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Laboratoire Sciences et Technologies de la Musique et du Son UMR 9912

Interplay between multisensory integration and social interaction in auditory space

Towards an integrative neuroscience approach of proxemics

par Lise Hobeika

Thèse de doctorat de Sciences Cognitives

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Abbreviations

AIP: Anterior Parietal Area

CCE: Crossmodal Congruency Effect

DPSP: Defensive Peripersonal Space

HBR: Hand Blink Reflex

HRTF: Head-Related Transfer Function

ILD: Interaural Level Difference

ITD: Interaural Time Difference

LH: Left-Handed

PPS: Peripersonal Space

RH: Right-Handed

TTC: Time To Contact

VIP: Ventral intraparietal area

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The initial PhD project was centered on prosocial effects of different motor interactions in humans. As we did not find a satisfying measure to assess prosocial effects, we decided to study if peripersonal space could be an appropriate tool of measurement. The complexity of peripersonal space led us to investigate its characteristics and modulations as the main topic of interest.

The present work aimed at further understanding human space perception in social contexts. It is now well known that space is not a unified percept. A critical distinction exists between the space near the body - called peripersonal space (PPS) by neuroscientists - and the space far from the body. In neuroscience, PPS is a motor interface coded by multisensory neurons. It is both a space of defense, and a space of interaction with the external world. It has been repeatedly evidence that the size of this space is flexible. It depends on various factors as individual motor abilities or emotional contexts. Social psychologists have widely studied spatial rules in society, arguing for a special space management in social contexts. Even if psychologists have emphasized the complexity of space management in society, the impact of social contexts on PPS size remains relatively undiscovered in the field of neuroscience.

In this work, I conducted three studies to investigate the factors that contribute to the permeability and adaptive aspects of PPS. The first study investigates the characteristics of PPS for individuals in isolation and their links with individual motor abilities as defined by handedness. The second study focuses on PPS in social contexts, looking at the impact of minimal social interaction induced in the laboratory on space perception. The third study is a methodological investigation aiming at overcoming limitations of the paradigm I used to measure PPS in the first two studies. These findings contribute to the field of multisensory integration research and the field of social cognition research.

This manuscript is divided in two parts: the first part introduces the theoretical framework (chapters 1 to 4) and the second part describes the three studies that were conducted (chapters 6 to 8) and discusses them separately and generally (chapter 9).

Part I

Introduction

Chapter 1

Space management

1.1 Animal spatial behaviors

In animals, space management is strictly regulated. Animals need to keep a certain distance between themselves and others to avoid potential danger. In social species, individuals also need to get close enough to interact. In 1955, the zoologist Hediger analyzed animals' spacing behaviors in a systematic way [Hediger, 1955]. He described different types of distances that individuals keep between themselves and others to interact with conspecifics while staying safe. In social species, spacing rules apply to members of the same social group. First, the personal space refers to the area that individuals keep between themselves. Its size can vary, depending on the hierarchical status of individuals in the group for example (the more dominant member having the larger personal space). A second distance described by Hediger in social groups is the social distance. This area refers to the maximal distance individuals from the same social group keep between them. This maximal distance enables them to receive sensory inputs - be they visual, auditory, or olfactory - from the rest of the group. The loss of contact would have serious consequences for many reasons, from the inability to alert others of a danger to the real loss of the group.

When two individuals from different species meet, the situation is potentially dangerous. Two types of distances regulating safety behaviors are at stake: fighting and fleeing. A wild animal let another approach up to a certain distance before fleeing. The limit at which an animal tolerates an approach is called "the flight distance". The size of this area seems to depend on the size of the animal, but also on other factors such as group size or as the distance to a safe shelter [Dill and Houtman, 1987, Ydenberg and Dill, 1986]. If an individual continues to

approach an animal below the flight distance, he is in the critical zone. This is the area between flight distance, and the fight distance, i.e the limit at which the animal will attack the invader.

The inability to maintain appropriate distances between individuals of the same species can have serious consequences. Evidence points out that social crowding provokes both behavioral and physiological changes, in rodents or non-human primates [Djordjevic et al., 2005, Judge and De Waal, 1997]. First, it is clear that crowding provokes stress that can lead to multiple physiological consequences such as cardiac dysfunction for example [Grippe et al., 2010]. Behavioral consequences are not that clear, and vary across species. A famous experiment performed by J. Calhoun in the 60's found dramatic consequences to social crowding in rats [Calhoun, 1962]. Aggressive behaviors increased, females showed abnormal maternal behavior leading to a high mortality rate among infants (up to 96%). However, studies on non-human primates found more variability in behavioral responses to stress, leading to aggressiveness but also to the increase of behavioral strategies reducing social stress as grooming and huddling [Judge and De Waal, 1997].

1.2 Human spatial behaviors

Defining personal space based on spatial behaviors

In the 1960's, Edward Hall developed the notion of proxemic defending the existence of socio-psychological rules to manage space in society [Hall, 1966], getting inspiration in Hediger's work. Hall described how inter-personal distances, i.e. the distance that individuals keep between them, differ in function of social contexts. Four ranges of interpersonal distances are used: the intimate distance, the personal distance, the social distance and the public distance (see figure 1.1). The intimate distance (0 to 0.5m) is the smallest one, where touch is possible. It refers to the adopted distances for wrestling, lovemaking, comforting or protecting. The personal distance (0.5 to 1.2m) is the term taken from Hediger's work to name distances that members of non-contact species keep between them. Hall refers to it as a protective bubble around the self that individuals maintain between them and others to avoid discomfort. Its size is putting the other around arm's reach. The social distance (1.2 to 3m) refers to distances that people use in most non-intimate social situations. Its range goes from the distance to have formal discussion to the distance of two people's desks in an office. The public distance (>3m) refers to distances used mostly when

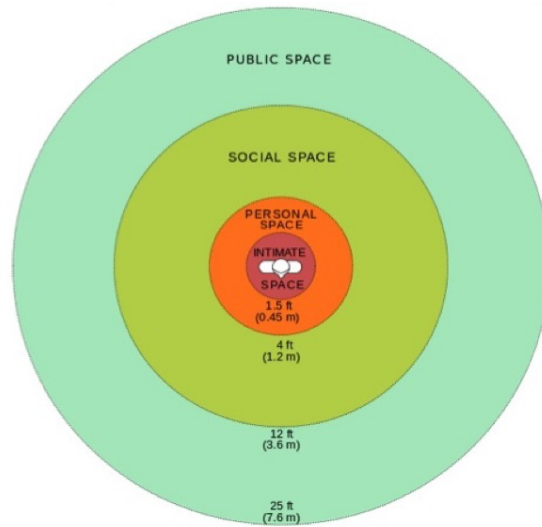


Figure 1.1: Representation of the four interpersonal distances described by Edward T. Hall: the intimate, the personal, the social and the public spaces.

one individual is addressing a group, during a political speech for example. The adopted distances are highly linked to the amount of sensory information shared by individuals. In the intimate space, people have high visual, auditory and tactile access to others, whereas in the public space the information about the others is limited: just rough visual information is available, voices need to be amplified to be perceived. Experimental works support this idea of social norms of spatial arrangements. As examples, standard interpersonal distances are used during group discussions [Batchelor and Goethals, 1972]. Interpersonal distances during natural conversations are kept below a limit [Sommer, 1962].

In social and cognitive psychology, a large portion of the literature focuses on the study of Hall's personal space, described as "the area with invisible boundaries that individuals actively maintain around themselves, into which others cannot intrude without arousing discomfort" [Aiello, 1987, Hayduk, 1978, Sommer, 1959]. Personal space is measured by individuals' interpersonal distances during social interactions. This field of research has widely investigated personal space in social contexts, to understand its mechanisms and factors that can modulate it.

Hall relied on real-life observations of interpersonal distances and on volunteers' interviews to establish his taxonomy. Measuring chosen interpersonal distances, be it in real-life environment or in tasks in the laboratory, is the simplest method to study personal space. For example, Lockard and colleagues measured distances that people keep between themselves in an elevator [Lockard et al., 1977]. Alternatively, Batch-

elor and colleagues performed tasks in the laboratory, observing distances at which people sit from each other to perform a task together [Batchelor and Goethals, 1972].

Another common psychology method to study personal space is to directly ask participants to place themselves at a distance they find appropriate and comfortable to interact with another individual, to have a conversation for example. The chosen distance is considered as the limit of participants' personal space [Aiello, 1987]. Two versions of the task exist, we are going to call them stop-approach and stop-distance tasks. In the stop-distance task, a participant walks towards an individual and stops when he finds the distance between them comfortable. The stop-approach task is a variant, in which the participant is immobile while an individual is walking towards him. The participant's task is to stop the approach as soon as he experiences discomfort. A possible option in both tasks is to continue the approach below the comfort distance and measure the distance at which the discomfort is becoming intolerable. The size between those two distances can be interpreted as the thickness of the boundary, or as the permeability of the personal space. It is common to use both stop-approach and stop-distance tasks in the same study as they do not always lead to the same results. The divergences in results could be due to differences in participants' sense of control. In the stop-approach task, participants do not control the speed of the approach. Furthermore, in the stop-approach task, still participants are observing an individual approaching towards them. This approach could be seen as a potential threat and elicit a defensive mechanism, which may not be at stake in the stop-distance task.

We can also mention the silhouette placement technique, a task that has been used to some extent in the 60's and 70's. Participants are asked to place two small cardboard silhouettes in space, with specific instructions on their activities or identities [Kuethe, 1962]. Those measures have been found to correlate to the stop-distance ones [Greenberg et al., 1980], thus they may reflect similar mechanisms.

Determinants of spatial behaviors

Personal space size is flexible. It depends on individuals' characteristics such as age, gender, personality traits (for a review [Aiello, 1987]). Personal space is already implemented at the age of 6, and evolves until adolescence by increasing its size with age [Aiello and Carlo Aiello, 1974, Jones and Aiello, 1973]. Adults change their spatial behaviors according to the age of others: they tolerate better personal space intrusion if children rather than adults do it. Adults start to expect of children

"adults-standards" personal space when they pass the age of 10. Gender effects have been reported in a small fraction of the studies; with smaller inter-personal distances in women dyads than men dyads [Sommer, 1962, Iachini et al., 2016]. The origin of those gender differences is discussed: they may be fully due to others factors as personality traits, and body schema as arm lengths [Bruno and Muzzolini, 2013]. Nevertheless, consistent results found that men and women better tolerate intrusions of their personal space by women than men. Culture also modulates personal space size [Sussman and Rosenfeld, 1982, Remland et al., 1995]. Remland and colleagues studied interpersonal distances in different countries analyzing recordings of natural interactions occurring on public sites. They found larger interpersonal distances for Scottish and Irish dyads than English, French, Italian and Greek ones.

Personality traits change interpersonal distances: individuals with low confidence and low self esteem tend to have a larger personal space [Karabenick and Meisels, 1972, Frankel and Barrett, 1971]. Anxiety impacts interpersonal distances. Social anxiety increases inter-personal distances whereas tendency to affiliate decreases them. Anxiety trait and induced anxiety increase interpersonal distances [Iachini et al., 2015, Brady and Walker, 1978]. Studies testing veterans with post-traumatic stress disorders and violent inmates found that exposure to violence tends to increase personal space, particularly in the back space [Bogovic et al., 2014]. Schizophrenia is linked to a larger and more variable personal space [Holt et al., 2015, Horowitz, 1968]. However a recent study affirms that schizophrenic patients with paranoid traits only have a larger personal space [Schoretsanitis et al., 2016].

Emotional contexts also modulate interpersonal distances. In a study using the stop-approach distance as measure of personal space, Tajadura-Jiménez and colleagues found that music inducing positive emotions listened by headphones decreases personal space extent, whereas music inducing negative emotions listened with loudspeakers increases personal space [Tajadura-Jiménez et al., 2011].

Interpersonal distances depend on individuals' perception of others and on the social relations between themselves [Gifford, 1982, Hayduk, 1978, Sommer, 1962, Tedesco and Fromme, 1974]. Affective or attractiveness evaluations of others modulate personal space. Social relations between individuals change space behaviors [Sommer, 1961]. Affiliation tends to reduce interpersonal distances. People at the same hierarchical level tend to maintain smaller space between themselves than people in a hierarchical relation. Affiliative signals as smiling reduce interpersonal distances [Lockard et al., 1977]. Collaborative social contexts, as group problem-solving

or cooperative set-up rather than a competitive one reduce inter-personal distances. People working together as a group adopt standardized distances between themselves. Minimal in-group members tends to sit closer to each other [Novelli et al., 2010]. In this study, authors created minimal groups based on an arbitrary criterion ('dot over-estimators' or 'dot under-estimators'). They randomly assigned participants' group membership. Then, participants had to place a chair for another participant that would come to interact with them. Participants placed the chair closer to their own chair when the experimenter described the other individual as an in-group member. Even without social interaction, people adopted closer interpersonal distance with individuals perceived as members of a common in-group category. The social relation between individuals, and mostly the level of affiliation between them seems to be crucial parameters to allow people in the space near the body.

Personal space is usually depicted as a round bubble for protection around the body, but it appears to not be symmetrical in all the directions. No consensus was found on the anisotropy of the personal space. Left and right limits of personal space appear to be closer to the body than the one in the front [Lloyd et al., 2009]. Studies found larger space in the front than in the rear [Hayduk, 1981], others found the opposite conclusion [Lloyd et al., 2009]. Bogovic and colleagues found a larger space in the front than the back for healthy subjects, but the opposite results for post-traumatic stress disorders patients [Bogovic et al., 2014]. Those unclear results could be explained by the variability across studies of the level of sensory information participants received, and especially the control of auditory information in the back space measures. Nevertheless, those results indicate an anisotropy of personal space.

Violation of the socio-psychological rules of spatial behaviors

We discussed in section 1.1 that in animal behaviors, intrusions of the personal space lead to appropriate behaviors to protect the self: fight or flight reactions. Are human reactions to personal space invasions similar? Several studies found that a common reaction to personal space intrusion is to escape the situation by leaving or by stepping away to recreate the appropriate distance [Felipe and Sommer, 1966, Barash, 1973]. The problem is that in our societies, those kinds of reactions are not always possible. Social rules and norms imply that individuals have to stand intrusions of their personal spaces in some situations, during a crowded subway ride for example.

Behavioral strategies in case of forced proximity consist in the reduction of sen-

sory information coming from the others, for example by turning away [Barash, 1973]. A psychophysical study found that people showing signs of discomfort in the presence of a stranger nearby shifted their visual attention away from the intruder [Szpak et al., 2015]. Forced proximity increases reported stress and discomfort, measured at both behavioral and physiological levels [Middlemist et al., 1976]. Evans and colleague studied the behavioral and physiological changes, and performances aftereffects of participants after a subway ride, depending on the number of people surrounding them in the subway [Evans and Wener, 2007]. The density of passengers in the subway increased stress reports, salivary cortisol levels (neurohormone related to stress [Pruessner et al., 1997]) but also deteriorated performances in a proofreading task. Personal space intrusion also provokes elevation of electrodermal activity [McBride et al., 1965, Aiello, 1987]. All those evidence pointed out that humans can stand forced spatial proximity but that increases arousal and stress.

At the neural level, amygdala activity seems linked to the negative outcomes linked to space intrusion. A brain damage patient with specific bilateral amygdala lesion showed abnormal space behaviors. She seemed to lack the notion of personal space. She chose smaller interpersonal distances than control participants. She never felt discomfort due to proximity, even when she was nose to nose with the experimenter [Kennedy et al., 2009]. The same article presents fMRI data on space intrusion in healthy subjects. Amygdala activation increased when an experimenter was at a close distance from the participants. This link between amygdala activation and space intrusion has been found in several studies [Wabnegger et al., 2016, Schienle et al., 2015].

Overall, space management is a complex phenomenon in social species. In humans, personal space is studied in social psychology by the measure of interpersonal distances for social interactions. The violation of personal space induces discomfort and stress. The size of personal space is variable, depending on personal traits as age and gender but also on socially-constructed factors as hierarchical status or group membership.

Chapter 2

Multisensory coding of peripersonal space

Perception of space has been widely studied in non-human primates, mainly in neurophysiology studies in macaques. A cerebral system coding specifically for space directly around the body has been evidenced and called peripersonal space (PPS). This space is coded by multisensory neurons. Multisensory integration is an automatic process that has been widely studied across species. We perceive the world through multiple modalities. We can see, hear, smell and touch what is located near us. When we receive sensory information from different modalities at the same time, we need to appropriately combine this sensory information into one or more percepts in order to create a coherent perception of the world.

2.1 Multisensory integration

2.1.1 Multisensory integration processes

Multisensory integration is a strong automatic process, which combines events from different modalities into unified percepts [McGurk and Macdonald, 1976]. Those sensory stimulations need to be close in time and space to be combined. A large part of the literature focuses on audiovisual integration, and agrees on the fact that there is a spatial and temporal window of integration [Stein and Stanford, 2008, Lewald and Guski, 2003]. The temporal window is not symmetrical: the multisensory integration neural system expects sound information to arrive before visual information. This difference is explained by the fact that the multisensory integration processes take into account the time that different sensory systems take to make

the transduction from the signals to the brain. Indeed, retina cells take longer time to convert light into neural signals than cells of the auditory system cells need for sounds transduction [Fain and Fain, 2003]. Perfect subjective alignment of sound and image appears when the visual stimulus is presented before the auditory one. Simultaneity windows for audiovisual stimuli are larger for events near the body than far from the body [Noel et al., 2016].

Superadditivity principle

Multisensory integration processes were first studied on non-human animals, with single neurons recording techniques. The first brain area to be studied was the superior colliculus, as this sub-cortical structure has the particularity of receiving visual, auditory and somatosensory inputs. Stein and colleagues recorded single neuron activity in cats' superior colliculus in response to visual, auditory or audiovisual stimulations [Stein et al., 1993]. They found multisensory integrative neurons. Those neurons discharge when visual or auditory unimodal stimuli appear in their receptive fields. The same neurons discharge with bimodal audiovisual stimuli. Neural responses for bimodal events were larger than both unimodal responses separately, but also larger than the sum of the two unimodal responses. This increased response for bimodal events is called superadditivity (see figure 2.1). This effect was also found for visuotactile and audiotactile events. However, if the two sensory events are too far in space to be considered as one event, a response depression occurs.

Inverse effectiveness principle

The size of the superadditivity effect depends on the strength of the stimulations. Specifically, it depends on the effectiveness of each unimodal stimulus. If one of the sensory stimulations is effective, i.e. it evokes a high neuronal response when it is presented alone, the multisensory enhancement is low. The multisensory enhancement is the largest when both sensory stimulations taken individually evoke to the neuron a small response or no response (see figure 2.2). This relation of bimodal responses strength to unimodal ones is called the inverse effectiveness principle [Stanford et al., 2005]. It suggests that multisensory integration is the strongest when individual sensory stimuli are not effective enough to assure detection of the event. Those results were found for audiovisual, visuotactile and audiotactile neurons.

