 blocks of 48 trials, lasting about 5 min each.

3 Results

The analyses were conducted on 49 participants (21 RH and 28 LH). We first excluded trials with outlier tactile RTs. Given that it is well known that the distribution of RTs is not normal (Luce 1986; Ulrich and Miller 1993), we used the natural logarithm transformation of RTs (ln) in order to trim outlier RTs from the analyses. For each participant

and each DELAY condition separately, we calculated the mean and the standard deviation of our transformed data. Ln(RTs) were considered outliers if they exceeded more than two standard deviations from the mean ln(RTs) and trimmed from the analyses (4.51% of trials). The remaining data were averaged for each participant, for each HEMISPACE condition and each DELAY condition and the means we obtained were transformed back with an exponential function.

We then conducted an ANOVA on the mean RTs with the within-subjects DELAY (11 levels: Tbefore, T1, T2, T3, T4, T5, T6, T7, T8, T9, Tafter) in order to verify that the experimental paradigm had worked, i.e. that the task-irrelevant sound interacted with tactile processing. The main effect of DELAY was significant ($F(10,480) = 77.30$, $p < 0.001$, $\eta_p^2 = 0.617$) suggesting that RTs were influenced by the temporal delay of tactile stimulation delivery from sound onset. RTs in the unimodal trials at the delay Tafter ($M \pm SEM = 332.4 \pm 6.8$) were significantly faster than RTs in the unimodal trials at the delay Tbefore ($M \pm SEM = 369.1 \pm 7.0$) (Post-hoc Newman-Keuls' test: $p < 0.001$). However, given that RTs at Tafter were significantly slower than RTs at T7 ($M \pm SEM = 316.5 \pm 6.5$), T8 ($M \pm SEM = 304.6 \pm 5.8$) and T9 ($M \pm SEM = 300.1 \pm 5.5$) (Post-hoc Newman-Keuls' test: $p < 0.001$ in all cases), we can exclude the possibility that participants were faster at late delays solely because of the increasing probability of receiving a tactile stimulation along trials (Kandula et al. 2017). RTs in the unimodal trials at Tbefore were significantly slower than RTs in bimodal trials at T2, T3, T4, T5, T6, T7, T8, and T9 (Post-hoc Newman-Keuls' test: $p < 0.001$ in all cases) however it was not the case when the tactile stimulation synchronously occurred with sound onset (at the temporal delay T1). RTs in the bimodal trials at T1 ($M \pm SEM = 369.7 \pm 7.0$) did not significantly differ from RTs in the unimodal trials at Tbefore (Post-hoc Newman-Keuls' test: $p = 0.88$). RTs at T1 were also significantly slower than RTs in all the other bimodal trials (T2, T3, T4, T5, T6, T7, T8, and T9; Post-hoc Newman-Keuls' test: $p < 0.001$ in all cases). These results show that the sound did interact with tactile RTs except when the tactile stimulation occurred at T1. When the tactile stimulus was delivered synchronously with sound onset, the latter had no impact on tactile RTs. This suggests that sound was not processed when the tactile stimulation occurred at this delay. Consequently, tactile RTs at T1 were excluded from the rest of the analyses.

We then performed an ANOVA on the mean RTs measured in the bimodal trials only, with the between-subjects factor HANDEDNESS (2 levels: RH/LH) and the within-subjects factors HEMISPACE (2 levels: Left/Right) and DELAY (8 levels: T2, T3, T4, T5, T6, T7, T8, T9). The ANOVA revealed a significant three-way interaction between HANDEDNESS, HEMISPACE and DELAY factors [$F(7,239) = 3.865$, $p < 0.001$, $\eta_p^2 = 0.076$]. The ANOVA also revealed a significant main effect of the factor DELAY [$F(7,329) = 56.50$, $p < 0.001$, $\eta_p^2 = 0.546$], and a significant interaction of the factors HEMISPACE * DELAY [$F(7,329) = 3.478$, $p < 0.01$, $\eta_p^2 = 0.069$]. The others factors and interactions were not significant: there was no significant main effect of HEMISPACE ($p = 0.61$), of HANDEDNESS ($p = 0.52$) and no significant interaction of HANDEDNESS * HEMISPACE ($p = 0.24$) or HANDEDNESS * DELAY ($p = 0.40$). To understand the meaning of the significant three-way interaction, we then conducted two separated ANOVA for the RH and the LH groups with the within-subjects factors HEMISPACE (2 levels: Left/Right) and DELAY (8 levels: T2, T3, T4, T5, T6, T7, T8, T9).

In the RH group, the ANOVA revealed a significant effect of DELAY [$F(7,140) = 23.82$, $p < 0.001$, $\eta_p^2 = 0.544$]. The effect of the two-way interaction HEMISPACE * DELAY was also significant [$F(7,140) = 4.82$, $p < 0.001$, $\eta_p^2 = 0.194$], suggesting that RTs were differently modulated by the temporal delay of tactile stimulation delivery from sound onset and as a function of whether the sound came from the left or right hemispace. No significant effect of HEMISPACE ($p = 0.52$) was found. As shown in the left graph of Fig. 2a, when the sound came from the left hemispace, the first significant decrease of RH participants' RTs occurred when the tactile stimulus was delivered at T5. RH participants' RTs were significantly faster when the tactile stimulus occurred at T5 compared to when the tactile stimulus occurred at T4 (Post-hoc Newman-Keuls' test: $p < 0.01$). RTs further decreased at the later delays. RH participants' RTs were significantly faster when the tactile stimulus occurred at T7 than at T6 (Post-hoc Newman-Keuls' test: $p < 0.001$) and RTs were also significantly faster when the tactile stimulus occurred at T9 than at T8 (Post-hoc Newman-Keuls' test: $p < 0.05$). Moreover, RTs were significantly faster when the tactile stimulus was delivered at T5, T6, T7, T8 and T9 as compared to when the tactile stimulus was delivered at T2, T3 and T4 (Post-hoc Newman-Keuls' test: $p < 0.002$ in all cases). As shown in the right graph of Fig. 2a, when the sound came from the right, the first significant decrease of RH participants' RTs occurred when the tactile stimulus was delivered at T7. RH participants' RTs were significantly faster when the tactile stimulus occurred at T7 compared to when the tactile stimulus occurred at T6 (Post-hoc Newman-Keuls' test: $p > 0.01$). RTs further decreased at the later delay T8. RH participants' RTs were significantly faster when the tactile stimulus occurred at T8 than at T7 (Post-hoc Newman-Keuls' test: $p < 0.001$). Moreover, RTs were significantly faster when the tactile stimulus was delivered at T7, T8 and T9 as compared to when the tactile stimulus was delivered at T2, T3, T4, T5 and T6 (Post-hoc Newman-Keuls' test: $p < 0.002$ in all cases). These results suggest that, in the RH group, the sound began to boost tactile RTs at a farther distance in the left hemispace than in the right hemispace.

In the LH group, the ANOVA revealed a significant effect of DELAY [$F(7,189) = 32.97$, $p < 0.001$, $\eta_p^2 = 0.550$]. No significant effect of HEMISPACE ($p = 0.52$) or of the two-way interaction HEMISPACE * DELAY ($p = 0.23$) were found. As shown in Fig. 2b, both when the sound came from the left and the right hemispaces, the first significant decrease of LH participants' RTs occurred when the tactile stimulus was delivered at T7. LH participants'
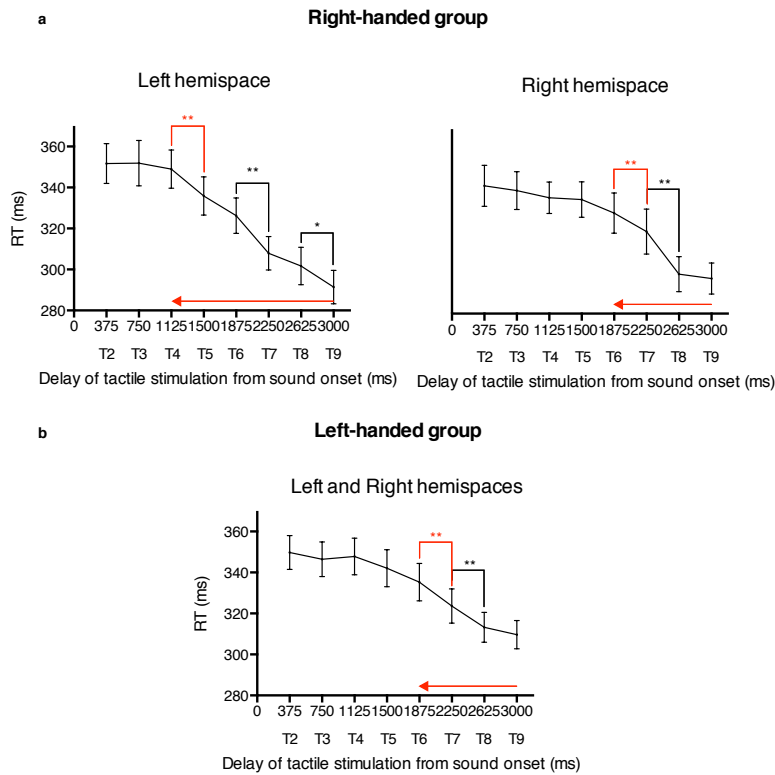
Fig. 2 Audiotactile test results. Two groups of participants – right-handers (RH) and left-handers (LH) – performed the audiotactile test. They responded to a tactile stimulation while a task-irrelevant sound was looming toward them from the left or right hemispace. This figure reports the mean tactile reaction time (± SEM) for (**a**) the RH group (n=21) and for (**b**) the LH group (n=28) as a function of the delay of tactile stimulation delivery from sound onset (T2, T3, T4, T5, T6, T7, T8, T9). In the LH group, the data in the left and right hemispaces are combined because they were merged in the post-hoc analyses given that the effect of the interaction between hemispace and delay of tactile stimulation on reaction times (RTs) was not significant. The distance of the sound source from participants' body when tactile stimulation occurred was the farthest at T2 (the shortest time between tactile stimulation and sound onset) and the closest distance at T9 (the longest time between tactile stimulation and sound onset). Asterisks indicate significant differences in RTs between temporal delay conditions (* p < .05, ** p < .01). The significant decrease of RTs corresponding to the temporal delay, at which sound starts to boost tactile processing is indicated by means of red asterisks. The red arrows illustrate the corresponding relative distance of the sound source from participants' body when it started boosting tactile RTs. While in the RH group the sound began to boost tactile RTs at a farther distance in the left hemispace than in the right hemispace, in the LH group the sound began to boost tactile RTs at a similar distance in both hemispaces.