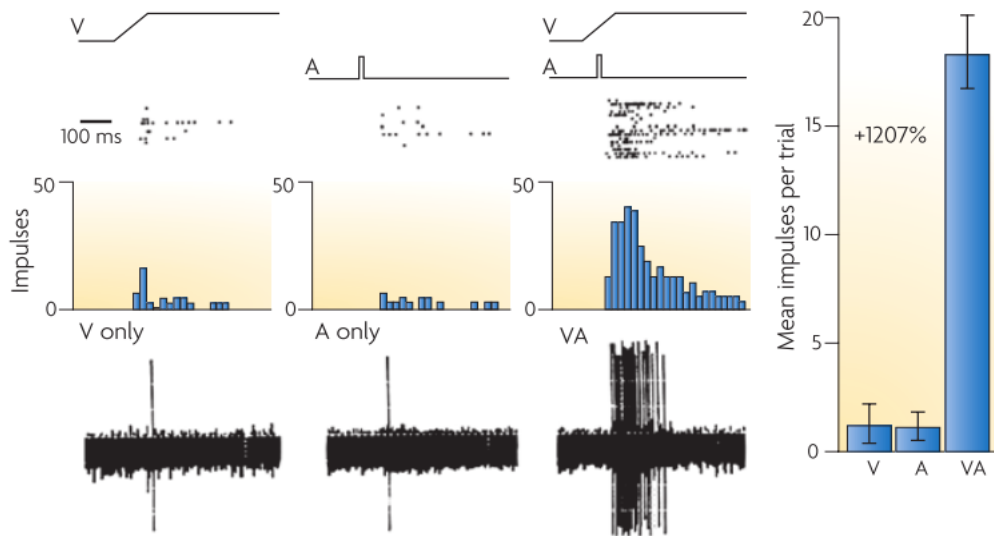


Figure 2.1: Neural responses of a bimodal neuron in cat superior colliculus to visual or auditory unimodal stimuli and audiovisual bimodal stimuli. Bimodal responses are enhanced compared to unimodal ones, this phenomenon is called superadditivity. Taken from [Stein and Stanford, 2008]

Behavioral consequences of multisensory integration processing

Multisensory integration enhances neural response to multisensory events compared to unimodal ones, but it also impacts behavioral reactions to them. Multisensory coding gives multiple advantages in terms of behavioral responses. First of all, bimodal events are detected faster than unimodal ones [Hershenson, 1962, Spence et al., 1998, Suied et al., 2009]. This effect is usually named the Redundant Signal Effect (RSE) [Kinchla, 1974]. Multisensory events also increase detection accuracy. In noisy situations for example, having a visual access to a speaker's face increases speech comprehension [Sumbly and Pollack, 1954]. Different modalities can bring complementary information, thus the number of different sensory information available usually improves event comprehension.

Furthermore, multisensory integration increases detection sensitivity. Sensory stimulations at the detection threshold are detected more often when they are combined with another modality signal. This phenomenon has been described for audiovisual integration, with bimodal events increasing detection of sub-threshold visual [Lovelace et al., 2003] and auditory events [Bolognini et al., 2005]. The sensitivity gain can depend on stimuli movements. Studies found that visual stimuli approaching a part of the body increase tactile sensitivity only on this part of the

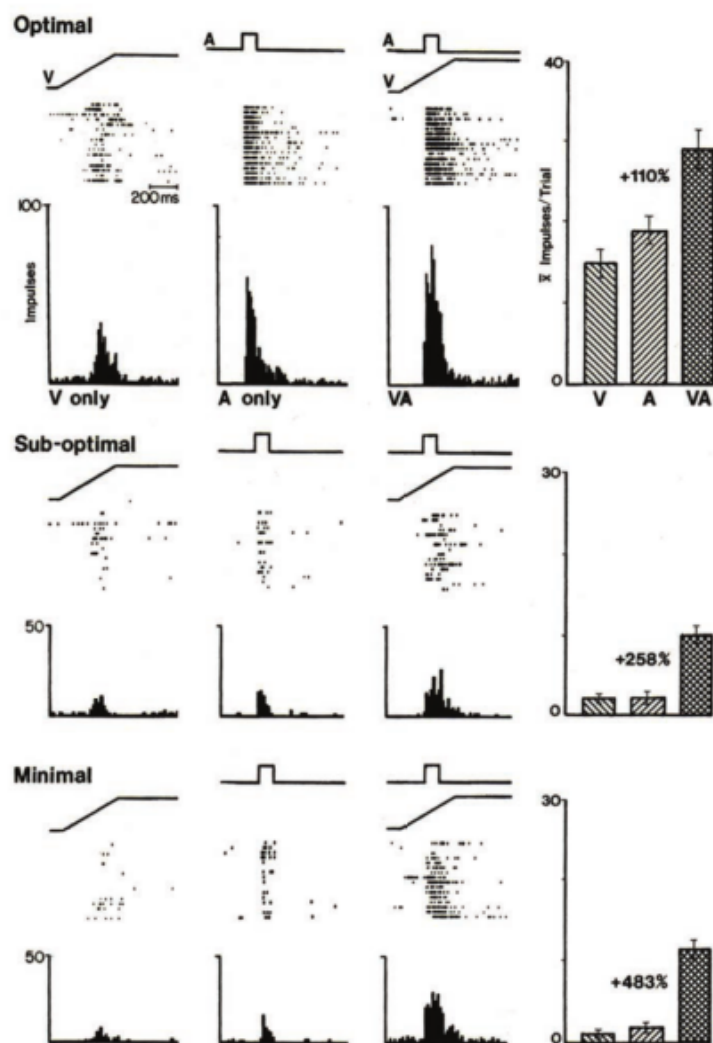


Figure 2.2: Neural responses of a bimodal neuron in cat superior colliculus to visual or auditory unimodal stimuli and audiovisual bimodal stimuli. Bimodal responses is enhanced compared to unimodal ones, this phenomenon is called superadditivity. Taken from [Stein et al., 1993]

body [Kandula et al., 2015, Van der Biest et al., 2016]. More precisely, Cléry and colleagues showed that the sensitivity increase only at the time and place of the expected collision of the object with the body [Cléry et al., 2015a].

2.2 Multisensory coding of near space in primates

2.2.1 Peripersonal space definition based on multisensory neurons activity

Specific neurons of the pre-motor ventral cortex [Rizzolatti et al., 1981], parietal cortex [Colby et al., 1993] and putamen [Graziano and Gross, 1993] discharge only in response to sensory events near the body. Looking at the places where those neurons discharge describes a space around the body: PPS. An important aspect of this space is that it is coded by multisensory neurons. Multisensory neurons discharge in the presence of two or three different types of sensory stimulation. These neurons are mainly audiotactile, visuotactile and audiovisual neurons. For example, visuotactile neurons coding for the space around the face discharge when the macaque's face is touched, but also when visual stimulations are near the face (for a review [Holmes and Spence, 2004]).

2.2.2 Two distinct fronto-parietal networks for peripersonal space representation?

PPS representation is based on fronto-parietal networks. In macaque brains, PPS is coded in the areas AIP (anterior parietal area), 7b and VIP (ventral intraparietal area) of the parietal cortex, and F4 and F5 of the area 6 of the pre-frontal cortex (see figure 2.3). A recent review looking at the anatomical connections and functional similarities of those areas claims that they constitute two separated fronto-parietal sub-networks [Cléry et al., 2015b].

The VIP-F4 parieto-frontal network: coding a defensive space?

The VIP - F4 network is thought to have a defensive function as it is linked to the implementation of protective behaviors for the body with an over-representation of the face and hands areas. Micro-stimulations of those two regions provoke stereotypical defensive behaviors such as eye blinking and squinting, retraction of the head, withdrawal of the hand or blocking arm movements [Graziano and Cooke, 2006].

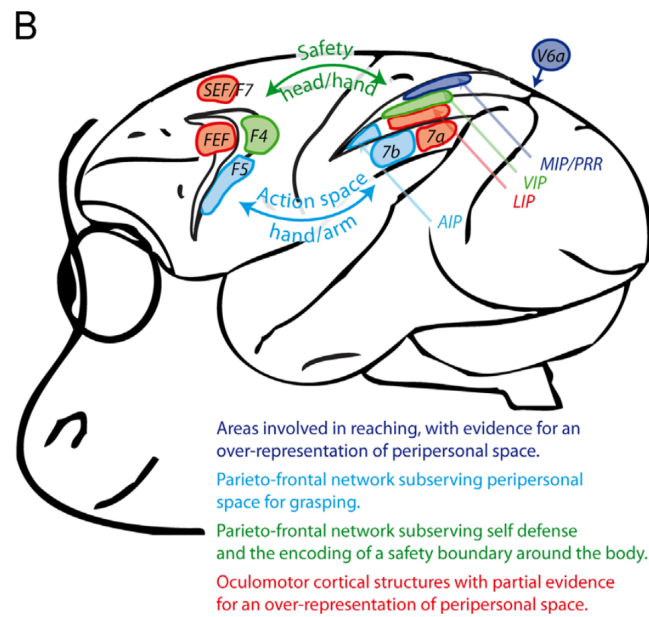


Figure 2.3: Neural basis of PPS and 3D vision in non-human primates. Taken from [Cléry et al., 2015b]

Furthermore, multisensory neurons in those brain areas are sensitive to movements. More specifically, they can be considered as looming detectors [Rizzolatti et al., 1981, Graziano and Gross, 1993, Colby et al., 1993]. Those neurons discharge preferentially for stimuli approaching the body, but not moving away from it (see figure 2.4). Objects in the environment vary in importance to the self depending on their movements. In particular, stimuli looming towards the self have a strong threatening meaning: their potential impact can endanger the body. Perceiving approaching events near the body elicits stereotyped defensive behaviors [Schiff, 1965]. Neurons of VIP and F4 could be a part of a larger network dedicated to body protection. Their roles are more likely to detect potential threat approaching the body and to produce the appropriate defensive motor responses.

The 7b, AIP and F5 parieto-frontal network: coding space for voluntary actions?

A second fronto-parietal network coding the space around the body is constituted of the parietal area AIP, 7b and the frontal area F5. Their neural activities seem to be linked to the coding of the reaching space and to the implementation of voluntary actions, especially grasping. Most AIP neurons respond during the observation of graspable objects, and all discharge during grasping actions. The temporary inac-

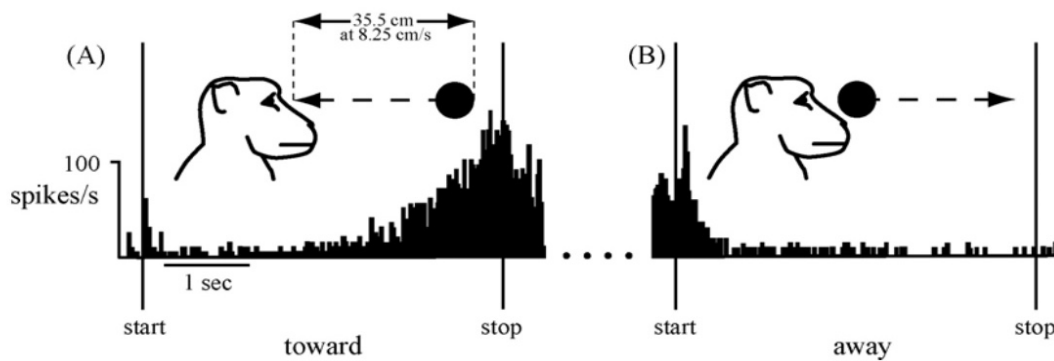


Figure 2.4: Neurons of macaque brain of the F4 area, responding to looming stimuli but not receding ones. Taken from [Graziano and Cooke, 2006]

tivation of AIP neurons and of a part of F5 neurons provokes troubles for grasping. Monkeys became unable to correctly shape their hands to fit presented objects [Gallese et al., 1994, Fogassi et al., 2001]. In area 7b, a large proportion of neurons discharge during motor actions. In area F5, 20% of neurons respond differently to the 3D shape of objects. Their answer depends on the size and shape of the presented objects, coded in motor terms [Murata et al., 1997]. This network activity is linked to voluntary motor actions, coding possible motor interactions of an individual in near space.

2.2.3 Flexibility of peripersonal space

Peripersonal space and tool-use

Personal space size, measured by interpersonal distances, is variable. PPS limits are also flexible. Studies on macaques found that PPS size is modulated by tool use. Authors gave monkeys a small rake that they used to collect objects far from their body. They studied the activity of neurons coding for the space around the hand and found that neurons coding for the space around macaques hand started coding also for the space around the rake after they had been using the rake for a while [Iriki et al., 1996]. This effect does not exist if monkeys just hold the rake without being trained to use it (see figure 2.5). Those modulations were found in both parietal and frontal regions [Maravita and Iriki, 2004, Obayashi et al., 2001]. Thus, PPS is sensitive to motor factors. Tool use is thought to change body schema, as the tool is incorporated into the individual body image after use [Maravita and Iriki, 2004]. The expansion of PPS with tool use in macaques is considered as a consequence of the extended body schema, thus as a reflection of the expansion of the reaching

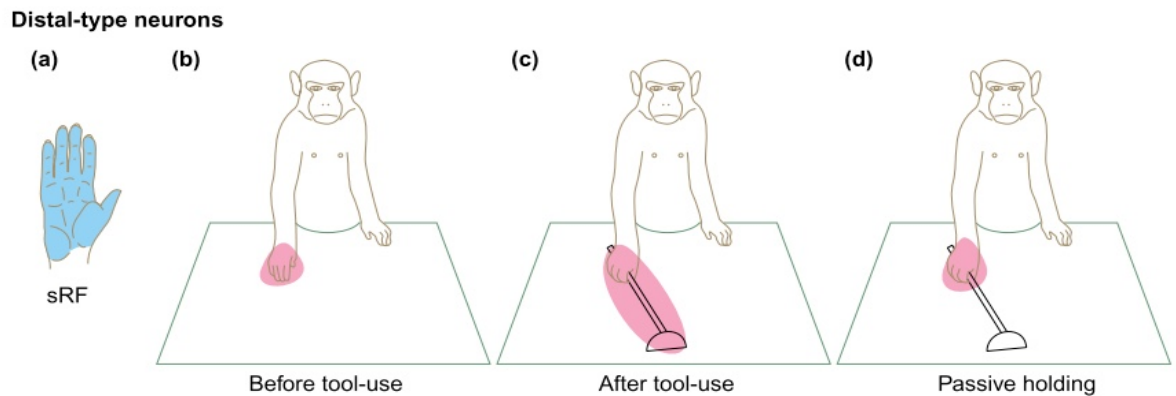


Figure 2.5: Effect of tool use on peri-hand space extension in macaque monkeys. After active practice with the tool, neurons coding for the peri-hand space increase their receptive fields and respond to stimulation around the tool. Taken from [Maravita and Iriki, 2004]

space.

Social coding of peripersonal space?

Some evidence points to possible links between PPS implementation and social cognition, making possible PPS modulations in presence of others. A well-known discovery in neurophysiology is the existence of mirror neurons in premotor cortex and parietal cortex. Those neurons discharge when monkeys are performing a motor action, but also when they observe someone else doing the same action [Rizzolatti and Craighero, 2004]. Both PPS and mirror neurons exist in the frontal area F5. Neurons with both characteristics have also been found [Fogassi et al., 2005, Caggiano et al., 2009], making a possible link between one's own actions and others. Neurons with PPS and social features have also been discovered in the parietal area [Ishida et al., 2010]. Authors found VIP neurons that they called "body matching neurons", as they discharge when stimuli are located around a specific monkey body part, but also when stimuli are located around the corresponding body part of the experimenter

The space near the body, called PPS, is coded in macaque brain by multisensory neurons separately from the far space. It relies on two fronto-parietal networks whose activity is linked to the coding of defensive behaviors and voluntary actions. Multisensory neurons integrate information according to specific rules, that control

the binding of sensory events in space and time. Multimodal coding of events leads to perceptual and behavioral gains, that facilitate appropriate reactions in PPS.

Chapter 3

Peripersonal space in humans

Neuropsychological investigation in brain damaged patients demonstrated a dichotomy in space processing, with different neural bases for the representation of near and far space in human. Patients with a right brain damage can present a specific neglect of one of the hemisphere, most usually the left one (for a review [Làdavas, 2002]). Some of those patients have an impairment only for stimuli located near their body [Halligan and Marshall, 1991]. Other patients neglect stimuli only when they are located in the far space [Cowey et al., 1994]. Overall, these double dissociation shows that human brains code separately the near and far spaces.

Neuroimaging studies in humans also suggests a dichotomy in space processing, with a multisensory coding of PPS [Serino et al., 2011, Bremmer et al., 2001]. A recent meta-analysis confirms the implication of fronto-parietal regions in the coding of PPS, looking at studies investigating brain regions sensitive to unimodal or multimodal stimulations near the body [Grivaz et al., 2017]. The identified brains areas correspond to those identified on monkey brain studies.

3.1 Behavioral measuring methods of peripersonal space

3.1.1 Peripersonal space as a multisensory integration area

The most obvious behavioral method to measure PPS as defined in neurophysiology studies is to measure multisensory integration around the body. As discussed in chapter 2, the multisensory integration leads to faster and more accurate behavioral responses. Those behavioral effects are used to measure PPS in humans.

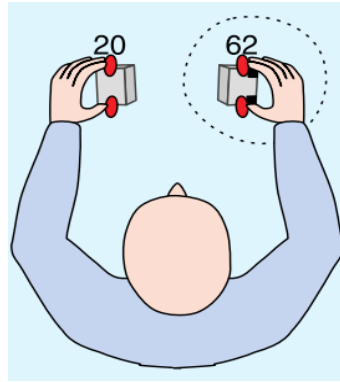


Figure 3.1: Crossmodal Congruency Effect, taken from [Maravita and Iriki, 2004]: participants have to respond to tactile stimulation while irrelevant visual information appears. When the visual is near the tactile, detection is sped up compared to when the visual stimuli is far. Differences of RTs give information on the multisensory integration effect near the body, therefore on PPS. The numbers give the CCE tactile stimulations on the right hand only but for visual distracters located on the left or right hemispaces.

Crossmodal Congruency Effect

The crossmodal congruency effect is based on the fact that multisensory events are detected more rapidly than unimodal ones. In this task, participants need to react as fast as possible to tactile stimulations on their hands. At the same time, they perceive irrelevant sensory information (usually visual stimulation). In the traditional version of the task, participants hold foam cubes. The tactile stimulations and the visual stimulations can appear on the upper part or lower part of the cube (see figure 3.1). The visual stimulations could appear at a congruent or incongruent position in space compared to the tactile one. For example, when participants receive a tactile stimulation on the upper part, the condition is congruent if the visual stimulus is on the upper part too, and incongruent if it is on the lower part. The difference of RTs for tactile detection in the congruent and incongruent conditions is called the crossmodal congruency effect (CCE). The crucial point is to compare the CCE for different positions of the visual distracters in space. As an example, the number in figure 3.4 depicts the CCE values for tactile stimulations on the right hand, but with visual stimuli on the right or left hand. CCE is larger when visual stimuli are near the right hand, indicating a modification of multisensory integration in space.

Multisensory interaction tasks

PPS can be measured by studying audiotactile or visuotactile integration in space. A simple paradigm is to measure the window of space in which auditory or vi-

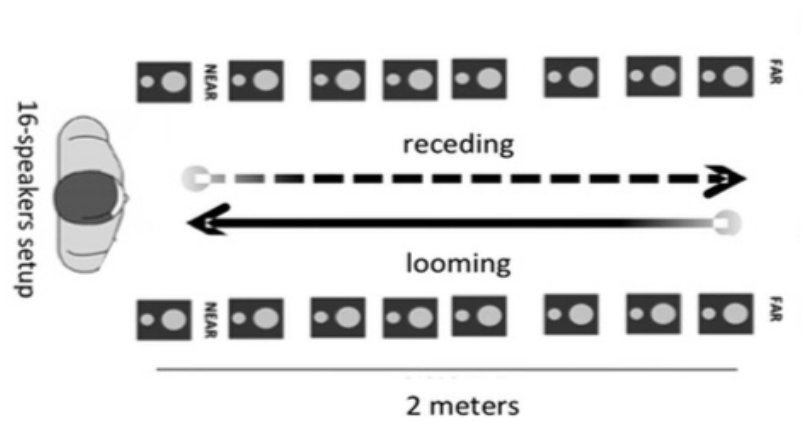


Figure 3.2: PPS measuring technique, by Canzoneri et al 2012. Participants have to detect a tactile stimulation while irrelevant looming or receding sounds are played.

sual stimuli are bound with tactile stimulations. Serino and colleagues compared RTs of tactile detection while irrelevant auditory information appeared near or far from the body to study PPS [Serino et al., 2007]. Recently Canzoneri and colleagues developed a variation of this method, based on audiotactile integration [Canzoneri et al., 2012, Canzoneri et al., 2013b]. The task is still to detect, as fast as possible, tactile stimulations in the presence of spatialized auditory information. Instead of comparing only two positions of sounds in space, they compared RTs for sounds at five different positions in space. They determined PPS boundaries by determining the space in which the presence of the auditory stimuli speed up tactile detection. The granularity of measures in space gives information on the PPS morphometry.