RTs were significantly faster when the tactile stimulus occurred at T7 compared to when the tactile stimulus occurred at T6 (Post-hoc Newman-Keuls' test: *p* = 0.003). RTs further decreased at the later delay T8. LH participants' RTs were significantly faster when the tactile stimulus occurred at T8 than at T7 (Post-hoc Newman-Keuls' test: *p* = 0.009). Moreover, RTs were significantly faster when the tactile stimulus was delivered at T7, T8 and T9 as compared to when the tactile stimulus was delivered at T2, T3, T4, T5 and T6 (Post-hoc Newman-Keuls' test: *p* < 0.003 in all cases). These results suggest that, in the LH group, the distance at which the sound began to boost tactile RTs what similar in both the left and right hemispaces.

4   Discussion

Our results suggest that both handedness and hemispatial processing influence the multisensory integration boost of tactile detection provided by the proximity of an auditory stimulus. The pattern of results for left-handers did not correspond to a mirror image of the pattern for right-handers. For right-handed participants, the sound differentially boosted tactile processing in the left and right hemispaces. The boost was observed at a farther distance for the left as compared to the right hemispace, suggesting that the left hemispace is larger than the right hemispace of right-handers' peri-trunk PPS. In contrast, for left-handed participants the sound started to boost tactile reaction times at similar distances in the left and in the right hemispace suggesting that peri-trunk PPS size of left-handers was similar

in the left and right hemispaces. It is important to note that we did not find any main effect of sound hemispace location on tactile detection: our findings cannot be explained by the mere spatial compatibility between participants' responding hand and sound hemispace (Michaels 1988), or by a global effect of right hemispheric dominance for spatial processing that would boost attentional processing in the left hemispace.

The results confirm that participants have perceived distance in a coherent way, given that tactile reaction time was depending on how close the sound was, reflecting the participants' higher sensitivity for sounds entering the PPS (Camponogara et al. 2015). Still, the paradigm used in our study does not allow distinguishing biases in auditory subjective localization from differences in PPS boundaries location. A possible explanation of our results is indeed that right-handers underestimate the distance of auditory sources in the left hemispace as compared to the right hemispace whereas left-handers estimate distance similarly in both hemispaces. It has been repeatedly shown that the distance of auditory sources located in the midsagittal plane is overestimated for sources closer than 1m and underestimated for farther sources (see Zahorik et al. 2005 for a review). However, the influence of binaural cues that vary with lateral position on auditory distance perception is not clear and its link to handedness has never been investigated. Studies, which have questioned the effect of handedness on auditory space perception, have mainly examined the differences in the perception of the azimuth of auditory sources. They reported either similar phenomena for left-handed and right-handed subjects (e.g. greater sound localization accuracy in the left hemispace (Burke et al. 1994) and rightward shift in the perceived location (Dufour et al. 2007)) or opposite phenomena with a rightward shift for left-handed participants and a leftward shift for right-handed participants in the perceived location of sounds (Ocklenburg et al. 2010). If both right-handers and left-handers show similar biases in distance perception in the left and right hemispace, then these biases could not explain the difference in the patterns of results that we found between right- and left-handers. If right-handers and left-handers had opposite biases in distance perception, we would expect left-handers' PPS to mirror the pattern of right-handers, which is not the case.

We have found that tactile detection is speeding up at multiple locations (for the right-handed group, between sound source location at T4/T5, T6/T7, and T8/T9 in the left hemispace). Reaction times further decreased after the first boost, as the sound came closer within PPS. A recent study examining visuotactile interactions has shown that the distance from an approaching visual stimulus influences tactile detection times (de Haan et al. 2016). Our results also suggest that, within PPS, the distance between the auditory and the tactile stimulus continues to influence tactile reaction time: the closer the two sensory stimuli, the stronger the multisensory boost of the detection times is.

Whereas right-handers' peri-trunk PPS was found to be larger in the left hemispace, this anisotropy was not observed in left-handed participants. A right hemispheric dominance in spatial processing could explain the boost of tactile detection at a farther distance from the right-handers' body in the left hemispace. The effect of handedness that we found could be linked to differences in cortical spatial sound processing: left-handers might be less strongly lateralized in terms of spatial function (McGlone and Davidson 1973; Vogel et al. 2003). Alternatively, the anisotropy could be explained in terms of action preparation. A previous study investigating perceived reachability in right and left hemispaces in relation to handedness also reported an asymmetric pattern for right-handers and a symmetric pattern for left-handers. Whereas left-handed subjects estimated being able to reach as far in the left as in the right hemispace, right-handed subjects underestimated their reaching possibility in the left as compared to the right hemispace (Linkenauger et al. 2009). Together with the facts that right-handers' movements in space are faster and more precise when using their right rather than their left hand, this suggest that right-handers' asymmetric PPS could be related to their asymmetric motor abilities.

Right-handers' peri-trunk PPS was indeed larger on the side where their motor abilities are limited. A study on spatial behavior during locomotion has also demonstrated a similar lateral anisotropy in right-handers (Gérin-Lajoie et al. 2008). In this study, participants had to walk towards a goal, circumventing a cylindrical obstacle that could remain stationary or move. The adopted trajectory was found to be farther from the obstacle when the latter was on participants' left side than when it was on their right side. The authors interpreted this difference as an indication that the safety margin required on the dominant side is smaller. The anisotropy reported in our study is also in accordance with the definition of PPS as a defense margin (Graziano and Cooke 2006; Sambo and Iannetti 2013): PPS should be larger in the hemispace of the non-dominant hand, where actions are slower and less precise, in order to provide additional time for the elaboration of defensive behaviors. However, we did not find any lateral PPS anisotropy in left-handed participants. Left-handers constitutes around 10-13% of the population (Marchant et al. 1995; Raymond et al. 1996), and are consequently largely outnumbered by right-handers. Living in a world structured for right-handers, left-handers are more likely to use both hands in everyday tasks than right-handers (Mamolo et al. 2006; Gonzalez et al. 2007), and they also observe globally more actions being performed with the right hand by right-handers, since everyday lateralized tools are mass-produced for right-handers. Among the participants of our study, only 14% of the left-handers use their left hand to manipulate a computer mouse whereas 100% of the right-handers manipulate it with their right hand. Precision movements in right-handers are preferentially executed with the dominant hand (Annett 1970; Carnahan 1998; Gonzalez et al. 2007) whereas it is not the case for left-handers, suggesting that visuomotor control might therefore be strongly linked to the left hemisphere. The absence of PPS lateral asymmetry could be related to the fact that left-handers are required to be more ambidextrous than right-handers, as well as to perceptual factors linked to living in a right-handers' world. In line with studies on bimanual

action control and visual processing in peri-hand space (Le Bigot and Grosjean 2012), audio-tactile integration could be impacted by the different ways in which left and right-handers use their hands.

A lateral asymmetry of PPS has never been reported before with a similar paradigm than the one we used. Nevertheless, several differences between the current paradigm and the previous studies have to be taken into account. First, auditory looming stimuli are not usually proposed in the two hemispaces in the studies reported in the literature (Canzoneri et al. 2013a; Maister et al. 2015; Serino et al. 2015). Second, the direction of the sound trajectory is generally parallel to the mid-sagittal plane of the participant. In contrast, in the present study, the direction of the sound trajectory is towards the mid-sagittal plane. This kind of sound direction only has been shown to have an effect on the modification of minimum comfortable interpersonal distance after a long tool use (Quesque et al. 2016). A sound looming towards the body mid-sagittal plane might be more prone to connect the external space with the body space, making more relevant the motor nature of PPS.