The particularity of Canzoneri’s task is that auditory stimuli are not flashing. The sound, which usually lasts three seconds, is moving in space at a constant speed, looming towards the participant’s body or receding from him (see figure 3.2). PPS in monkeys is coded by neurons sensitive to movements and particularly to looming movements towards the body (see section 2.2.2). Canzoneri and colleagues used PPS sensitivity to movements to elicit larger behavioral effects. They showed that looming sounds have larger effects on RTs than receding ones, as expected.

The cross modal extinction phenomenon

In patients with unilateral brain lesions, a methodology to study multisensory coding of PPS is to measure extinction phenomena. Those patients might fail to identify a stimulus presented on the side opposed to their lesion when a competing

stimulus is presented on the side of the lesion [Bender, 1952, Gainotti et al., 1989]. This phenomenon is called extinction. Extinction happens when both hands are touched simultaneously, but also when one hand is touched while the other one received near by a visual [di Pellegrino et al., 1997, Làdavas et al., 1998] or auditory [Ladavas et al., 2001] stimulation. This effect depends not on the position of the hands, but on the distance between the hand and the visual or auditory stimuli. Those studies shows that the space near the body is coded by multisensory neurons in an egocentric spatial referential, as found for monkeys.

3.1.2 Peripersonal space as a reaching area

One aspect of PPS is to code the possible motor actions in the space. Multiple experimental paradigms are based on reaching possibility to study PPS.

Perceived reachability

This technique aims to measure the perceived reaching space of individuals. Objects are presented to participants at different distances from them. Participants' task is to indicate whether they think that the objects are near enough for them to reach [Valdés-Conroy et al., 2012, Quesque et al., 2016]. Distances at which the objects are evaluated as reachable are considered to be located within PPS boundaries.

Affordances and compatibility effect

An implicit measure of reaching abilities is the study of affordances. Affordances are defined as actions incitement that the environment creates on viewers [Gibson, 1979]. Individuals represent possible actions that they can perform on their environment. This motor representation, called affordances, impacts behavior. People's sensitivity to affordances is measured by the compatibility effect [Ellis and Tucker, 2000, Tucker and Ellis, 1998]. In this task, participants are asked to grasp a grip with their left or right hand at a given signal. At the same time, they look at pictures of graspable objects, typically a cup. The crucial point is that when the handle of the mug is turned to the right for example, participants represent the action of grasping the mug with their right hand. Thus, participants are faster to grasp the grip with their right hand when they are looking at a cup with a handle turned towards their right hand (congruent trials) than towards their left hand (incongruent trials). The difference of RTs between congruent and incongruent trials is called the compatibility effect. This compatibility effect depends on the reaching possibilities

of the participants. There is no compatibility effect when the cup is unreachable: for example if the cup is too far from the participants, or if it is separated from him by a transparent panel [Costantini et al., 2010]. The size of compatibility effects depending on the position of objects in space gives an implicit measure of reaching space of individuals, thus PPS as a reaching area.

Demonstratives use

A possible approach to the distinction between far and near space is through language. Different demonstratives are used to describe objects that are near or far from the body. In English, studies look at the use of *this* vs *that* and *here* vs *there* to designate objects located at different distances in front of them. The distance at which participants stop to use *this* and *here* and start to use *that* or *there* is considered as the limit between the far and near spaces, that could be linked to PPS limit [Kemmerer, 1999].

3.1.3 Peripersonal space as a defensive margin

Another attributed function of PPS is to code a safety margin around the self. The following experimental methods to study PPS are based on behavioral reactions to threat.

The Hand-Blink Reflex

A recent method was developed by Sambo and Iannetti to measure the defensive space around the eyes [Sambo et al., 2012b, Sambo et al., 2012a]. The technique relies on the blink reflex elicited when a potential danger is moving near the eyes. It is a prototypical defensive reflex that may be elicited by abrupt and intensive stimuli in various sensory modalities (visual, auditory and somatosensory). The authors record the electromyographic activity of the orbicularis oculi muscle bilaterally, which is involved in this blink reflex [Berardelli et al., 1999]. To elicit a blink reflex, authors send electrical stimulations on the median nerve on participants wrists [Alvarez-Blanco et al., 2009]. They manipulate the position of the hand in space, to measure the blink reflex when the potential danger is located at different positions in space (see figure 3.3). The intensity of the hand blink reflex (HBR) is not modulated in a linear way by the distance of the hand. There is a critical distance at which the proximity of the hand to the eye starts increasing the HBR: this distance is considered as the limit of the defensive PPS around the eyes (DPPS).

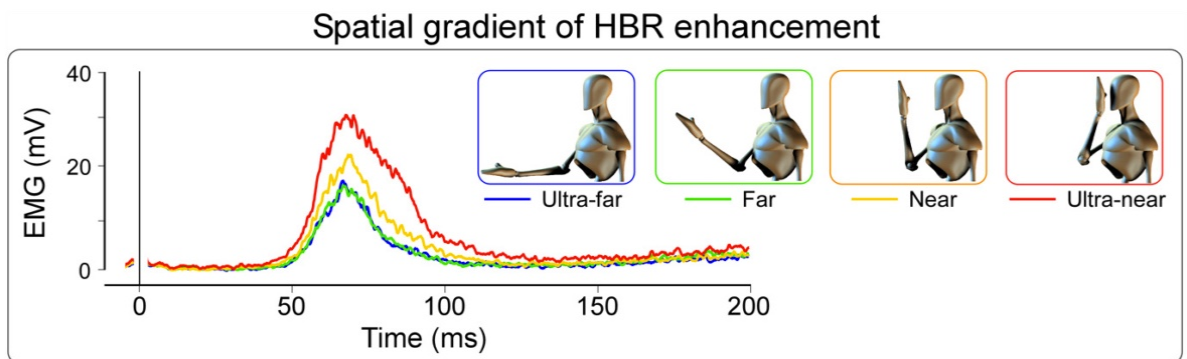


Figure 3.3: Defensive PPS measuring technique, taken from Sambo et al 2013. The activity of the muscle responsible for the blink reflex is recorded by EMG, while an electrical stimulation is administered on participants' wrists. The blink reflex intensity depends on the position of the participants' hand in space.

Time to contact

In this method, participants watch an object looming towards them during one second. Their task is to estimate the time at which the looming stimulus will collide with them. The estimation of time to contact (TTC) is modulated by the emotional valence of the stimuli [Vagnoni et al., 2012], with an underestimation of the time for negative stimuli. This measure would be linked to the protective function of the PPS.

3.1.4 Attentional bias

The line bisection task is based on the fact that healthy humans have a slight leftward attentional bias in the near space, called pseudoneglect. Authors asked participants to cross a line at its middle. The line could be near or far from the participants. When the line was near the body, subjects had a slight leftward bias. When the line was far from the body, participants tended to shift their answer towards the right, closer to the middle of the line. Authors link the dynamic bias in space to a dissociation between PPS and the extrapersonal space [Longo and Lourenco, 2006, Lourenco and Longo, 2009].

3.2 Modulating factors of peripersonal space

3.2.1 Peripersonal space extent is body-centered

As a space of action, we expect PPS to be linked to body characteristics. In macaques, PPS is a body-centered space which can be modulated by body schema extension with tool use. Body schema is a classic concept in neurosciences, referring to individuals' knowledge of their own body structure, that they access through proprioceptive signals and prior knowledge [Berlucchi and Aglioti, 1997].

PPS: multiple sizes for different limbs

First of all, PPS is body-centered. CCE measures with visuotactile tasks found that multisensory integration effects around the hands are linked to the distance between visual information and the hand. It is not affected by the position of the body in space, confirming that PPS is defined in the body reference frame [Maravita et al., 2003]. Furthermore, a study using Canzoneri's method found that PPS of different limbs do not have the same size. Authors measured PPS of participants' face, trunk or hand by placing tactile stimulations on those different limbs [Serino et al., 2015]. The larger PPS is around the trunk, then the hand and the face. Interestingly, hand PPS depends on hand position in space. When the hand is near the trunk, hand PPS merges into the trunk PPS.

The link between body schema and PPS has been found using several experimental paradigms. Arm length is linked to PPS extent measured by line-bisection task, with an increased PPS for longer arms [Longo and Lourenco, 2007]. Body perception can be strongly manipulated with illusions. A paradigm to modify body perception is the full body illusion. Participants see a virtual body being stroked while receiving the similar stroke on their own body. When touches are synchronized, participants can experience an out of body experience, feeling that their own body is shifted towards the virtual one. Noel and colleagues found that PPS is shifted towards the virtual body during a full body illusion, with a PPS extension in the front area (towards the virtual body) and a contraction in the back space [Noel et al., 2015]. Maister and colleagues used the same type of paradigm, but only in the face. The en-face illusion consists of feeling a touch on the face while observing a synchronous one on a partner's face. A feeling of ownership over the other's face is reported in this situation. A partial remapping of PPS is observed in this case, with an increased multisensory integration around the face of the partner [Maister et al., 2015]. Other

types of body perception manipulation impact PPS. Seeing one's hands in a mirror increased CCE for the space near the mirror [Maravita et al., 2002b], and CCE is increased around their hands' shadows [Pavani and Castiello, 2004].

Tool use

Tool use is a specific motor ability, widespread across species which give a consistent advantage in terms of survival. We already discussed in part 2.2.3 that PPS is extended with tool use for macaque monkeys. Indeed, multisensory integration near the body is increased around a tool when a macaque uses it. This PPS modulation is usually interpreted as the result of the extension of reaching abilities due to the incorporation of the tool into the individual body schema [Maravita and Iriki, 2004].

In humans, studies also found extension of PPS with tool use. First, hemineglects studies bring strong evidence that space near the body perception is changed with tool use. Berti and colleagues looked at the effect of tool use on the hemineglect bias of patient with near space neglect [Berti and Frassinetti, 1996]. Those patients have a bias in line bisection tasks in the near space but not in the far space. However, the bias appears in the far space if the bisection line task in the far space is performed using a stick, interpreted as a PPS extension. In healthy participants, a shift in bisection line bias has also been found with tool use, arguing for PPS extension [Longo and Lourenco, 2006].

Extensions of PPS with tool use have also been demonstrated in patients suffering from crossmodal extinction. A crossmodal extinction was found for tactile stimulation on one hand and visual stimulation near the other hand. After tool use, the extinction was also present when visual stimulation was located near the extreme part of the tool [Farnè and Làdavas, 2000, Farnè et al., 2007]. This effect depends on the length of action of the tool: no PPS extension was found after short tool use, or after long tool use with short area of effectiveness. It also depends on the exposure to the tool: holding a tool without practicing with it before does not extend PPS [Farnè et al., 2005].

The effect of tool use on PPS was investigated with multisensory integration methods. Studies using cross-modal congruency effects consistently found PPS extension to the extreme part of the tool after time of practice. Maravita and colleagues did a audiotactile CCE measure, with tactile stimulations and visual stimulations located at the extremity of tools (see figure 3.4) [Maravita et al., 2002a]. They found an interference effect between tactile integration and visual distracters located at the

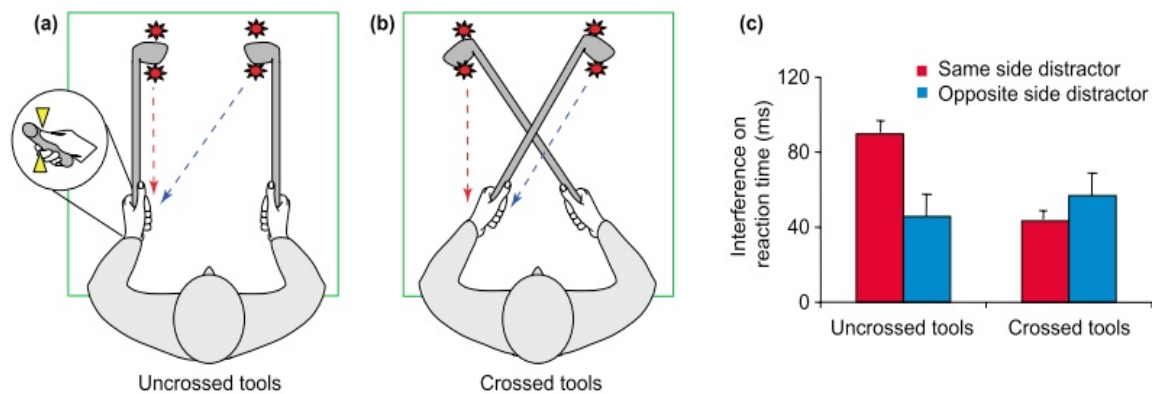


Figure 3.4: Effect of tool use on peri-hand space extension, measured by a crossmodal congruency effect task. Taken from [Maravita and Iriki, 2004]

extremity of the tool, arguing for an extension of the visuotactile integration area of the hand. The CCE was stronger when tactile stimulation was applied on the same hand that was holding the tool, and this regardless the location of the tool in space. This result goes in the direction of the inclusion of the tool in the body schema, as an extension of the hand. CCE modulations were also found using a computer mouse as a tool linking the personal space to the related computer screen space [Bassolino et al., 2010]. Using Canzoneri's PPS measurement task, extension of PPS size was found after tool use [Canzoneri et al., 2013b], and also with a wheelchair after a passive training [Galli et al., 2015]. Moreover, PPS of amputees is increased when they wear their prosthesis [Canzoneri et al., 2013a].

Studies on PPS as a reaching space also found extension with active tool use. In their study, Bourgeois and colleagues asked participants reachability judgments about objects located in front of them. They had to evaluate if they could reach the objects with their hand, and with the given tool [Bourgeois et al., 2014]. Reachability measures of the tool and the hand were higher when participants hold the tool. Moreover, while holding the tool, the reachability judgments of the hands became more variable. Those results argue for an inclusion of the tool in the body schema that leads to an increased reaching space, but also for a less precise representation of the hand action space. Finally, tool use modified demonstratives use to refers to objects. An increase of the space of the use of near space demonstratives (*this* in english, and *este* in spanish) was found after long tool use [Coventry et al., 2008].

Motor coding of peripersonal space

PPS implementation is linked to action production near the body. As a space coded for the purpose of action, PPS is dependent of motor factors.

Motor constraints change PPS extent. In a line bisection paradigm, Lourenco and colleagues found that changing arm motor abilities by hanging wrist weights to participants lead to a decrease of the bias in bisection line, interpreted as a contraction of PPS [Lourenco and Longo, 2009]. Object affordances are diminished when arms are constrained, only when objects are near the body [Iachini et al., 2014b]. Paradigms using looming stimuli also found changes with motor constraints. Time-to-contact evaluations are underestimated when participants are constrained by a chin-rest. This result is interpreted as a PPS extension, an increase of the body safety margin [Vagnoni et al., 2017]. Physical fitness could impact PPS. Time to contact underestimation is correlated with fitness [Neuhoff et al., 2012], as if the weak abilities to behaviorally respond to physical threat increased the safety margin around the body. Finally, Bassolino and colleagues also found evidence for PPS contraction after arm immobilization, measured with Canzoneri's audiotactile paradigm [Bassolino et al., 2014]. They found no effect of arm overused on PPS.

Furthermore, PPS depends on the possible actions that we can perform on the external world. In the presence of objects, the easiness to act with those objects changes action possibilities, thus changing PPS. For example, a cup is easier to grasp when its handle is turned towards the subjects. Affordances are increased with the easiness to act with the environment [Ellis and Tucker, 2000]. Furthermore, PPS measured with reachability judgments also increases with the easiness to grab objects presented in front of participants [Valdés-Conroy et al., 2012]. This effect is modulated by handedness [Linkenauger et al., 2009], suggesting that perceived reachability really depends on the relation between the external world and motor abilities. The multisensory integration also depends on the easiness to interact with objects, as CCE is stronger during the observation of objects of high manipulability (as a cell phone) compared to low manipulability ones (as a computer screen) [van Elk and Blanke, 2011].

It has been shown that PPS linked to defense mechanisms (DPPS) as measured by the blink reflex is influenced by gravitational cues. Gravity makes objects fall in one particular direction [Bufacchi and Iannetti, 2016]. DPPS is larger in the direction where it is more probable to be hit by falling objects. When individuals are standing, DPPS is more developed above the head than below the head. When participants

lie down, it becomes symmetrical.

3.2.2 Emotional influence on peripersonal space

Emotional valence

PPS is described as a personal, defensive margin for the self. We expect emotional valence of stimuli to modulate PPS, and especially threatening cues. First, PPS is increased in frightening contexts. Taffou and colleagues investigated PPS size using Canzoneri's technique, for dog-phobic and control participants, in presence of dog growls (phobic situation) or sheep bleats (non-phobic situation). PPS extended in the phobic condition, in the phobic group only [Taffou and Viaud-Delmon, 2014]. With the same audiotactile protocol, Ferri and colleagues measured PPS size with positive, negative and neutral sounds. They found an increase of PPS size only with negative sounds compared to the neutral. Positive sounds did not modify PPS compared to neutral ones [Ferri et al., 2015]. Evidence for a contraction of PPS with negative stimuli also comes from patient studies, with a reduction of the cross-modal extinction with negative stimuli [Vuilleumier and Schwartz, 2001].

Emotional valence of stimuli also modulates PPS measured as a reaching space. Coello and colleagues found that dangerous objects decreased reaching space, but only when the objects are spatially oriented to threat participants (the blade of the cutter box directed towards the participant body) [Coello et al., 2012]. An extension of reaching space with positive stimuli compared to neutral and negative ones has also been reported [Valdés-Conroy et al., 2012]. Studies on reachability space also found modulation in anxious situations. Induced anxiety decreases perceived reachability space [Graydon et al., 2012]. Rock climbers underestimate their reaching space when they feel anxious because of high heights [Nieuwenhuys et al., 2008]. Emotional stimuli valence also change time to collision estimation: threatening stimuli are evaluated as colliding sooner than neutral ones [Vagnoni et al., 2012].

Anxiety and Claustrophobia

Trait anxiety is linked to PPS size. Sambo and colleagues modeled the HBR size modulation with distances [Sambo and Iannetti, 2013]. They found that the size of the DPPS correlated with trait anxiety, but not with claustrophobia. A second study relates PPS and anxiety. Using line bisection, Lourenco and colleagues found that claustrophobic fear traits predicted the size of PPS [Lourenco et al., 2011].

Threat perception from looming stimuli

In the described methods to study PPS, different types of stimuli are used. Line bisection tasks always use still stimuli, cross-modal congruency effects use flashing events, whereas Canzoneri's method and time to contact tasks use moving stimuli. This difference is important, as moving stimuli have different relevance for the self and could trigger different responses. The relevance of looming stimuli compared to receding ones is documented.

Looming stimuli appear to be a fundamental component of threat for the body surface [Gibson, 1986]. Detection of looming movements is a fundamental capacity across species. As described in section 2.2.2, looming and receding events are coded differently by multisensory neurons for macaque monkeys, with looming processing integrated preferentially in the defensive neural network. Looming detector neurons were found on pigeon and locust brains [Sun and Frost, 1998, Rind et al., 2008]. Authors claim that those neurons have a role during flight for obstacles avoidance. Psychophysical studies in adult humans found a sensitivity to looming visual stimuli at early stages of visual processing [Regan and Beverley, 1978]. Newborns make a distinction between looming and receding stimuli [Orioli et al., 2017]. Newborns and infants produce stereotypical defensive reactions to looming stimuli but not receding ones [Ball and Tronick, 1970, Nández and Yonas, 1994]. Thus, looming stimuli processing elicits mechanisms linked to the defense of the body.

The method of Canzoneri uses both looming and receding sounds. It seems that the direction of the moving sound changes the behavioral reaction of participants, as a differences are usually observed between looming and receding sounds [Canzoneri et al., 2012, Serino et al., 2015]. Looming sounds increase the multisensory boosting effect compared with receding sounds.

3.3 Peripersonal space as safety zone or space of voluntary motor actions

Space perception is distinct for near and far spaces, in both human and non-human primates. The space near the body is dependent on body schema, motor abilities, emotional and social factors. The biological function of this space is not clear. As in monkey studies, two main functions are usually attributed to PPS. PPS could be a safety zone for the body, and/or the space of possible motor actions [de Vignemont and Iannetti, 2015]. Multiple arguments defend both possible

functions.

PPS can be a defensive margin for the body. Multisensory integration near the self would allow a better defense of the body, as it speeds up motor reactivity and detection accuracy. PPS modulations in negative emotional contexts go into the direction of defensive mechanisms. Multisensory integration space increases in threatening contexts, thus the area where people are faster to react increases [Taffou and Viaud-Delmon, 2014, Ferri et al., 2015]. In climbing, estimated reaching space decreases in anxious situations, decreasing risk taking [Nieuwenhuys et al., 2008].

Another common function attributed to PPS is that it codes the reaching space, the space where individuals can make motor actions. The main result in this direction is that PPS is increased by tool use, which increases reaching distances. Also, motor affordances depend on the possibility to grab the object. When objects are far or when a glass window separates people from the objects, affordances disappear.

Those two functions are not incompatible, even if their expected modulations are not the same direction (extension or contraction) as in the threatening context example. Those two functions could rely on two separated fronto-parietal networks, as suggested in monkey brain studies [Cléry et al., 2015a]. Furthermore, it is not possible to know nowadays if different experimental methods to study PPS are linked to one suggested function, to both or to something else. Clearly, the so-called defensive PPS (DPPS), measured by the eye-blink reflex, should be linked to defensive reactions. The space measured by affordances seems more linked to the possibility to grab objects. In experimental threatening contexts, we can expect to elicit the defensive function. As looming stimuli could represent danger, time to contact method and Canzoneri's task may be linked to a defensive representation of space. Below those considerations, it is unclear what PPS characteristics are elicited by different methods.

As in monkeys, human brains code differently the space near the body. Multiple behavioral methods have been developed to measure PPS in humans. They are based on identified PPS characteristics: PPS is coded by multisensory neurons for the purpose of actions. PPS size is flexible and can be modulated by motor and emotional factors.

Chapter 4

Peripersonal space in social contexts

4.1 Space perception and social cognition

Humans are a social species, most of our time is spent in social contexts. The human mind and brain have specific social abilities, that allow people to live in group, cooperate with each other and coordinate their actions. Fundamental aspect of social cognition are affiliation and the constitution of a trustworthy social group that cooperates [Bowles and Gintis, 2003]. Affiliation can be manipulated experimentally by minimal group attribution: formation of group identity on an arbitrary assigned criterion. That experimental minimal group assignment appears to be relevant for participants, as they change their behavior according to it. Participants tend to reward more and punish less perceived in-group members [Hewstone et al., 1981]. People are more likely to help an injured individual when he is perceived as in-group [Levine et al., 2005]. Emotion perception of others' changes depending on their group assesment [Montalan et al., 2012].

Furthermore, another main aspect of social cognition is that humans have high abilities to perform collective actions. They are able to coordinate their action in space and time to perform joint actions. To be able to perform joint actions, people need to understand others' behaviors and produce appropriate behavioral response. They need to understand motor actions, infer others people intentions and take into consideration others' spatial perspective [Sebanz and Bekkering, 2006]. This coordination happens in everyday life with little conscious effort, as during a conversation, dancing, or lifting an object together.

Recent studies tackle the question of possible social influences on space perception. During joint action, participants automatically represent the action of the partner. This representation of the other's task could necessitate taking the other's perspective, and thus changing the spatial reference frame. Samson and colleagues found that individuals automatically compute the spatial perspective of others [Samson et al., 2010]. Computation of the other's perspective was found even when subjects were suggested to ignore the other participant, indicating that the process is fast, involuntary and requires small cognitive resources. This process was recently studied more precisely. On a mental rotation task, Böckler and colleagues showed that when two people co-attend to the same stimuli, they automatically take the other's perspective into consideration [Böckler et al., 2011]. In the study, two subjects, facing each other, have to do a mental rotation task of a hand picture. Authors showed a flattening of the performance rotation curve when participants jointly attended to the stimuli. Interestingly, this effect was not sensitive to the social status of the co-actor (cooperation or competition). Those studies suggest that the frame of reference of an individual during joint action is not strictly egocentric, but a mix (or a switch) between egocentric and allocentric reference frames.

The Simon effect reveals also a social impact on space perception. This effect is based on a spatial compatibility effect: an overlap in the spatial location between stimuli and responses occurs, so that stimuli appearing on the right are responded to faster with a right than a left response key (see [Simon and Rudell, 1967]). In a study of Sebanz and colleagues, subjects had to press a left response key when red stimuli appeared and to press a right response key when green stimuli appeared [Sebanz et al., 2003]. In addition, a picture of an index finger pointing to the left or to the right was presented. Due to the spatial compatibility effect, participants were faster to respond to red stimuli (thus with the left key) when the finger pointed to the left than to the right (see figure 4.1). Similarly, participants were faster to respond to green stimuli (thus with the right key) when the finger pointed to the right. This effect did not occur when participants were instructed to respond to only the red or only the green stimuli. However, when participants shared the task with a partner - one responded to red stimuli only and the other to green stimuli only - the spatial compatibility effect reappeared. Participants were slower to respond when the finger was pointing at their partner. One possible interpretation of those results is that participants attributed a part of the space to their partner.

The spatial compatibility effect is also modulated by the spatial position of the

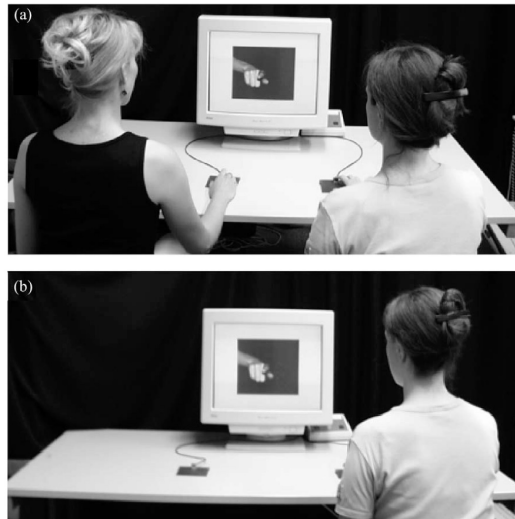


Figure 4.1: Setting of the social Simon task for the joint and individual conditions, taken from [Sebanz et al., 2003]

two co-actors: the effect exists only when the co-actors are seated within arm reach but not when they are farther away [Guagnano et al., 2010]. It is also modulated by social contexts. Mc Clung and colleagues investigated the impact of minimal group attribution on the social Simon effect. They found a social Simon effect when participants performed the task with an in-group member, but not with an out-group member [McClung et al., 2013]. Overall, those studies showed that human's use of space can be modulated by social factors.

4.2 Social modulation of peripersonal space

Some recent studies looked at multisensory integration based PPS in social contexts. Heed and colleagues tested the effect of joint action on a visuo-tactile CCE task [Heed et al., 2010]. Two participants were facing each other, both holding the same foam cubes. Participants performed a joint action, they "shared the task": one participant had to respond to the position of the tactile stimuli while the second was judging the visual ones. Only the RTs of the tactile task were analyzed. Authors found a decrease of the CCE when participants performed a joint action, an indirect evidence of a contraction of PPS during joint action. The effect disappears if participants are far from each other, or if they perform a similar task rather than a complementary one. The same results are found for an audiovisual task shared by two partners, with stimuli located further away from their body (50cm from participants) [Wahn et al., 2017]. Recent studies using Canzoneri's task tested if the social

relationship between two individuals can change PPS. Teneggi and colleagues found that after performing an economical task with a cooperative partner rather than a selfish one, people extended their PPS towards this partner [Teneggi et al., 2013]. The same results were found with moral attributions to a virtual partner: PPS extends towards moral partners but not immoral ones [Pellencin et al., 2017].

Reaching space is also modulated in social contexts. In presence of another individual in the near space, the estimated reaching space is extended [Fini et al., 2014, Fini et al., 2015]. Those studies are performed in virtual reality. The effect is specific to the social aspect of the stimuli, and also depends on the motor capacities of the other. The reaching space is not modified when the other individual can not act (in the experiment, the virtual partner is tied to a pole). Affordances are also impacted by social environment. A spatial alignment effect is found around objects unreachable by participants but reachable by a confederate [Costantini et al., 2011].

Finally, the DPPS is enlarged in presence of others. HBR also exists when the hand of the participants is near a partner's face [Fossataro et al., 2016]. The size of the HBR is correlated with the participant's empathy trait.

4.3 Peripersonal space and personal space

An open question is to understand whether the personal space studied by psychologists through interpersonal distances modulations and the PPS defined by neuroscientists are linked. Both concepts refer to space just surrounding the body. They are linked to motor abilities, sensitive to body representation, to emotional and social factors. What links could there be personal space and PPS?

A few recent studies try to make the link between those two concepts. Two studies compared the impact of tool use on both personal space and PPS as a reaching space, in a within participants design. In both studies, manipulation of long tools increases reachability judgments [Patané et al., 2016, Quesque et al., 2016]. Patane and colleagues found no modulation of interpersonal distances with tool use, whereas Quesque and colleagues found increased interpersonal distances with tool use.

Social factors seems to modulate in the same way personal space and reachability estimations, judged with 3d virtual avatars [Iachini et al., 2014a]. Both distances were larger for male compared to female avatars. A recent study found that anxiety traits increases both personal space and reaching space [Iachini et al., 2015]. However, another study found distinct modulations of personal space and PPS as

reachability space after a collaborative task [Patané et al., 2017].

Those experimental studies do not allow to draw a conclusion on the relationship between personal space and PPS, as results between studies are not consistent. Moreover, those studies just tested PPS as the reachability space.

Space perception in social condition has been widely studied by social psychologist, but not by neuroscientists. For a long time, social neurosciences focused on single-subject studies, looking at processing of social stimuli. Nowadays, more and more studies focus on real social interaction with multiple-participants paradigms, making possible the study of space perception in social contexts. Few recent studies found modulation of PPS during joint action, but also PPS modulation by high-level cognitive processes, such as moral attribution to a partner. As PPS coding is linked to actions, it is likely to be modulated during shared actions.

Part II

Experimental contribution

Three studies have been conducted during this PhD. Each one is reported in a chapter.

- **Chapter 6** investigates lateral PPS in isolation and its links with handedness
- **Chapter 7** investigates the impact of social context on PPS boundaries.
- **Chapter 8** interrogates the limits of the audiotactile PPS measuring technique used in the first two studies. Variations and alternative options are described.

Chapter 5

General Methodology

In order to study how social factors could impact space management in human, we choose a task measuring PPS that would address low level sensory integration mechanisms. We chose Canzoneri’s audiotactile paradigm to measure PPS because of its precision on the description of PPS in space. To be able to test if the position of a partner impact PPS, we chose to measure PPS in the right and left hemispaces of two participants seated side by side. We first needed to measure the lateral PPS of participants in isolation, as previous studies only measured it in the front.

An important aspect of that task is that it is based on auditory-tactile integration mechanisms, and more specifically on the processing of auditory looming sound. Audiotactile integration is less studied than audiovisual integration. Auditory perception of distance, involved in perception of movement in depth, is not much studied as well.

5.1 Experimental methodology

In all the performed studies, we used a PPS measurement technique based on Canzoneri’s audiotactile detection task [Canzoneri et al., 2012]. In this task, participants had to detect tactile stimulations located under their index while an irrelevant sound was looming towards them. The 3s sound was followed by a silence of 3.7s to 4.3s (see figure 5.1). In one trial, a tactile stimulation could arrive at different delays after the time onset, corresponding to different distances from the participant body. Furthermore, unimodal tactile trials were tested before and after the sound appearance (Tbefore and Tafter), to measure an eventual effect of expectancy during a trial. Rather than measuring PPS in the front, we chose to investigate PPS in the left and

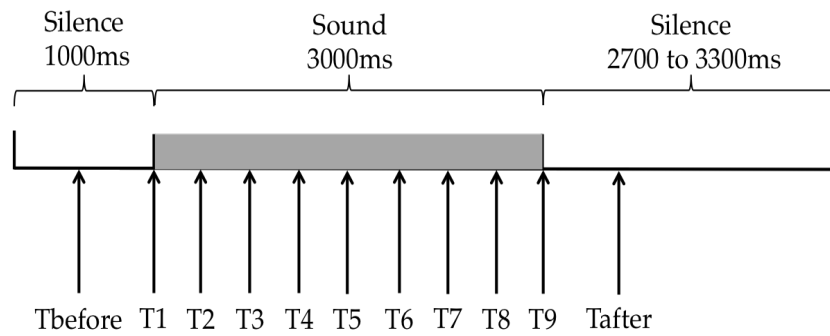


Figure 5.1: Time description of a trial

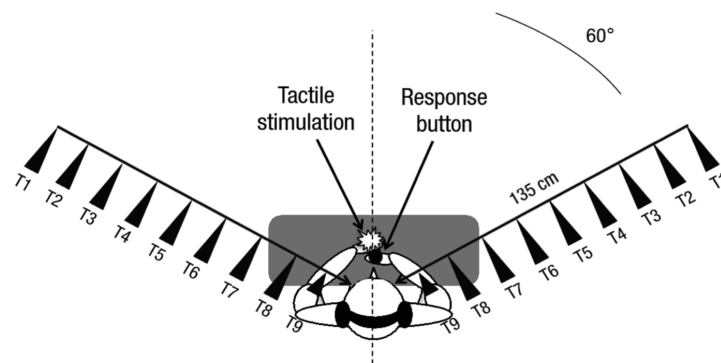


Figure 5.2: Protocol used to measure PPS boundaries in the experimental studies. Sounds are looming from the right or left hemispace while the participant is performing a speeded tactile detection task. The tactile stimulation can happen when the sound is at different distances from the body.

right front hemifields (see figure 5.2). Analysis of reaction times indicates PPS size. We took as a proxy of PPS boundary the further distance at which the presence of the sound source started to boost tactile detection.

5.2 The auditory space

Perception of sound in depth

Localizing a sound in 3D space is a complex cognitive process that takes into account many different acoustic parameters. Sound-source localization can be divided into two processes: localization of the direction of the source and of the distance to the source. The perception of the sound direction is mainly based on interaural differences [Rayleigh, 1907]. As our two ears have different positions in space, they receive different sound signals. If the sound source is not located in the median plane, the

incoming sound wave will not reach both ears at the same time. Moreover, the presence of the listener's head between the two ears will also create a sound shadowing effect (level attenuation) on the ear opposite to the direction of incidence. These interaural time difference (ITD) and interaural level difference (ILD) are important cues to process sound lateralization. More precisely, the frequency-spectrum of the signal reaching each ear canal will be strongly affected by the complex sound diffraction effects occurring on the listener's torso, head and pinnae. These frequency cues are especially important to localize the elevation of the source and to discriminate sounds coming from the front or the rear hemispaces. Taken together, the interaural differences and the frequency-spectrum variations generated by body diffraction, provide the listener with effective cues for assessing the direction of a sound source.

For the localization of sound in depth, the main acoustic cues are the sound level and the reverberation [Shinn-Cunningham, 2000]. The sound level is the most important cue, as a listener easily detects its variation. In open-air conditions, the sound level decreases by 6 dB when the distance to the source is doubled. Thus, the sound level is a relative cue: it does not allow an estimation of the absolute distance to the source without any prior information on the signal it actually emits. The second acoustic cue for distance perception is reverberation. This phenomenon is caused by the multiple reflections of the acoustic waves occurring on obstacles and space boundaries and creates a diffuse surrounding sound field. In contrast with the level of the direct sound, in a closed space, the level of the reverberated sound field does not depend on the distance to the source. Consequently, the ratio between the level of the direct sound and that of the reverberated field gives an absolute cue on the sound-source distance.

The absolute distance estimation of stationary sound sources is usually a difficult task [Zahorik et al., 2005], in which participants are not accurate for non-familiar sounds. However, participants are accurate in the comparison of distances between two sources at different distances. In our task, we are using looming sounds, and compare the effect of continuously varying sound distances. As distance perception in depth is accurate for relative comparison but not in term of absolute distance, we will not present the results in terms of geometrical distances but in terms of delay from the sound onset.

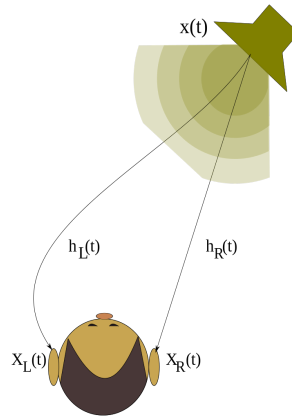


Figure 5.3: HRTF or head-related transfer function are filters applied to sounds to create virtual 3D spatialized sounds. It describes sound modulations between the source and the inner ears, taking into account the propagation in space and the reflection on the body and inside the auricle

Spatialization of auditory stimuli in 3D space

This audiotactile protocol requires a high level of precision of the sound localization in 3D space. The 3D audio spatialization techniques developed at IRCAM allow us to control precisely the spatial aspect of the auditory information in our studies. Several techniques exist to create 3D sounds, e.g. binaural rendering on headphones or Ambisonics on an array of loudspeakers surrounding the listener. In this study, we chose the binaural rendering technique on headphones.

Binaural sound-rendering on headphones provides the participants with all necessary cues to perceive sound in their own referential. The technique uses the Head-Related Transfer Function filters (or HRTF) that characterize the transformation of the signal during its propagation from a particular point in space to the entrance of the listener's ear canals (see figure 5.3). The HRTFs convey all the above described acoustical cues linked to interaural differences as well as to spectral cues caused by the diffraction on the listener's torso, head and pinnae. In addition to HRTFs, the reflections and the reverberation of the room are added, and the sound intensity of the direct sound is modulated to create a perception of moving sound in three dimensions. The sound spatialization was performed with IRCAM's Spat real-time signal processing library running in the Max/MSP environment.