Observing an impact of handedness on the PPS of the trunk contributes to the accumulation of data indicating that PPS is coded in motor terms (Dijkerman and Farnè 2015; Noel et al. 2015; Vagnoni et al. 2017). In a previous study measuring lateral peri-trunk PPS boundaries, we did not find any lateral anisotropy of PPS when the sound was looming from the back space towards right-handed participants (Taffou and Viaud-Delmon 2014), which is coherent with fact that the back space is not a space of action (Viaud-Delmon et al. 2007). Few studies on spatial behavior have reported a front/back anisotropy that seems to follow the asymmetry of the motor abilities, with a larger extent of personal space on the front space (Hayduk 1981; Lloyd et al. 2009). As the lateral anisotropy seems to be linked to the motor nature of PPS, it seems logical not to observe it with stimuli coming from behind.

In the present study, participants received tactile simulations on one hand and responded with the other hand. Previous findings suggest that peri-hand PPS merges with peri-trunk PPS when hands are located near the body (Serino et al. 2015). Our aim was therefore to study peri-trunk PPS by applying tactile stimulation on the non-dominant hand, with both hands positioned in contact with the trunk. However, we cannot exclude the possibility that the present results are somehow associated to the peri-hand PPS of the non-dominant hand. Further experiments using a set up assessing stimulation on the trunk with vocal responses would be required to confirm that there is no link between the asymmetry in the PPS and the opposite location of tactile stimulus and hand of response.

In sum, the present study explored PPS boundaries in relation to handedness and hemispace and revealed an expanded PPS on the side of the non-dominant hand for right-handers and a rather symmetrical PPS for left-handers. This suggests that PPS is sensitive to individual factors impacting the possibility of acting as efficiently as possible with the upper limb. This result has important consequences on future studies on PPS, and invites new interpretations of previous results where handedness and side of stimulation might have had a confounding role. The literature agrees on the fact that PPS is an area where objects are coded in motor terms for the purpose of action. It is therefore important to take into account the interactions between hemispace and motor skills when attempting to unravel the general sensory and motor constraints on proxemics.

5   Acknowledgments

6   References

Alais D, Newell FN, Mamassian P (2010) Multisensory processing in review: from physiology to behaviour. Seeing Perceiving 23:3–38 . doi: 10.1163/187847510X488603

Annett M (1970) the Growth of Manual Preference and Speed. Br J Psychol 61:545–558 . doi: 10.1111/j.2044-8295.1970.tb01274.x

Aspell JE, Lavanchy T, Lenggenhager B, Blanke O (2010) Seeing the body modulates audiotactile integration. Eur J Neurosci 31:1868–73 . doi: 10.1111/j.1460-9568.2010.07210.x

Bassolino M, Finisguerra A, Canzoneri E, et al (2014) Dissociating effect of upper limb non-use and overuse on space and body representations. Neuropsychologia 70:1–9 . doi: 10.1016/j.neuropsychologia.2014.11.028

Bassolino M, Serino A, Ubaldi S, Làdavas E (2010) Everyday use of the computer mouse extends peripersonal space representation. Neuropsychologia 48:803–811 . doi: 10.1016/j.neuropsychologia.2009.11.009

Bertelson P, Aschersleben G (1998) Automatic visual bias of perceived auditory location. Psychon Bull Rev 5:482–489

Bremmer F, Schlack A, Shah NJ, et al (2001) Polymodal motion processing in posterior parietal and premotor cortex: A human fMRI study strongly implies equivalencies between humans and monkeys. Neuron 29:287–296

Bresciani J-P, Dammeier F, Ernst MO (2006) Vision and touch are automatically integrated for the perception of sequences of events. J Vis 6:554–64 . doi: 10.1167/6.5.2

Brozzoli C, Gentile G, Petkova VI, Ehrsson HH (2011) fMRI Adaptation Reveals a Cortical Mechanism for the Coding of Space Near the Hand. J Neurosci 31:9023–9031 . doi: 10.1523/JNEUROSCI.1172-11.2011

Burke KA, Letsos A, Butler RA (1994) Asymmetric performances in binaural localization of sound in space. Neuropsychologia 32:1409–1417 . doi: 10.1016/0028-3932(94)00074-3