5.3 Multisensory integration processes involved in the audiotactile method

Our task is based on the effect of sound on tactile detection. First, it is important to note that tactile perception is the most appropriate sensory information to study PPS. Tactile stimulations are always per definition within PPS. Experimental evidence supports the idea that auditory information can influence tactile perception. Sounds can modulate tactile perception of a surface: sound frequency can change the tactile perception of smoothness [Guest et al., 2002]. More precisely, there are interactions between the frequency of sounds and the perceived frequency of a tactile stimulation [Yau et al., 2009]. Moreover interaction between sounds and tactile stimulation can be dependent on their position in space. Kitagawa and colleagues found that sound distractors interfere with the localization of tactile stimulations only if the sounds are near the body [Kitagawa et al., 2005]. Conversely, tactile information can also bias auditory perception. The localization of auditory information in space is biased by the presence of tactile stimuli [Caclin et al., 2002]. Taken together, auditory and tactile information are bound depending on their spatial proximity (see [Kitagawa and Spence, 2006] for a review).

Our task uses sounds moving in depth. Few studies looked at multisensory integration processes of cues moving in depth. Audiovisual integration takes into account the speed of propagation of auditory information and of visual information. As light speed is faster than sound velocity, the auditory cues of a stimulus are expected to arrive to the perceiver after the visual cues of the same event. The expected delay between both sensory inputs increases with the distance to the perceiver [Sugita and Suzuki, 2003, Alais and Carlile, 2005]. Thus, depth information is taken into account for multisensory integration. For looming stimuli, the speed of movement is also taken into account. Studies on visuotactile integration showed that tactile sensitivity is increased after looking at a visual looming stimulus, but only at the expected time and space of the collision [Kandula et al., 2015, Cléry et al., 2015a].

Several studies on PPS are based on audiotactile integration [Serino et al., 2007, Farnè and Làdavas, 2002, Bassolino et al., 2010]. We will try to accommodate the above-mentioned properties of both auditory and tactile stimulations and of their interaction to use the audiotactile detection task proposed by Canzonerri in order to

evaluate the flexibility of PPS.

Chapter 6

Handedness and peripersonal space

This work was presented at different scientific events:

- at the Joint Action Meeting 2017 (JAM) : "Impact of a shared goal on the perception of the space around the body", Londres, UK, July 2017 (oral presentation)

- at the Aegina Summer School 2017 : "Lateral PPS boundaries in social context", Aegina, Greece, June 2017 (poster)

- at the Frontiers du Vivant PhD Students Retreat 2017, "Lateral PPS boundaries are influenced by handedness", Hyères, France, June 2017 (poster)

- at the Mind, Brain and Body Symposium (MBBS 2017), "Lateral PPS boundaries are influenced by handedness", Berlin, Germany, March 2017 (poster), where It receives the Prize of the best Poster.

It is submitted for publication:

- Lise Hobeika, Isabelle Viaud-Delmon and Marine Taffou, *Anisotropy of lateral peripersonal space is linked to handedness*

6.1 Description of the study and main findings

PPS boundaries are flexible and dependent on the easiness to act. Humans have asymmetric motor abilities, in particular the dominant hand has advantages in term of movements precision and reaction time. We tested whether lateral PPS boundaries are differently modulated by motor abilities, measuring PPS of left-handed and right-handed participants. Data suggested that hand dominance and PPS extent are

linked. Right-hander, but not left-handers, had asymmetrical lateral PPS. This result is coherent with the literature showing that motor capacities change PPS extent. We found that right-handers PPS is anisotropic, right PPS hemisphere being smaller. Those results are coherent with the idea of PPS as zone of defense, where a larger safety margin is needed in the hemisphere of less precise motor actions. Finally, left-handers PPS is not asymmetrical, which could be explained by their proneness to use both hands for many everyday tasks.

6.2 Anisotropy of lateral peripersonal space is linked to handedness

See the study on the following pages.

Anisotropy of lateral peripersonal space is linked to handedness

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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 terms 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 hemisphere 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 hemispacial 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/equipements/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

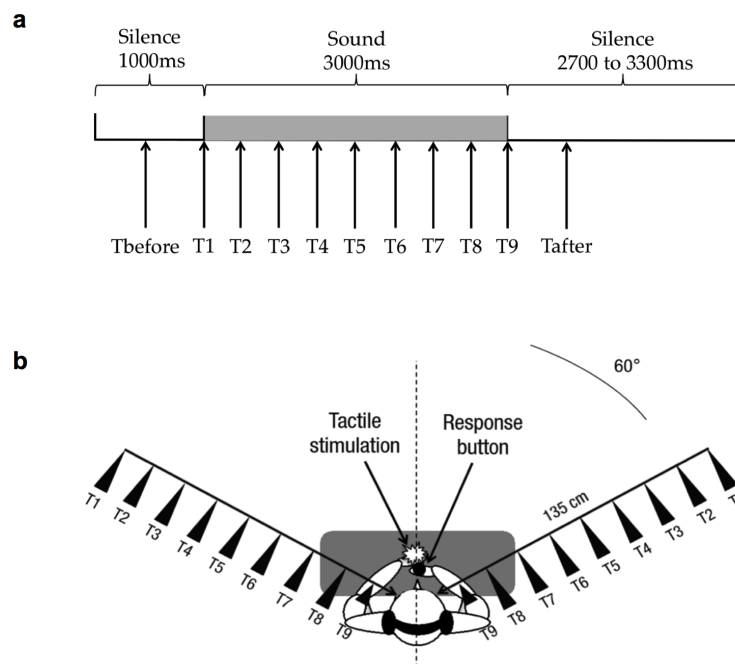


Fig. 1 Experimental paradigm. (a) Description of a trial. (b) The figure depicts a right-handed participant in the experimental setup. Participants responded with their dominant hand to a tactile stimulus delivered on their other hand while task-irrelevant sounds approached them from the frontal hemi-field, 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), HEMISPHERE (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. $\ln(\text{RTs})$ were considered outliers if they exceeded more than two standard deviations from the mean $\ln(\text{RTs})$ and trimmed from the analyses (4.51% of trials). The remaining data were averaged for each participant, for each HEMISPHERE 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 HEMISPHERE (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, HEMISPHERE 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 HEMISPHERE * 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 HEMISPHERE ($p = 0.61$), of HANDEDNESS ($p = 0.52$) and no significant interaction of HANDEDNESS * HEMISPHERE ($p = 0.24$) 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 HEMISPHERE (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 HEMISPHERE * 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 hemisphere. No significant effect of HEMISPHERE ($p = 0.52$) was found. As shown in the left graph of Fig. 2a, when the sound came from the left hemisphere, 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 hemisphere than in the right hemisphere.

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 HEMISPHERE ($p = 0.52$) or of the two-way interaction HEMISPHERE * 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'

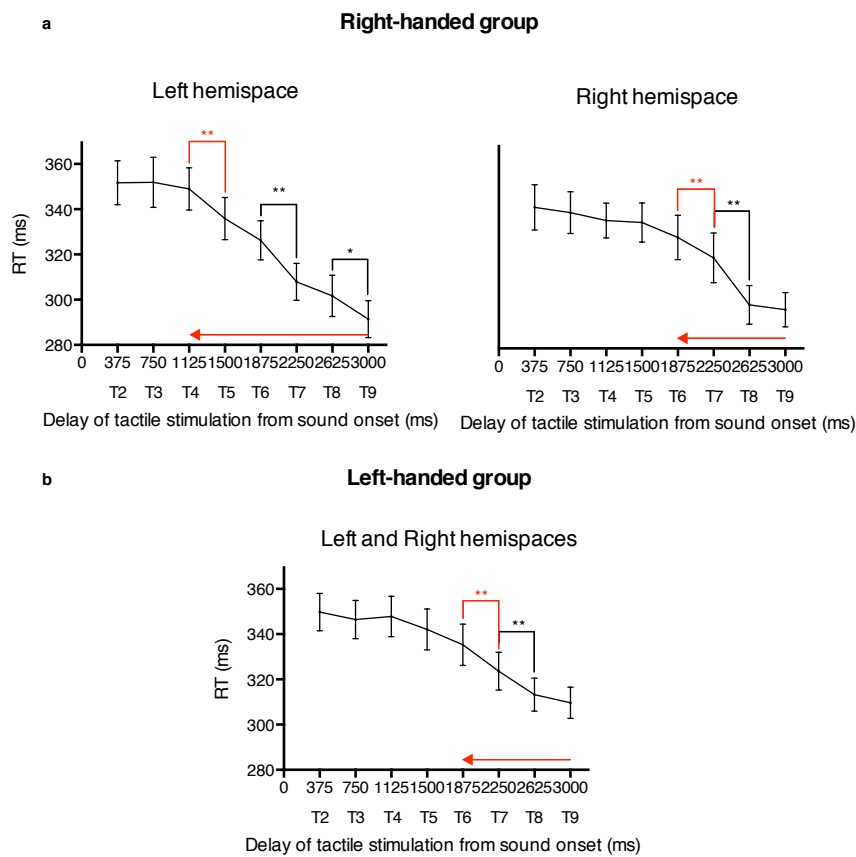


Fig. 2 Audiotactile test results. Two groups of participants – right-handers (RH) and left-handers (LH) – performed the audiotactile test. They responded to a tactile stimulation while a task-irrelevant sound was looming toward them from the left or right hemisphere. This figure reports the mean tactile reaction time (\pm 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 hemisphere 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 was 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 suggests 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 constitute 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.

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6.3 Additional analysis

6.3.1 Supplementary Information

Analysis of the impact of sound presence on tactile detection

We conducted an ANOVA on the mean RTs, with the within subject factor DISTANCE (11 levels: Tactile-Before, T1, T2, T3, T4, T5, T6, T7, T8, T9, Tactile-After). The main effect of DISTANCE was significant ($F_{(10,530)} = 82.59, p < .01, \eta_p^2 = .609$) suggesting that RTs were influenced by the time of tactile stimulation delivery. As shown in figure 6.1, RTs in the unimodal trials Tactile-After ($M = 334.08ms, SEM = 6.51$) were significantly faster than RTs in the unimodal trials Tactile-Before ($M = 372.02ms, SEM = 6.82$) (Post-hoc Newman-Keuls' test: $p < .001$). However, given that RTs at Tactile-After were significantly slower than RTs at T7 ($M = 315.89ms, SEM = 6.31$), T8 ($M = 305.24ms, SEM = 5.65$) and T9 ($M = 300.97ms, SEM = 5.48$) (Post-hoc Newman-Keuls' test: $p < .001$ in all cases), we can exclude the possibility that participants were faster at late delays because of the increasing probability of receiving a tactile stimulation along trials. RTs in the unimodal trials Tactile-Before were significantly slower than RTs in bimodal trials T2, T3, T4, T5, T6, T7, T8, and T9 (Post-hoc Newman-Keuls' test: $p < .001$ in all cases) however it was not the case when the tactile stimulation synchronously occurred with sound onset (at the T1 distance). RTs in the bimodal trials T1 ($M = 372.89ms, SEM = 7.00$) did not significantly differ from RTs in the unimodal trials Tactile-Before (Post-hoc Newman-Keuls' test: $p = .811$). 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: $p < .001$ in all cases). This suggests that at the distance T1 (tactile stimulation occurred at sound onset), the sound was not processed when tactile stimulation occurred.

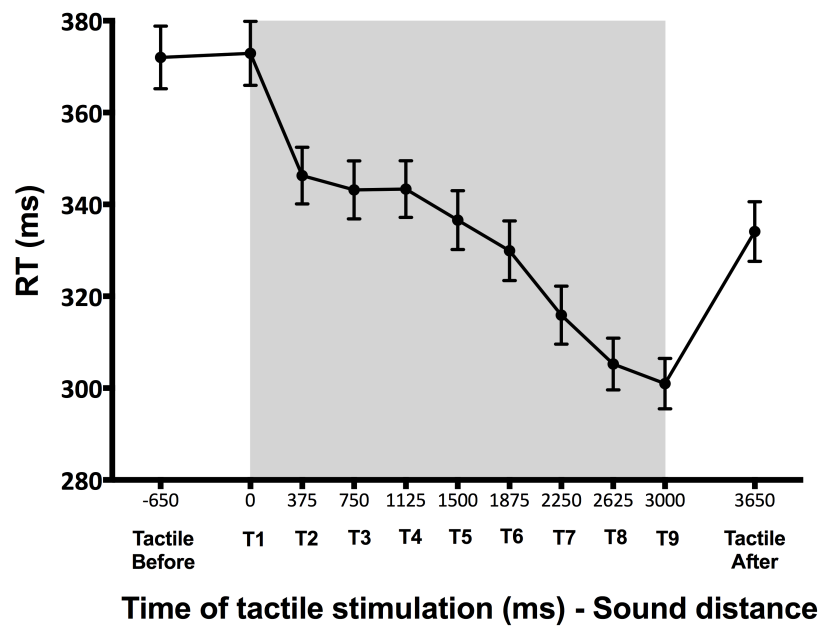


Figure 6.1: Impact of sound presence on tactile detection. This figure reports participants' mean tactile reactions times ($\pm SEM$) as a function of the distance of the sound source from participants' body when tactile stimulation occurred (from the farthest distance T1, corresponding to the shortest time between tactile stimulation and sound onset, to the closest distance T9, corresponding to the longest time between tactile stimulation and sound onset). It also represents reactions times (RTs) in response to tactile stimulations presented without sound, before the sound onset (Tactile-Before) or after the sound offset (Tactile-After). The shaded region indicates the duration of the sound.

Chapter 7

Peripersonal space in social contexts

This work was presented at different scientific events:

- at the Joint Action Meeting 2017 (JAM) : "Impact of a shared goal on the perception of the space around the body", Londres, UK, July 2017 (oral presentation)

- at the Aegina Summer School 2017 : "Lateral PPS boundaries in social context", Aegina, Greece, June 2017 (poster)

- at the Motor Behaviour and Emotion conference : "Lateral PPS boundaries in social context", Lille, France, November 2016 (poster)

- at the 17th International Multisensory Research Forum (IMRF2016) : "Peripersonal space boundaries in a social context", Suzhou, China, June 2016 (poster)

- at the Frontiers du Vivant PhD Students Retreat 2016, "Sharing a task modulates lateral peripersonal space boundaries.", Les Issambres, France, May 2016 (poster)

- at FdV/AIV Thematic Workshops 2016, "Are lateral peripersonal space boundaries shaped by social context?", Paris, France, March 2016 (poster)

This work is written in the form of a draft of research article in view of being submitted to a scientific journal for publication.

7.1 Study description and main findings

We investigated whether PPS boundaries were modulated in social contexts. We used a modified version of Canzoneri's audiotactile interaction task [Canzoneri et al., 2012]

in three groups of right-handed participants. In each group, participants performed the task both in isolation and with another participant, who was either inactive, doing the same task in collaboration or doing the same task in competition. PPS boundaries were modulated only when participants shared a goal with a partner, in the form of an extension on the right hemispace, and independently of the location of the partner. This suggests a complex modulation of PPS for tasks performed in collaboration.

7.2 Social coding of the multisensory space around us

See the study on the following pages.

Social coding of the multisensory space around us

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Abstract

Spatial arrangement of individuals is an important dimension during social interaction. The field of proxemics has widely studied humans' use of space when they interact with each other. Yet, little is known about how social context modulates the perception of space. Here, we showed that collaborating with others modulates the perception of near space. The extent of peripersonal space (PPS), i.e. the area coded in the brain as being near the body, changed during collaborative tasks. Specifically, when participants performed a task in collaboration with another individual seated next to them, their PPS extended on the right side. This effect was not due to the mere presence of the other person given that PPS lateral boundaries were not influenced if the individual seated beside is an auditor and does not perform the task. Moreover, no modulation was found when participants were in competition with one another. Those results indicate a complex modification of spatial information processing during tasks performed in collaboration, which questions the organization of motor control during actions in groups. When we collaborate with others, a supra-individual representation of the space of action could be at stake in order to adapt our individual motor control to an interaction as a group with the external world.

Keywords: peripersonal space, social interaction, audio-tactile integration, spatial perception, collaboration, 3D sound

1. Introduction

The space around the body, called PPS, is the space where physical interactions between the body and the external world occur. PPS is opposed to the more distant extra-personal space. In the field of neurosciences, neurophysiological studies in monkeys as well as brain imaging and lesion studies in humans have evidenced this dichotomy and showed that PPS is coded in the brain through multisensory integration mechanisms (Colby, Duhamel, & Goldberg, 1993; Farnè & Làdavas, 2002; Gentilucci et al., 1988; Graziano & Cooke, 2006; Graziano & Gross, 1993; Làdavas & Farnè, 2004). This dedicated multisensory representation is thought to have a role in apprehending events occurring in the space near the body, which require the implementation of particularly appropriate and precise behaviors: be it for dealing with imminent threat (Graziano & Cooke, 2006) or for attaining an object of interest (Brozzoli, Makin, Cardinali, Holmes, & Farnè, 2012). Furthermore, PPS displays flexible boundaries that are sensitive to motor action factors (Ladavas & Serino, 2008; Maravita & Iriki, 2004) as well as to affective components (Ferri, Tajadura-Jiménez, Väljamäe, Vastano, & Costantini, 2015; Taffou & Viaud-Delmon, 2014), so that multisensory integration related to the body can be adaptively boosted according to the context.

A turn in neuroscience has been recently introduced with the investigations of the brain mechanisms underlying social and affective psychological processes, spurred on by the fact that human species is a social species and that most of their behaviors are dependent on a social context (Cacioppo, 2010). For now, few studies have addressed the question of whether and how space perception mechanisms are influenced by social factors in humans. In social neurosciences, space perception studies are based on low-level multisensory integration tasks. Heed et al. measured the effect of task sharing on multisensory integration within PPS. They measured a crossmodal congruency effect (i.e. a spatial congruency acceleration effect (Pavani, Spence, & Driver, 2000)) as participants did a task alone or shared it with a partner located within their PPS. They observed that performing a task together with a partner modulates multisensory processes within PPS and propose that this modulation may allow others' actions in the space near the body (Heed, Habets, Sebanz, & Knoblich, 2010). A post-effect of the valence of social interaction was also found at the low sensorimotor level with a modification of PPS boundaries' location. Teneggi et al. measured participants' PPS extent in presence of an inactive person, who had had a cooperative or egoist behavior in an economical game performed before the measure. The study showed that, after the economical game, PPS boundaries extended towards the partner, allowing their integration to one's PPS, only if the social interaction had been satisfying (Teneggi, Canzoneri, di Pellegrino, & Serino,

2013).

This body of work emerging in neurosciences can be linked to the study of proxemics and spatial behavior in social psychology. This field has widely investigated spatial behaviors in social context by examining interpersonal distances, i.e. the distance that individuals keep between them. Interpersonal distance refers to an area around the body as the PPS, and is described as “an area with invisible boundaries that individuals actively maintain around themselves, into which others cannot intrude without arousing discomfort” (Aiello, 1987; Hall, 1966; Hayduk, 1978). Differences in the adopted interpersonal distances were observed as a function of age, gender, culture, affective evaluation of the other individual and the relationship between the individuals (Aiello, 1987; Hayduk, 1983). Whereas these studies investigated the impact of the social context established by knowledge about the other person’s characteristics on interpersonal distance, some studies have also examined interpersonal distances modulation when a social interaction establishes the social context. Specifically, it was found that participants seat closer when they are asked to solve a problem as a group compared to individually (Batchelor & Goethals, 1972). It was also observed that participants adopt closer distance with another individual after a cooperative compared to a competitive interaction (Gifford, 1982; Tedesco & Fromme, 1974). Moreover, group membership also affects interpersonal distances: assigning participants to minimal groups change their spatial behaviors (Novelli, Drury, & Reicher, 2010).