Camponogara I, Komeilipoor N, Cesari P (2015) When distance matters: Perceptual bias and behavioral response for approaching sounds in peripersonal and extrapersonal space. Neuroscience 304:101–108 . doi: 10.1016/j.neuroscience.2015.07.054

Canzoneri E, Magosso E, Serino A (2012) Dynamic sounds capture the boundaries of peripersonal space representation in humans. PLoS One 7:e44306 . doi: 10.1371/journal.pone.0044306

Canzoneri E, Marzolla M, Amoresano A, et al (2013a) Amputation and prosthesis implantation shape body and peripersonal space representations. Sci Rep 3:2844 . doi: 10.1038/srep02844

Canzoneri E, Ubaldi S, Rastelli V, et al (2013b) Tool-use reshapes the boundaries of body and peripersonal space representations. Exp Brain Res 228:25–42 . doi: 10.1007/s00221-013-3532-2

Carnahan H (1998) Manual asymmetries in response to rapid target movement. Brain Cogn 37:237–253 . doi: 10.1006/brcg.1997.0973

Cowey A, Small M, Ellis S (1994) Left visuo-spatial neglect can be worse in far than in near space. Neuropsychologia 32:1059–1066 . doi: 10.1016/0028-3932(94)90152-X

de Haan AM, Smit M, Van der Stigchel S, Dijkerman HC (2016) Approaching threat modulates visuotactile interactions in peripersonal space. Exp Brain Res 234:1875–1884 . doi: 10.1007/s00221-016-4571-2

Dietz MJ, Friston KJ, Mattingley JB, et al (2014) Effective Connectivity Reveals Right-Hemisphere Dominance in Audiospatial Perception: Implications for Models of Spatial Neglect. J Neurosci 34:5003–5011 . doi: 10.1523/JNEUROSCI.3765-13.2014

Dijkerman HC, Farnè A (2015) Sensorimotor and social aspects of peripersonal space. Neuropsychologia 70:309–312 . doi: 10.1016/j.neuropsychologia.2015.03.005

Dufour A, Touzalin P, Candas V (2007) Rightward shift of the auditory subjective straight ahead in right- and left-handed subjects. Neuropsychologia 45:447–453 . doi: 10.1016/j.neuropsychologia.2006.05.027

Farnè A, Iriki A, Làdavas E (2005) Shaping multisensory action-space with tools: Evidence from patients with cross-modal extinction. Neuropsychologia 43:238–248 . doi: 10.1016/j.neuropsychologia.2004.11.010

Farnè A, Serino A, Làdavas E (2007) Dynamic size-change of peri-hand space following tool-use: Determinants and spatial characteristics revealed through cross-modal extinction. Cortex 43:436–443 . doi: 10.1016/S0010-9452(08)70468-4

Finisguerra A, Canzoneri E, Serino A, et al (2015) Moving sounds within the peripersonal space modulate the motor system. Neuropsychologia 70:421–428 . doi: 10.1016/j.neuropsychologia.2014.09.043

Flowers K (1975) Handedness and Controlled Movement. Br J Psychol 66:39–52 . doi: 10.1111/j.2044-8295.1975.tb01438.x

Gentile G, Petkova VI, Ehrsson HH (2011) Integration of visual and tactile signals from the hand in the human brain: an FMRI study. J Neurophysiol 105:910–922 . doi: 10.1152/jn.00840.2010

Gérin-Lajoie M, Richards CL, Fung J, McFadyen BJ (2008) Characteristics of personal space during obstacle circumvention in physical and virtual environments. Gait Posture 27:239–247 . doi: 10.1016/j.gaitpost.2007.03.015

Gonzalez CLR, Whitwell RL, Morrissey B, et al (2007) Left handedness does not extend to visually guided precision grasping. Exp Brain Res 182:275–279

Graziano MSA, Cooke DF (2006) Parieto-frontal interactions, personal space, and defensive behavior. Neuropsychologia 44:2621–2635 . doi: 10.1016/j.neuropsychologia.2005.09.011

Graziano MSA, Gross CG (1993) A bimodal map of space: somatosensory receptive fields in the macaque putamen with corresponding visual receptive fields. Exp Brain Res 97:96–109

Hall ET (1966) The Hidden Dimension

Halligan PW, Marshall JC (1991) Left neglect for near but not far space in man. Nature 350:498–500 . doi: 10.1038/350498a0

Hayduk L a. (1981) The shape of personal space: An experimental investigation. Can J Behav Sci Can des Sci du Comport 13:87–93 . doi: 10.1037/h0081114

Heilman KM, Van Den Abell T (1979) Right hemispheric dominance for mediating cerebral activation. Neuropsychologia 17:315–321 . doi: 10.1016/0028-3932(79)90077-0

Iachini T, Ruggiero G, Ruotolo F, Vinciguerra M (2014) Motor resources in peripersonal space are intrinsic to spatial encoding: Evidence from motor interference. Acta Psychol (Amst) 153:20–27 . doi: 10.1016/j.actpsy.2014.09.001

Kandula M, Van der Stoep N, Hofman D, Dijkerman HC (2017) On the contribution of overt tactile expectations to visuo-tactile interactions within the peripersonal space. Exp Brain Res 235:2511–2522 . doi: 10.1007/s00221-017-4965-9

Kerr M, Rosemary M, Elithorn A (1963) Cerebral Dominance in Reaction Time Responses. Br J Psychol 54:325–336 . doi: 10.1111/j.2044-8295.1963.tb00887.x

Krumbholz K, Hewson-Stoate N, Schönwiesner M (2007) Cortical response to auditory motion suggests an asymmetry in the reliance on inter-hemispheric connections between the left and right auditory cortices. J Neurophysiol 97:1649–1655 . doi: 10.1152/jn.00560.2006

Krumbholz K, Schönwiesner M, Von Cramon DY, et al (2005) Representation of interaural temporal information from left and right auditory space in the human planum temporale and inferior parietal lobe. Cereb Cortex 15:317–324 . doi: 10.1093/cercor/bhh133

Làdavas E, Farnè A (2004) Visuo-tactile representation of near-the-body space. J Physiol Paris 98:161–170

Le Bigot N, Grosjean M (2012) Effects of handedness on visual sensitivity in perihand space. PLoS One 7: . doi: 10.1371/journal.pone.0043150

Linkenauger S a, Witt JK, Stefanucci JK, et al (2009) The effects of handedness and reachability on perceived distance. J Exp Psychol Hum Percept Perform 35:1649–1660 . doi: 10.1037/a0016875

Lloyd DM, Coates A, Knopp J, et al (2009) Don't stand so close to me: The effect of auditory input on interpersonal space. Perception 38:617–620 . doi: 10.1068/p6317

Longo MR, Lourenco SF (2007) Space perception and body morphology: Extent of near space scales with arm length. Exp Brain Res 177:285–290 . doi: 10.1007/s00221-007-0855-x

Longo MR, Lourenco SF (2006) On the nature of near space: Effects of tool use and the transition to far space. Neuropsychologia 44:977–981 . doi: 10.1016/j.neuropsychologia.2005.09.003

Lourenco SF, Longo MR (2009) The plasticity of near space: Evidence for contraction. Cognition 112:451–456 . doi: 10.1016/j.cognition.2009.05.011

Luce RD (1986) Response times: Their role in inferring elementary mental organization (No. 8), Oxford Uni

Maister L, Cardini F, Zamariola G, et al (2015) Your place or mine: Shared sensory experiences elicit a remapping of peripersonal space. Neuropsychologia 70:455–461 . doi: 10.1016/j.neuropsychologia.2014.10.027

Makin TR, Holmes NP, Zohary E (2007) Is that near my hand? Multisensory representation of peripersonal space in human intraparietal sulcus. J Neurosci 27:731–40 . doi: 10.1523/JNEUROSCI.3653-06.2007

Mamolo CM, Roy E a, Rohr LE, Bryden PJ (2006) Reaching patterns across working space: the effects of handedness, task demands, and comfort levels. Laterality 11:465–492 . doi: 10.1080/13576500600775692

Maravita A, Iriki A (2004) Tools for the body (schema). Trends Cogn Sci 8:79–86 . doi: 10.1016/j.tics.2003.12.008

Marchant LF, McGrew WC, Eibl-Eibesfeldt I (1995) Is Human Handedness Universal? Ethological Analyses from Three Traditional Cultures. Ethology 101:239–258 . doi: 10.1111/j.1439-0310.1995.tb00362.x

McGlone J, Davidson W (1973) The relation between cerebral speech laterality and spatial ability with special reference to sex and hand preference. Neuropsychologia 11:105–113 . doi: 10.1016/0028-3932(73)90070-5

Michaels CF (1988) S-R compatibility between response position and destination of apparent motion: Evidence of the detection of affordances. J Exp Psychol Hum Percept Perform 14:231–240 . doi: 10.1037//0096-1523.14.2.231