In the present study, we investigated whether minimal high-level social manipulations such as collaborating or competing with an unknown individual would influence low-level multisensory coding of the space around the body, i.e. PPS. Collaborating with a partner constitutes a core element of collective actions (Sebanz & Bekkering, 2006; Vesper, Butterfill, Knoblich, & Sebanz, 2010), being a necessary component to perform joint actions with others. Participants in a protest, supporters in a stadium are perfect strangers and unaware of others actions however they know that they are part of a collective action and share a goal together. In contrast, competitive context forces participants to perform self-centered, individualistic actions. Very few studies focused on the modification of space perception with high-level social manipulation. We hypothesized that social contexts would modulate PPS boundaries. Given that PPS is asymmetric for right-handers (right PPS being smaller than left PPS) (Hobeika, Viaud-Delmon, & Taffou, n.d.), we measured PPS boundaries on both those hemispaces.

To measure PPS boundaries, we used Canzoneri and colleagues’ audiotactile task (Canzoneri, Magosso, & Serino, 2012). Participants performed a speeded tactile detection task while irrelevant sounds were looming towards them from the frontal hemifield, either from the left or the right

hemisphere. Tactile stimuli were delivered at different delays from sound onset (T1, T2, T3, T4, T5, T6, T7, T8, T9). Thus, participants perceived the sound source at different distances from their body when they processed the tactile stimulus (from the farthest distance at T1 to the closest distance at T9). As the delay increased, the looming sound was perceived as closer. It is now well established that a sound speeds up tactile detection when located near, but not far from, the body, i.e. within PPS (Canzoneri et al., 2012; Serino, 2016). Consequently, we sought for the distance from participants' body, at which sound starts to boost tactile RTs as a proxy of PPS boundaries. In order to measure PPS of participants' trunk, participants were instructed to keep their hands aligned with their mid-sagittal plane and in contact to their body (Serino et al., 2015). We examined if being in collaboration (collaborative experiment) or in competition (competitive experiment) with an unknown individual modulates PPS boundaries. Moreover, in order to evaluate the contribution of the mere social presence on PPS modulation, we also measured the impact of the presence of another individual on PPS boundaries (audience experiment).

2. Experiment 1: collaboration

2.1 Material and methods

2.1.1 Apparatus

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. Participants were instructed to fix a visual target located at 65cm in front of them. Auditory stimuli were presented through Beyer Dynamic DD770 headphones. The auditory stimulus was a sound of bubbling water (32 bits, 44100 Hz digitization), processed through binaural rendering using a 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 small loudspeaker on the palmar surface of the left index finger of participants. 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.

2.1.2 Design and procedure

Participants were asked to place their left index finger on the vibrator and to press a button with their right 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 hemisphere (-60°), with a spatial location varying from 135 to 20 cm from the center of the participant's head. The sound velocity was $38.33 \text{ cm}\cdot\text{s}^{-1}$. 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 (see Figure 1).

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 respond as quickly as possible to the tactile stimuli. They were asked to emphasize speed, but to refrain from anticipating. Reaction times (RTs) were measured.

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. 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 -650 ms (Tbefore) and at 3650 ms (Tafter) from sound onset.

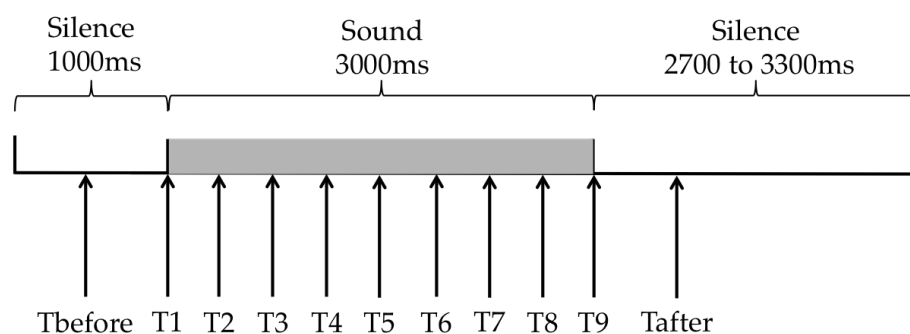


Figure 1: Description of a trial. On each trial, one tactile stimulation was delivered at one among eleven possible delays from sound onset (Tbefore, T1, T2, T3, T4, T5, T6, T7, T8, T9, Tafter).

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 total test consisted of a random combination of ten target stimuli in each of the 22 conditions. The factors were: CONDITION (two levels: isolated/in dyad), HEMISPHERE (two levels: left/right) and DELAY (eleven levels: Tactile before, T1, T2, T3, T4, T5, T6, T7, T8, T9 and Tactile after). There were a total of 440 trials with a tactile target, randomly intermingled with 40 catch trials. Trials were equally divided in 10 blocks of 48 trials, lasting about 5 min each.

Sample sizes were decided priori based on previous work examining PPS boundaries with the same audiotactile paradigm (Ferri et al., 2015; Taffou & Viaud-Delmon, 2014; Hobeika et al. n.d.).

2.1.3. Social Manipulation

Every participant performed the audiotactile task in a main condition and in a control condition: respectively paired with another participant (dyad) and isolated (see Figure 2 panel a). The order of the social conditions was counterbalanced between participants. In the dyad condition, participants were always paired with another participant of the same gender. The two participants were seated side by side, at 1m from each other. In the isolated condition, an empty chair remained beside the participant. Each participant was assigned to the left or right seat and stayed in that position during the whole experiment. In this experiment, the dyad of participants performed the audiotactile task as a team. We affiliated participants and created a group by giving them a shared goal. We told them that we were recording their global performance as a dyad and not their individual performance

2.1.4 Participants

Thirty individuals with normal audition and touch took part in the study. All of them were right-handed. Participants received a financial compensation of 10€/hour for their participation. They provided a written informed consent prior to the experiment, which was approved by the Institutional Review Board of the French National Institute of Health and Medical Research (INSERM, IRB00003888).

2.1.5 Data processing

The performances were analyzed in terms of RTs. Given that it is well known that the distribution of RTs is not normal (Luce, 1986; Ulrich & Miller, 1993), we used the natural logarithm transformation of RTs (\ln) before trimming outlier RTs from the analyses. For each subject, each

delay and each hemispace 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. For the analyses, ln(RTs) were averaged for each subject and for each of the 44 conditions separately (2 HEMISPACE * 11 DELAY * 2 CONDITION). The means we obtained were transformed back with an exponential function. Mean tactile RTs were submitted to repeated measures analysis of variance. A significance threshold of $p < .05$ was set for all statistical tests, and Newman-Keuls correction was applied for pairwise comparisons. All tests were two-tailed and the assumptions justifying their use were examined. The normality assumption was also tested and Greenhouse-Geisser adjustments were conducted when the homoscedasticity assumption was not verified.

2.2 Results

Among the participants, three participants had a high rate of misses in at least one of the social condition (isolated condition: 10% and 18.1% of miss, $m \pm sd$ of the sample: $1.8 \pm 3.8\%$, in a dyad condition: 14.5% of miss, $m \pm sd$ of the sample: $1.2 \pm 2.7\%$) and were therefore excluded from the RTs analyses. The remaining participants were accurate in performing the task as the rates of omissions ($0.70 \pm 1.8\%$) can attest. We also excluded one participant from the analyses because his mean RT was substantially elevated (497.67 ± 127.76 ms, $m \pm sd$ of the sample: 364.55 ± 57.88 ms), giving us reason to suspect that he did not correctly perform the task. There were twenty-six remaining subjects (14 females, age 24.08 ± 4.39).

2.2.1. Comparison between unimodal and bimodal trials

We first verified that multisensory integration globally speed up tactile detection in bimodal trials compared to unimodal trials. We conducted an ANOVA on the mean RTs, with the within subject factors DELAY (11 levels: Tactile_Before, T1, T2, T3, T4, T5, T6, T7, T8, T9 and Tactile_After). The global effect of DELAY was significant ($F_{(10,250)} = 61.23$, $p < .001$, $\eta_p^2 = .710$) suggesting that RTs were influenced by the time of tactile stimulation delivery (see appendix panel a).

RTs in the unimodal trials Tactile_Before were significantly slower than RTs in the bimodal trials T2, T3, T4, T5, T6, T7, T8 and T9 (Post-hoc Newman-Keuls' test: $p < .001$ in all cases). RTs at Tactile_Before did not significantly differ from RTs in the bimodal trials at T1 (Post-hoc Newman-Keuls' test: $p = .967$). RTs in the bimodal trials at T1 were also significantly slower than all the other RTs in the bimodal trials (at T2, T3, T4, T5, T6, T7, T8 and T9; Post-hoc Newman-Keuls' test: $p < .001$ in all cases) suggesting that, even though the sound started at the same time as

the tactile stimulus delivery in that condition, the auditory stimulus was not perceived by participants. Thus, RTs at T1 were excluded from the rest of the analysis.

RTs in the unimodal trials Tactile_After were significantly faster than RTs at Tactile_Before (Post-hoc Newman-Keuls' test: $p < .001$). Given that RTs at Tactile_After were significantly slower than RTs at T7, T8 and T9 (Post-hoc Newman-Keuls' test: $p < .001$), we can exclude the possibility that participants were faster at late delays because of the increasing probability of receiving a tactile stimulation along trial.

2.2.2 Verification of the anisotropy of lateral PPS

We first verified that PPS is anisotropic by examining the effect of HEMISPACE on bimodal RTs (Hobeika et al., n.d.). We conducted an ANOVA on the mean RTs with the within-subjects factors HEMISPACE (2 levels: Left/Right) and DELAY (8 levels: T2, T3, T4, T5, T6, T7, T8 and T9). The ANOVA revealed a main significant effect of DELAY ($F_{(7,175)} = 42.29$, $p < .001$, $\eta_p^2 = .629$). The analysis also revealed that the two-way interaction HEMISPACE x DELAY was significant ($F_{(7,175)} = 5.17$, $p < .001$, $\eta_p^2 = .171$), indicating that tactile detection were dependent on the temporal delay of tactile stimulation delivery from sound onset and the hemispace of origin of the sound source. The effect of the factor HEMISPACE was not significant. Thus, we analyzed the effect of the social manipulation with the others factors separately on the left and on the right PPS boundaries.

2.2.3 Effect of the social manipulation on PPS

We conducted separated ANOVA for the left and the right hemispace, with the between subject factor SEATING (2 levels: Left/Right) and the within subject factors SOCIAL CONDITION (2 levels: Isolated/In Dyad), and DELAY (8 levels: T2, T3, T4, T5, T6, T7, T8, T9).

In the left hemispace, analysis indicated only a significant effect of DELAY ($F_{(7,168)} = 36.77$, $p < .001$, $\eta_p^2 = .605$). The others factors and interactions were not significant. Sound in the left hemispace started to boost tactile detection when tactile stimulation is administrated at T4. 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: $p < .001$). RTs further decreased at the later delays. Participants' RTs were significantly faster when the tactile stimulus occurred at T7 than at T6 (Post-hoc Newman-Keuls' test: $p < .001$) and RTs were also significantly faster when the tactile stimulus occurred at T9 than at T8 (Post-hoc Newman-Keuls' test: $p < .05$). 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: $p < .01$ in all cases).

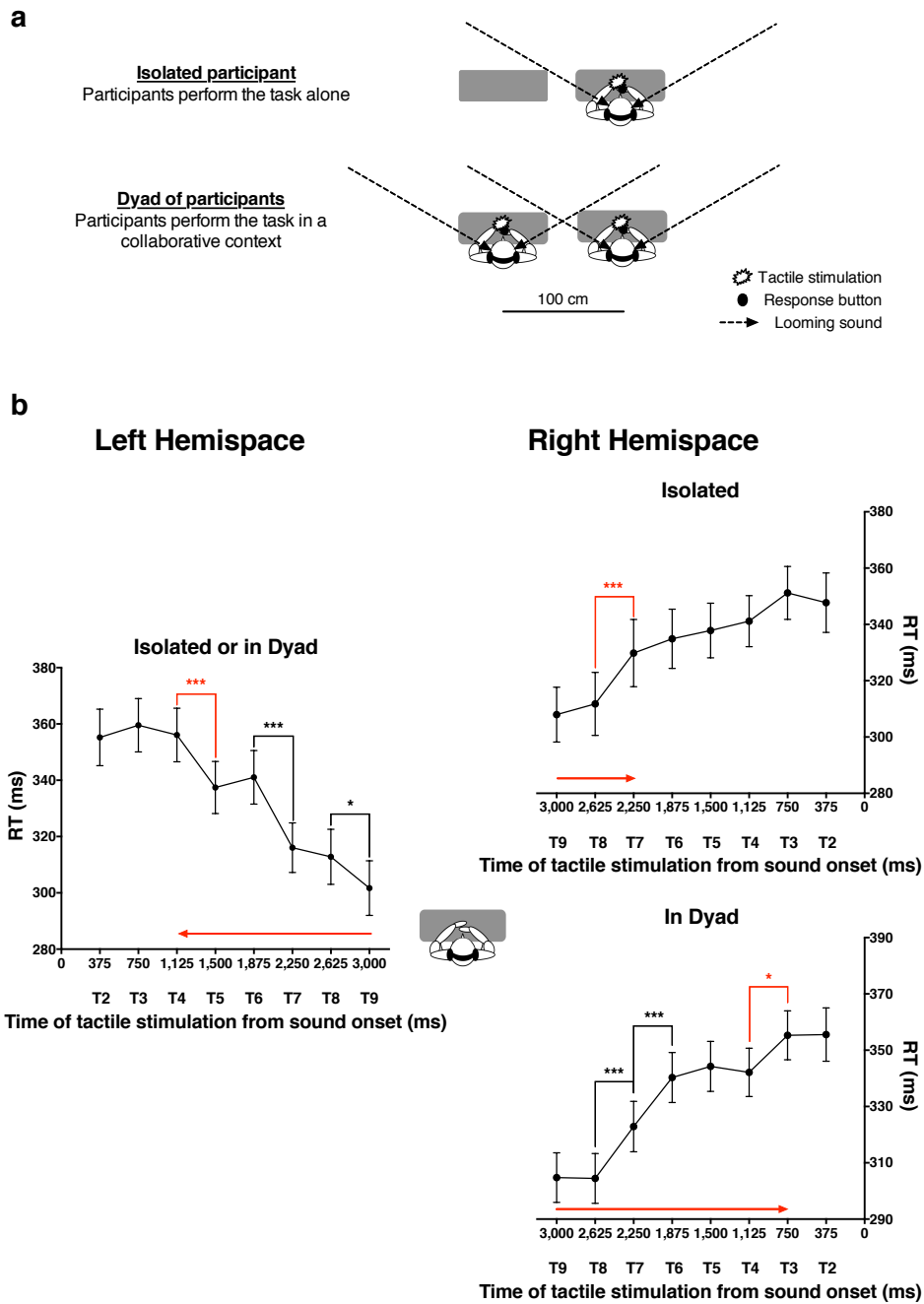


Figure 2. Influence of collaboration on near space coding. **a.** Participants performed the audiotactile task by responding to a tactile stimulation while a task-irrelevant sound was looming towards them from the left or right hemisphere and in two different social conditions: they were performing the task isolated or in a dyad in a collaborative context. **b.** This figure reports the mean

tactile reaction times (\pm SEM) as a function of the delay of tactile stimulation delivery from sound onset for the left hemispace (left graph) and for the right hemispace (right graphs). The significant decreases of RTs are indicated by means of asterisks. The significant decrease of RTs corresponding to the critical delay at which sound starts to boost tactile processing is indicated by means of red asterisks. The red arrows illustrate the extent of PPS boundaries from participants' body.

In the right hemispace, analysis revealed a significant two-way interaction SOCIAL CONDITION * DELAY ($F_{(7,168)} = 2.24$, $p = .033$, $\eta_p^2 = .085$), and a significant main effect of DELAY ($F_{(7,168)} = 27.13$, $p < .001$, $\eta_p^2 = .531$). The effect of the others factors and interactions were not significant. When participants performed the task in a dyad, sound in the right hemispace started to boost tactile detection when tactile stimulation was administrated at T4 (see Figure 2 panel b). Participants' RTs were significantly faster when the tactile stimulus occurred at T4 compared to when the tactile stimulus occurred at T3 (Post-hoc Newman-Keuls' test: $p = .016$). RTs further decreased at the later delays. Participants' RTs were significantly faster when the tactile stimulus occurred at T7 than at T6 (Post-hoc Newman-Keuls' test: $p < .001$) and RTs were also significantly faster when the tactile stimulus occurred at T8 than at T7 (Post-hoc Newman-Keuls' test: $p < .001$). 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: $p < .05$ in all cases), except for RTs at T4 and T6 which are just marginally different ($p = .074$). In contrast, when participants were isolated, sound in the right hemispace started to boost tactile detection when tactile stimulation was administrated at T8 (see Figure 1 panel b). Participants' RTs were significantly faster when the tactile stimulus occurred at T8 compared to when the tactile stimulus occurred at T7 (Post-hoc Newman-Keuls' test: $p < .001$). Moreover, RTs were significantly faster when the tactile stimulus was delivered at T8 and T9 as compared to when the tactile stimulus was delivered at T2, T3, T4, T5, T6 and T7 (Post-hoc Newman-Keuls' test: $p < 0.001$ in all cases).

2.3 Discussion

Collaborating with a partner modulates right PPS boundaries. PPS right boundaries were farther away when participants were performing the task together with another individual than when they were isolated. No significant effect of the factor Seating Position was found: the change in PPS boundaries' location did not depend on whether the partner was sitting on the left or on the right side of participants. Thus, our results show that PPS left boundaries were not influenced by the

social context, i.e whether participants were isolated or in a dyad. Right PPS boundaries were impacted by the social manipulation. The right PPS boundaries were located farther away from the body when participants were in a cooperative dyad than when participants were isolated.

3. Experiment 2: competition

In this experiment, we tested the impact of competition on PPS. Participants performed the audiotactile task either isolated or in dyad with a competitive task.

3.1 Material and methods

3.1.1 Apparatus

The apparatus are similar than in the previous experiment, see section 2.1.1.

3.1.2 Design and procedure

Design and procedure are similar than in the previous experiment, see section 2.1.2.

3.1.3. Social Manipulation

As in the previous experiment, every participant performed the audiotactile task in a main condition and in a control condition: respectively paired with another participant (dyad) and isolated (see Figure 3 panel a). The order of the condition, with which participants began, was counterbalanced between participants. In the dyad condition, participants were always paired with another participant of the same gender. The two participants were seated side by side, at 1m from each other. In the isolated condition, an empty chair remained beside the participant. Each participant was assigned to the left or right seat and stayed in that position during the whole experiment. In this experiment, the dyad of participants performed the audiotactile task in competition. We told them that at each trial, we were recording only the fastest answer and not their individual performance.

3.1.4 Participants

Thirty individuals with normal audition and touch took part in the study. All of them were right-handed. Participants received a financial compensation of 10€/hour for their participation. They provided a written informed consent prior to the experiment, which was approved by the Institutional Review Board of the French National Institute of Health and Medical Research

(INSERM, IRB00003888).

3.1.5 Data processing

Data processing is similar than in the previous experiment, see section 2.1.5.

3.2 Results

Among the participants, one had a high rate of misses (5.45% of miss, $m \pm sd$ of the sample $1.24 \pm 1.08\%$) and was therefore excluded from the analyses. The 29 remaining participants (16 females, age $m \pm sd$: 23.45 ± 4.15) were accurate in performing the task.