Nicholls MER, Thomas NA, Loetscher T, Grimshaw GM (2013) The flinders handedness survey (FLANDERS): A brief measure of skilled hand preference. Cortex 49:2914–2926 . doi: 10.1016/j.cortex.2013.02.002

Noel J-P, Grivaz P, Marmaroli P, et al (2015) Full body action remapping of peripersonal space: The case of walking. Neuropsychologia 70:375–384 . doi: 10.1016/j.neuropsychologia.2014.08.030

Ocklenburg S, Hirnstein M, Hausmann M, Lewald J (2010) Auditory space perception in left- and right-handers. Brain Cogn 72:210–217 . doi: 10.1016/j.bandc.2009.08.013

Quesque F, Ruggiero G, Mouta S, et al (2016) Keeping you at arm's length: modifying peripersonal space influences interpersonal distance. Psychol Res. doi: 10.1007/s00426-016-0782-1

Railo H, Tallus J, Hämäläinen H (2011) Right visual field advantage for perceived contrast: Correlation with an auditory bias and handedness. Brain Cogn 77:391–400 . doi: 10.1016/j.bandc.2011.08.019

Raymond M, Pontier D, Dufour A-B, Pape Moller A (1996) Frequency-dependent maintenance of left handedness in humans. Proc R Soc London B Biol Sci 1627–1633

Reuter-Lorenz P, Kinsbourne M, Moscovitch M (1990) Hemispheric control of spatial attention. Brain Cogn 266:240–266

Rizzolatti G, Fadiga L, Fogassi L, Gallese V (1997) The space around us. Science (80-) 277:190–191

Sambo CF, Iannetti GD (2013) Better safe than sorry? The safety margin surrounding the body is increased by anxiety. J Neurosci 33:14225–30 . doi: 10.1523/JNEUROSCI.0706-13.2013

Savel S (2009) Individual differences and left/right asymmetries in auditory space perception. I. Localization of low-frequency sounds in free field. Hear Res 255:142–154 . doi: 10.1016/j.heares.2009.06.013

Serino A (2016) Variability in Multisensory Responses Predicts the Self-Space. Trends Cogn Sci 20:169–170 . doi:

10.1016/j.tics.2016.01.005

Serino A, Bassolino M, Farnè A, Làdavas E (2007) Extended multisensory space in blind cane users. Psychol Sci 18:642–8 . doi: 10.1111/j.1467-9280.2007.01952.x

Serino A, Canzoneri E, Avenanti A (2011) Fronto-parietal Areas Necessary for a Multisensory Representation of Peripersonal Space in Humans: An rTMS Study. J Cogn Neurosci 23:2956–2967 . doi: 10.1162/jocn_a_00006

Serino A, Noel J-P, Galli G, et al (2015) Body part-centered and full body-centered peripersonal space representation. Sci Rep 5:doi: 10.1038/srep18603 . doi: 10.1038/srep18603

Spence C, Pavani F, Driver J (2004a) Spatial constraints on visual-tactile cross-modal distractor congruency effects. Cogn Affect Behav Neurosci 4:148–169 . doi: 10.3758/CABN.4.2.148

Spence C, Pavani F, Maravita A, Holmes NP (2004b) Multisensory contributions to the 3-D representation of visuotactile peripersonal space in humans: Evidence from the crossmodal congruency task. J Physiol Paris 98:171–189 . doi: 10.1016/j.jphysparis.2004.03.008

Taffou M, Viaud-Delmon I (2014) Cynophobic Fear Adaptively Extends Peri-Personal Space. Front Psychiatry 5:3–9 . doi: 10.3389/fpsyt.2014.00122

Ulrich R, Miller J (1993) Information processing models generating lognormally distributed reaction times. J Math Psychol 37(4), 513:

Vagnoni E, Andreanidou V, Lourenco SF, Longo MR (2017) Action ability modulates time-to-collision judgments. Exp Brain Res 1–11 . doi: 10.1007/s00221-017-5008-2

Viaud-Delmon I, Brugger P, Landis T (2007) Hemineglect: Take a look at the back space. Ann Neurol 62:418–422 . doi: 10.1002/ana.21176

Vogel JJ, Bowers CA, Vogel DS (2003) Cerebral lateralization of spatial abilities: A meta-analysis. Brain Cogn 52:197–204 . doi: 10.1016/S0278-2626(03)00056-3

Zahorik P, Brungart DS, Bronkhorst AW (2005) Auditory Distance Perception in Humans : A Summary of Past and Present Research. 91:409–420