3.2.1 Comparison between unimodal and bimodal trials

We first verified that multisensory integration globally speed up tactile detection in bimodal trials compared to unimodal trials. We conducted an ANOVA on the mean RTs, with the within subject factors DELAY (11 levels: Tactile_Before, T1, T2, T3, T4, T5, T6, T7, T8, T9 and Tactile_After). The global effect of DELAY was significant ($F_{(10,280)} = 76.34$, $p < .001$, $\eta_p^2 = .732$) suggesting that RTs were influenced by the time of tactile stimulation delivery (see appendix panel b).

RTs in the unimodal trials Tactile_Before were significantly slower than RTs in the bimodal trials T2, T3, T4, T5, T6, T7, T8 and T9 (Post-hoc Newman-Keuls' test: $p < .001$ in all cases). RTs at Tactile_Before also significantly differed from RTs in the bimodal trials at T1 (Post-hoc Newman-Keuls' test: $p = .011$). RTs in the bimodal trials at T1 were also significantly slower than all the other RTs in the bimodal trials (at T2, T3, T4, T5, T6, T7, T8 and T9; Post-hoc Newman-Keuls' test: $p < .001$ in all). Thus T1 significantly differed from Tactile_Before, but also to all others bimodal trials. The expected behavioral effect of multisensory is an acceleration of RTs around 25ms at least (as seen in the others two experiments, and in the literature (Canzoneri et al., 2012; Taffou & Viaud-Delmon, 2014)). As Tactile_Before differs from T1 of 7ms and from T2 of 24ms, it is likely that the stimulation was not perceived as bimodal. Thus, T1 was excluded of the rest of the analysis.

RTs in the unimodal trials Tactile_After were significantly faster than RTs at Tactile_Before (Post-hoc Newman-Keuls' test: $p < .001$). Given that RTs at Tactile_After were significantly slower than RTs at T7, T8 and T9 (Post-hoc Newman-Keuls' test: $p < .001$), we can exclude the possibility that participants were faster at late delays because of the increasing probability of receiving a tactile stimulation along trial.

3.2.2 Verification of the anisotropy of lateral PPS

We first verified that PPS is anisotropic by examining the effect of HEMISPACE on bimodal RTs (Hobeika et al., n.d.). We conducted an ANOVA on the mean RTs with the within-subjects factors HEMISPACE (2 levels: Left/Right) and DELAY (8 levels: T2, T3, T4, T5, T6, T7, T8 and T9). The ANOVA revealed a main significant effect of DELAY ($F_{(7,196)} = 44.27$, $p < .001$, $\eta_p^2 = .613$). The analysis also revealed that the two-way interaction HEMISPACE x DELAY was significant ($F_{(7,196)} = 2.90$, $p < .01$, $\eta_p^2 = .094$), indicating that tactile detection were dependent on the temporal delay of tactile stimulation delivery from sound onset and the hemispace of origin of the sound source. The effect of the factor HEMISPACE was not significant. Thus, we analyzed the effect of the social manipulation with the others factors separately on the left and on the right PPS boundaries.

3.2.3 Effect of the social manipulation on PPS

We performed separated ANOVA for the left and right hemispaces, with the between subject factor SEATING (2 levels: Left/Right) and the within subject factors SOCIAL CONDITION (2 levels: Isolated/In Dyad), and DELAY (8 levels: T2, T3, T4, T5, T6, T7, T8, T9).

In the left hemispace, analysis indicated a significant main effect of DELAY ($F_{(7,189)} = 49.25$, $p < .001$, $\eta_p^2 = .646$) (see Figure 3 panel b). Sound in the left hemispace started to boost tactile detection when tactile stimulation is administrated at T5. Participants' RTs were significantly faster when the tactile stimulus occurred at T4 compared to when the tactile stimulus occurred at T5 (Post-hoc Newman-Keuls' test: $p < .01$). RTs further decreased at the later delays. Participants' RTs were significantly faster when the tactile stimulus occurred at T7 than at T6 (Post-hoc Newman-Keuls' test: $p < .001$) and RTs were also significantly faster when the tactile stimulus occurred at T8 than at T7 (Post-hoc Newman-Keuls' test: $p < .01$). 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: $p < .01$ in all cases). Analysis also revealed a significant main effect of the SOCIAL CONDITION ($F_{(1,27)} = 25.60$, $p < .001$, $\eta_p^2 = .488$). Participants RTs were significantly faster when participants performed the task in a dyad than alone (Post-hoc Newman-Keuls' test: $p < .001$). The effect of the others factors and interactions were not significant.

In the right hemispace, analysis indicated a significant main effect of DELAY ($F_{(7,189)} = 56.56$, $p < .001$, $\eta_p^2 = .677$). Sound in the right hemispace started to boost tactile detection when tactile stimulation is administrated at T7. 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: $p < .001$). RTs further decreased at the later delays. Participants' RTs were significantly faster when the tactile stimulus occurred at T7 than at T6 (Post-hoc Newman-Keuls' test: $p < .001$) and RTs were also significantly faster when the tactile stimulus occurred at T8 than at T7 (Post-hoc Newman-Keuls' test: $p < .001$). Moreover, RTs were significantly faster when the tactile stimulus

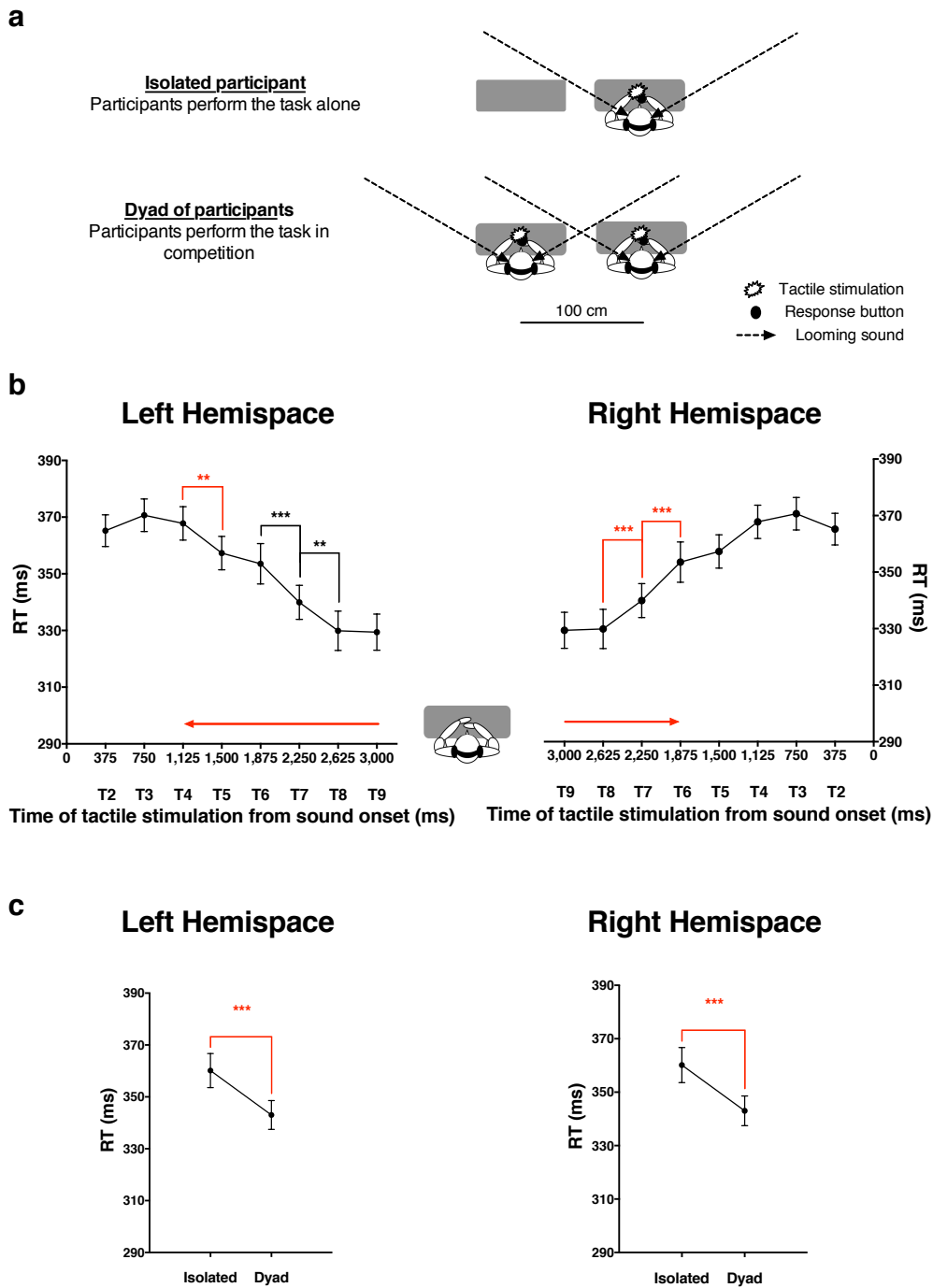


Figure 3. Influence of social competition on near space coding. **a.** Participants performed the audiotactile task by responding to a tactile stimulation while a task-irrelevant sound was looming towards them from the left or right hemispace and in two different social conditions: they were performing the task isolated or in a dyad in a competitive context. **b.** This figure reports the mean tactile reaction times (\pm SEM) as a function of the delay of tactile stimulation delivery from sound onset for the left hemispace (left graph) and for the right hemispace (right graphs). The significant decreases of RTs are indicated by means of asterisks. The significant decrease of RTs corresponding to the critical delay at which sound starts to boost tactile processing is indicated by means of red asterisks. The red arrows illustrate the extent of PPS boundaries from participants' body. **c.** This figure reports the mean tactile reaction times (\pm SEM) for the different social conditions – in isolation and in dyad - in left hemispace (left graph) and for the right hemispace (right graphs). RTs are significantly lower when participants performed the task in a dyad in competition than alone.

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: $p < .001$ in all cases). Analysis also revealed a significant main effect of the SOCIAL CONDITION ($F_{(1,27)} = 28.90$, $p < .001$, $\eta_p^2 = .517$). Participants RTs were significantly faster when participants performed the task in a dyad than alone (Post-hoc Newman-Keuls' test: $p < .001$) (see Figure 3 panel c). The effect of the others factors and interactions were not significant.

3.3 Discussion

Our results show that, when participants were performing the task in competition with another individual, their RTs were globally speeded-up. Participants were globally faster when they were in competition, confirming that participants took into account the competitive instruction. This speed-up effect does not interact with the delay: PPS boundaries did not differ in a competitive context. Thus, lateral PPS were not modulated by the presence of a rival.

4. Experiment 3: audience

In order to investigate the effect of the mere presence of another individual, we also examined whether and how the presence of an inactive individual modulates PPS boundaries. In a third experiment, participants performed the audiotactile task either isolated or in dyad, seated side-by-side with an unknown individual. Both participants from the dyad were clearly told that one of them was doing the task while the other one remained inactive.

4.1 Material and methods

4.1.1 Apparatus

The apparatus are similar than in the previous experiment, see section 2.1.1

4.1.2 Design and procedure

Design and procedure are similar than in the previous experiment, see section 2.1.2

4.1.3. Social Manipulation

As in the previous experiment, every participant performed the audiotactile task in a main condition and in a control condition: respectively paired with another participant (dyad) and isolated (see Figure 4 panel a). The order of the condition, with which participants began, was counterbalanced between participants. In the dyad condition, participants were always paired with another participant of the same gender. The two participants were seated side by side, at 1m from each other. In the isolated condition, an empty chair remained beside the participant. Each participant was assigned to the left or right seat and stayed in that position during the whole experiment. In this experiment, only one of the two participants from the dyad performed the audiotactile task while the other one was asked to stay inactive and immobile. This context, in which participants had no common task, was clearly explained to both participants in the instructions.

4.1.4 Participants

Twenty-eight individuals with normal audition and touch took part in the study. All of them were right-handed. Participants received a financial compensation of 10€/hour for their participation. They provided a written informed consent prior to the experiment, which was approved by the Institutional Review Board of the French National Institute of Health and Medical Research (INSERM, IRB00003888).

4.1.5 Data processing

Data processing are similar than in the previous experiment, see section 2.1.5

4.2 Results

Among the 28 participants who took part to the Audience experiment, two had a high rate of misses in at least one of the two social conditions (Isolated condition: 15.9% of miss, $m \pm sd$ of the sample:

1.4 ± 3.1%; In Dyad condition: 17.3% and 28% of miss, $m \pm sd$ of the sample: 2.7 ± 6.4 %) and were therefore excluded from the RTs analyses. The 26 remaining participants (11 females, age $m \pm sd$: 25.27 ± 3.58) were accurate in performing the task as the rates of omissions ($0.87 \pm 2.0\%$) can attest.

4.2.1 Comparaison between unimodal and bimodal trials

We first verified that multisensory integration globally speed up tactile detection in bimodal trials compared to unimodal trials. We conducted an ANOVA on the mean RTs, with the within subject factors DELAY (11 levels: Tactile_Before, T1, T2, T3, T4, T5, T6, T7, T8, T9 and Tactile_After). The global effect of DELAY was significant ($F_{(10,250)} = 50.30$, $p < .001$, $\eta_p^2 = .668$) suggesting that RTs were influenced by the time of tactile stimulation delivery (see appendix panel c).

RTs in the unimodal trials Tactile_Before were significantly slower than RTs in the bimodal trials T2, T3, T4, T5, T6, T7, T8 and T9 (Post-hoc Newman-Keuls' test: $p < .001$ in all cases). RTs at Tactile_Before did not significantly differ from RTs in the bimodal trials at T1 (Post-hoc Newman-Keuls' test: $p = .260$). RTs in the bimodal trials at T1 were also significantly slower than all the other RTs in the bimodal trials (at T2, T3, T4, T5, T6, T7, T8 and T9; Post-hoc Newman-Keuls' test: $p < .001$ in all cases) suggesting that, even though the sound started at the same time as the tactile stimulus delivery in that condition, the auditory stimulus was not perceived by participants. Thus, RTs at T1 were excluded from the rest of the analysis.

RTs in the unimodal trials Tactile_After were significantly faster than RTs at Tactile_Before (Post-hoc Newman-Keuls' test: $p < .001$). Given that RTs at Tactile_After were significantly slower than RTs at T7, T8 and T9 (Post-hoc Newman-Keuls' test: $p < .02$), we can exclude the possibility that participants were faster at late delays because of the increasing probability of receiving a tactile stimulation along trial.

4.2.2 Verification of the anisotropy of lateral PPS

We first verified that PPS is anisotropic by examining the effect of HEMISPACe on bimodal RTs (Hobeika et al., n.d.). We conducted an ANOVA on the mean RTs with the within-subjects factors HEMISPACe (2 levels: Left/Right) and DELAY (8 levels: T2, T3, T4, T5, T6, T7, T8 and T9). The ANOVA revealed a main significant effect of DELAY ($F_{(7,175)} = 35.99$, $p < .001$, $\eta_p^2 = .590$). The analysis also revealed that the two-way interaction HEMISPACe x DELAY was marginally significant ($F_{(7,175)} = 1.81$, $p = .08$, $\eta_p^2 = .067$), suggesting that tactile detection were dependent on the temporal delay of tactile stimulation delivery from sound onset and the hemispac of origin of the

sound source. The effect of the factor HEMISPAC was not significant. Thus, we analyzed the effect of the social manipulation with the others factors separately on the left and on the right PPS boundaries.

4.2.3 Effect of the social manipulation on PPS

We performed separated ANOVA for the left and right hemispaces, with the between subject factor SEATING (2 levels: Left/Right) and the within subject factors SOCIAL CONDITION (2 levels: Isolated/In Dyad), and DELAY (8 levels: T2, T3, T4, T5, T6, T7, T8, T9).

In the left hemispac, analysis indicated a main effect of DELAY ($F_{(7,168)}= 24.93$, $p < .001$, $\eta_p^2 = .509$). The others factors and interactions were not significant. Sound in the left hemispac started to boost tactile detection when tactile stimulation is administrated at T5. 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: $p < .05$). RTs further decreased at the later delays. Participants' RTs were significantly faster when the tactile stimulus occurred at T7 than at T6 (Post-hoc Newman-Keuls' test: $p < .01$) and RTs were also significantly faster when the tactile stimulus occurred at T8 than at T7 (Post-hoc Newman-Keuls' test: $p < .05$). 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: $p < .05$ in all cases), except for T3 which is only marginally different from T5 (Post-hoc Newman-Keuls' test: $p = .067$).

In the right hemispac, analysis indicated a main effect of DELAY ($F_{(7,168)}=32.03$, $p < .001$, $\eta_p^2 = .572$). The others factors and interactions were not significant. Sound in the right hemispac started to boost tactile detection when tactile stimulation is administrated at T7. 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: $p < .01$). RTs further decreased at the later delays. Participants' RTs were significantly faster when the tactile stimulus occurred at T8 than at T7 (Post-hoc Newman-Keuls' test: $p < .05$). 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 and T5 T6 (Post-hoc Newman-Keuls' test: $p < .01$ in all cases).

4.3 Discussion

In this experiment, no effect of the social condition was found in both hemispaces. As in the previous experiment, participants' PPS left boundaries were located farther than PPS right boundaries but none of them were influenced by the presence of another individual. Thus, lateral

PPS are not influenced by the presence of an inactive unknown partner. Those results affirm that the social effects reported in the collaborative experiment and the competitive experiment are not due to the mere presence of another individual.

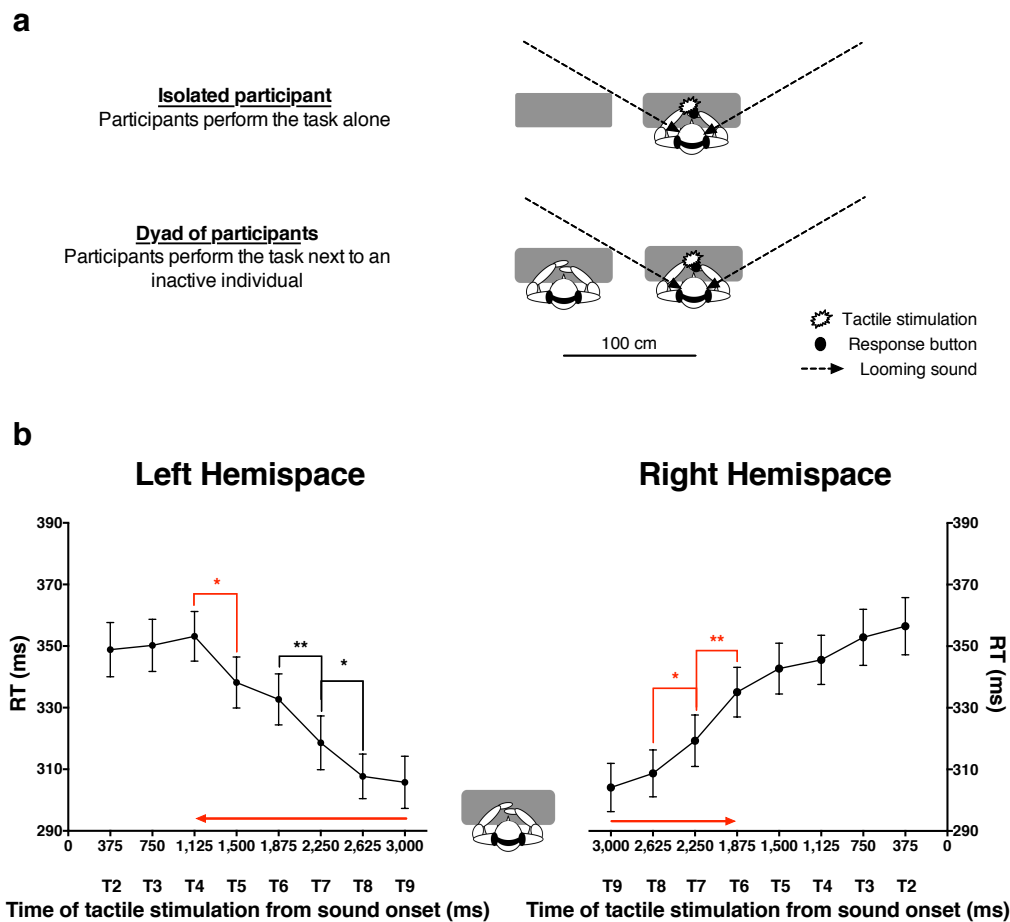


Figure 4. Influence of another individual's presence on near space coding. **a.** Participants performed the audiotactile task by responding to a tactile stimulation while a task-irrelevant sound was looming towards them from the left or right hemisphere and in two different social conditions: they were isolated or in a dyad with an inactive partner. **b.** This figure reports the mean tactile reaction times (\pm SEM) as a function of the delay of tactile stimulation delivery from sound onset for the left hemisphere (left graph) and for the right hemisphere (right graph). The significant decreases of RTs are indicated by means of asterisks. The significant decrease of RTs corresponding to the critical delay at which sound starts to boost tactile processing is indicated by means of red asterisks. The red arrows illustrate the extent of PPS boundaries from participants' body.

6. Discussion

In this study, we investigated whether high-level social manipulation influences the integration of the multisensory information related to a stimulus approaching the body, determining PPS boundaries. We conducted experiments in which we measured PPS boundaries of participants when they were isolated or when they were performing a task in a dyad, in collaborative or competitive contexts. In order to understand if the effect of the presence of another individual is enough to modulate lateral PPS boundaries, we conducted the Audience experiment, in which participants' PPS boundaries were measured when they were isolated or in the presence of an inactive individual.

Being implicated in a collaborative task influenced PPS boundaries. In this condition, participants' PPS extended in the right hemisphere. Simply affiliating two persons who did not interact with each other influenced the multisensory coding of the space around them. These results are comparable to the study of McClung and colleagues, who showed that affiliating participants at the same minimal group change their representation of others action in space (McClung, Jentzsch, & Reicher, 2013). McClung, Jentzsch and Reicher (2013) observed an impact of perceived group membership on the process of stimuli in space during co-action, i.e. "a situation in which individuals all simultaneously engaged in the same activity and are in view of each of other" (Zajonc, 1965). In this study, a social Simon effect (a spatial compatibility task shared by two participants (Sebanz, Knoblich, & Prinz, 2003; Simon & Rudell, 1967)) was observed only during co-actions performed by individuals of the same minimal group (McClung et al., 2013). This impact of group membership on the multisensory coding of near space can be related to the impact of group membership on adopted interpersonal distances (Novelli et al., 2010).

Competitive contexts did not modulate PPS boundaries. Teneggi et al. found no modulation of PPS in the presence of a non-cooperative individual (Teneggi et al., 2013). This result goes into the direction that only affiliative signals impact PPS. Participants globally speeded up their tactile detection in the competitive condition, confirming that they took into account the instruction.

Individuals' PPS was not impacted by the presence of an inactive partner. The distance at which sound started to boost tactile detection was similar in the isolated and dyad conditions, be it in the left or right hemispaces. The fact that our participants did not adjust their PPS in the dyad condition is in opposition with the conclusion of Teneggi et al., who observed a contraction of PPS when participants were in presence of another person (Teneggi et al., 2013). In Teneggi et al. study, participants were facing another individual standing at 1m whereas, in our experiment, the inactive partner was seated at 1m beside participants. Studies on interpersonal distances have shown that

participants tolerate smaller distances with another individual when the latter is located at their left or right side, comparing to when they are facing each other (Hayduk, 1981; Lloyd, Coates, Knopp, Oram, & Rowbotham, 2009). Our findings may be linked to frontal PPS boundaries being located farther than lateral PPS boundaries. Whereas it would be necessary to accommodate one's PPS when facing someone, it would not be required when the other is at the same distance on the side.

7. Conclusion

The main finding of this work is that a high-level social manipulation modulated a low-level process - as multisensory integration near the body. The influence of social context on PPS boundaries highlights the complicated relationships existing between motor capacities, multisensory integration, and our complex social environment. The PPS modulation in a collaborative context is impressive as it goes against the natural anisotropy of PPS. Indeed, a recent study showed that lateral PPS depends on handedness (Hobeika et al., n.d.). As we verified here, right-handers individuals have an asymmetric PPS, right boundaries being closer to the body than left boundaries. The brain and behavioral asymmetry in humans and other vertebrates are thought to give an evolutionary advantage (Levy, 1977). However, in the collaborative experiment, participants' PPS were more symmetrical. Modulations of individuals' motor possibilities during collaborative actions could be the explanation of this complex remapping of PPS.

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Author contributions

L.H., M.T. and I.V.D designed the experiments reported in the paper. L.H collected the data; L.H. and M.T performed the analyses. L.H., M.T. and I.V.D wrote the article.

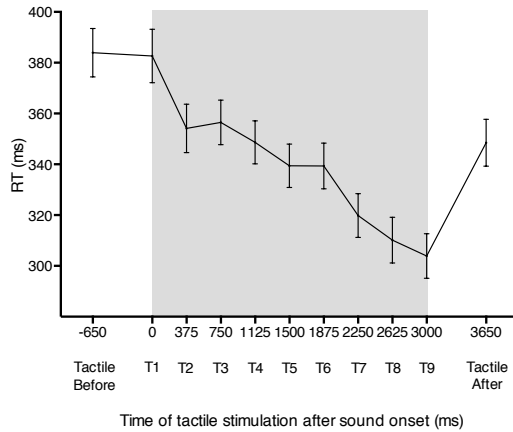
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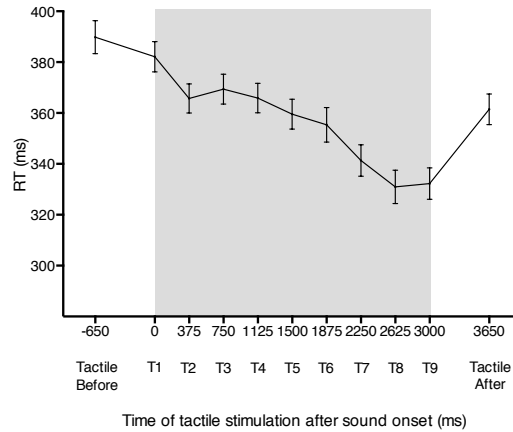
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Appendix

a. Collaborative experiment



b. Competitive experiment



c. Audience experiment

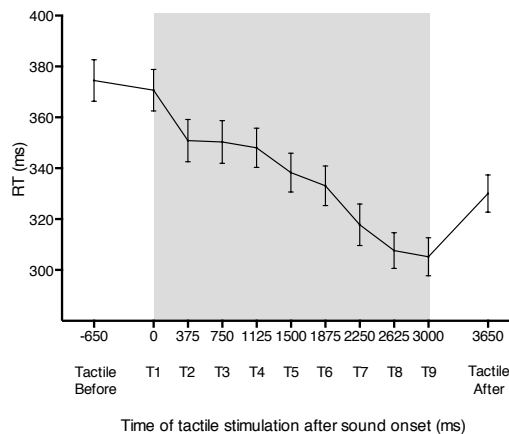


Figure S1: Impact of sound presence on tactile detection for the three experiments: a) in the collaborative experiment, b) in the competitive experiment and c) in the audience experiment. Those figures reports participants' mean reaction times (\pm SEM) as a function of the time after the sound onset when tactile stimulation occurred (with T1 corresponding at the sound onset, when the sound is the furthest from participants' body to T9 corresponding to the moment when the sound is the closest from participants' body). It also represents reactions times (RTs) in response to tactile stimulations presented without sound, before the sound onset (Tactile_Before) or after the sound offset (Tactile_After). The shaded region indicates the duration of the sound.

Chapter 8

Measuring PPS in human: a methodological investigation

This chapter discusses an on-going project that has not been presented in conferences yet.

8.1 Introduction

8.1.1 Limits of the actual method

The method used in chapters 6 and 7 to measure PPS characteristics is derived from the method exposed in Canzoneri's study [Canzoneri et al., 2012]. This method has several assets. First, it is an implicit measure: participants are not aware that the sound position can modulate their reaction times. The technique is based on multisensory integration behavioral effects that have been extensively studied. Before this method, studies on multisensory integration in space were comparing RTs for tactile detection while an irrelevant sensory information was presented in near or far space. The irrelevant sensory information was static in space [Serino et al., 2007, Bassolino et al., 2010]. In Canzoneri's method, the irrelevant information source is moving into space. Movement and especially looming stimuli are interesting for the study of PPS, as we discussed before the sensitivity of PPS for movements towards the body. Furthermore, this technique measures the integration at multiple positions of the space, which gives a higher spatial resolution to locate PPS boundaries. However, this method has limitations.

The first limitation of the paradigm is a possible expectancy effect. Recent experimental work emphasize the effect of expectation on motor preparation and RTs

[Umbach et al., 2012, Kandula et al., 2017]. In our study, a tactile stimulus is presented during the sound in 91.7% of the trials. Therefore, the probability that a tactile event arrives during a sound event is high. If the looming sound has arrived near the body and a tactile event has not arrived yet, the probability that it will arrive is really strong. Thus, the probability that a tactile event arrives knowing that it has not arrived yet is increasing with the factor delay. The problem here is that we cannot disentangle the possible expectancy effect from our variable of interest which is the delay. A way to control that the effect on RTs is due to multisensory integration and not expectancy is to compare RTs in unimodal trials, that are send to participants 350ms before the beginning of a sound or 350ms after the end of the sounds. In our previously described experiments, RTs for the two different unimodal tactile stimulations were significantly different: RTs were faster when the tactile stimulation arrived just after the sound than just before. This difference could be the mark of an expectancy effect. It could also be explained by other factors like an attentional effect. Another possible explanation is an increase of tactile sensitivity due to the presence of the sound near the body just before, when the tactile event is after the sound [Cléry et al., 2015a, Kandula et al., 2015]. It is important to note that the previously presented results on PPS can not be fully explained by expectancy effects, mainly because RTs for the unimodal tactile events are different from RTs for the multimodal trials surrounding them. Moreover if RTs were explained only by expectancy effects, the same results should be found for looming and receding sounds which is not the case [Canzoneri et al., 2012, Serino et al., 2015]. At this stage, we cannot exclude the possibility that expectancy effects are entangled with the multisensory integration effect we are looking for. It would be interesting to try to measure or control for these possible effects.

Another possible limitation of this method is the method of analysis. First, our results are based on RTs analysis. Usually, RTs analysis requires a large number of repetitions of the same event to allow a reliable precision of the measure. In the original study, there were 8 repetitions per condition. We used 10 repetitions in the experiments of chapters 6 and 7. The reason of the weak number of repetitions is the length of a single trial. As the trial-length mean is 7s, the experiment duration of the chapter 7 is around 50min of pure experiment. This duration is already long for attentional resources, especially as we are looking at a speed up effect on RTs.

Furthermore, the performed analysis (ANOVA) may not be the best in term of statistical power. If we look at the experiment of chapter 6 about PPS and handed-

ness as an example, we compared RTs in two groups in two hemispaces, and for 8 delays. The anova is a 2x2x8 statistical analysis. As we expect a shift of PPS, only one or two points in space should be statistically different. This analysis does not give a lot of statistical power. Moreover, increasing the number of delays tested increases the spatial resolution of PPS but decreases the statistical power. In some articles using this method, authors performed data fitting to extract relevant features of the data [Canzoneri et al., 2012, Canzoneri et al., 2013b, Bassolino et al., 2014]. They use sigmoid fitting, a function with four parameters: the upper asymptote, the lower asymptote, the slope of the curve and the 50% threshold point. The last two parameters are the crucial ones for the PPS characteristics. The threshold could be representative of the size of PPS, whereas the slope would be linked to the permeability of the PPS boundary. This type of analysis reduces the number of factors in the anova, thus increasing the statistical power. It also gives the possibility to perform intra-individual analysis, as correlation between individual traits as anxiety trait or body image to PPS characteristics. We tried to fit the data of the experiments of chapters 6 and 7. The problem of this fitting method is that the quality is not satisfying. For the majority of the individual fitting, obtained parameters were highly dependent of the initial conditions used in the fitting. Furthermore, is not clear that the sigmoid fit is better than the linear fit. Those models are usually compared without taking into account the difference in the number of parameters. Fitting difficulties could be due to the lack of precisions of RTs. It can also be that RTs evolution with sound distances is not following a sigmoidal law.

8.1.2 Paths to overcome the limitations?

To try to improve the method and better understand its results, we propose several ways to go under the presented limitations.

The expectancy effect

We explained that an expectancy effect could be at stake in the method, and this effect is not disentangled from the delay effect. Different procedures could be used to measure this effect or to avoid it.

One possibility is to overcome the possible expectancy effect. Changing the probability that a tactile event arrives during a trial could erase the expectancy effect. There are two obvious ways to do it. The first one is to add a lot of catch trials, i.e. trials with sound but no tactile event. If the probability that a tactile

event arrives during a sound is lower (for example 50% instead of currently 91.7%), participants will not expect a tactile event to arrive when a sound begins. The problem with this solution is that it will increase significantly the duration of the experiment, or decrease the number of collected data if we do not want to increase the experiment duration.

Another experimental possibility is to manipulate the expectancy in the paradigm, to disentangle it from the sound distances. We could use several looming sounds with the same duration but travelling across different distances. The tactile stimulus would always arrive at the same delay from the sound onset, but the sound location when the time the tactile stimulus arrives will vary.

Changing the variable of interest

To overcome the variability of measure of RTs, a possibility is to change our data of interest from RTs to percentage of detection. A number of studies found that the tactile detection rate follows a sigmoidal psychometric function [Johansson and Vallbo, 1979, Ferrington et al., 1977, Gibson and Craig, 2005]. As discussed in section 3.1.1, multisensory coding of an event increases detection accuracy. We could study PPS as the space were sound presence starts to increase tactile detection rate. As tactile stimuli at the tactile detection threshold is supposed to be detected 50% of the time, expectancy should also be automatically lower [Umbach et al., 2012]. Working at the tactile detection threshold and analyzing percentage of detection could lead us to data easier to fit.

Length of a trial

To increase precision in the PPS measure, we could increase the number of repetitions of each trial. To do this, we can diminish the length of a trial. In our previous experiments, trials lasted 7s with 3s of sound. Diminishing the length of looming sounds would shorten the length of a trial. The important stimuli features in this experiment are that sounds are perceived in space looming towards the participants. The localization of sounds in space is a fast process, which can be performed for sounds lasting less than a second [Zahorik and Wightman, 2001]. Instead of having only one stimulus per hemispace, we can create several stimuli with different starting and ending distances. Thus, sounds can be shorter than 3s and the number of trials multiplied.

8.2 PPS measured with detection rates

In this study, we wanted to test the first step of a different protocol. The tactile stimulus was calibrated at the individual detection threshold, thus the new variable of interest was detection rates. The rest of the protocol remained globally the same as described in section 5.1. All participants were right-handed. Their task remained to respond as fast as possible with their right index when they detect a tactile stimulation under their left index. At the same time, they were listening to looming sounds moving towards them in their left or right hemisphere. The number of tested distances is reduced to seven to increase the number of repetitions per distance. As the tactile stimulus intensity is fixed at the individual detection threshold, participants should detect the tactile stimulus in around 50% of the trials. Thus the probability that a tactile stimulus arrived during a single sound event was manipulated, and lower than in the previous experiments. A first step in the experiment is to measure the tactile detection threshold for each individual. We introduced the hemisphere factor in this experiment to compare the effect sizes obtained with this paradigm.

8.2.1 Method

Participants

Ten healthy individuals (5 females; age $M \pm SD = 23.40 \pm 1.17$) with normal hearing and touch participated in the study. As PPS is linked to handedness, the participants' handedness was verified with a questionnaire measuring skilled hand preference (Flanders Handedness survey, FLANDERS) [Nicholls et al., 2013]. The questionnaire scores range from -10 for strong left-handed individuals to +10 for strong right-handed individuals. The participants' Flanders scores ranged from 8 to 10 ($M \pm SD = 9.80 \pm 0.63$). 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 guidelines. Participants received a financial compensation of 10€/hour for their participation.

Procedure

All participants performed two similar sessions of the experiment. The first part of the experiment consisted in measuring the tactile detection threshold of the participant. The second part was the audiotactile task. During the whole experiment, a

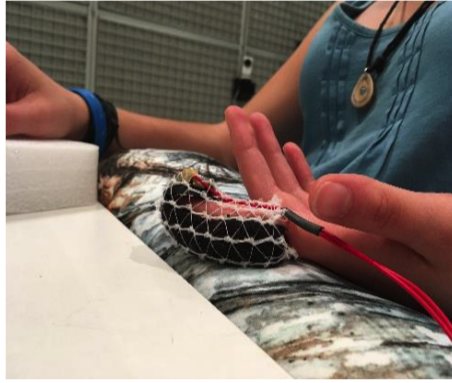


Figure 8.1: The tactile stimulator was held in place with a medical restraint filet to avoid any shift in position on the surface of the index

vibrator (a small loudspeaker) was fixed on the index finger of participants' left hand with a medical restraint filet, to avoid the vibrator to moving during the test (see figure 8.1).

Tactile detection threshold determination

The tactile detection threshold was measured using a three-interval three-alternative forced choice (3I-3AFC) adaptive procedure. In each trial, one observation interval contained the target tactile stimuli, and the two remaining intervals no tactile stimulation. The visual intervals were separated by 500 ms. Visual intervals were indicated by a number: 1, 2, or 3 displayed on the participant's monitor. The interval containing the tactile stimulation was randomized from one trial to another. Participants were asked to select the interval containing the tactile stimulus, no feedback was given. The tactile stimulus was a sinusoid signal of 20 ms at 250Hz. The variation step size was initially set to 5dB; it was reduced to 3dB after the second reversal and to 1dB from the fourth reversal until the end (the 8th reversal). A three-down/one-up rule was used during the whole procedure, to attain a 73% detection level [Levitt, 1971]. For one run, the threshold was calculated as the mean of the target sound duration across the last four reversals. Participants performed four runs of calibration simultaneously, with random selection of the run to play at each trial. The final threshold for one participant was the mean of the four runs.

Audiotactile detection task

An auditory stimulus was presented for 3000ms for each trial. The sound source approached from the front hemifield, either from the right (-60°) or from the left

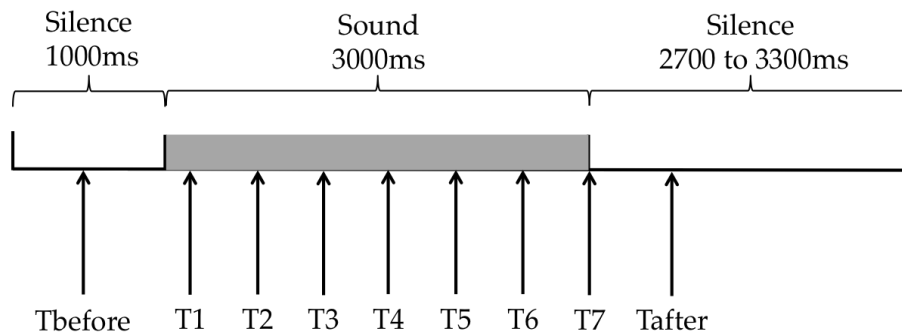


Figure 8.2: Description of a trial of the experiment measuring PPS with detection rates, described in section 8.2

hemisphere (60°), with a spatial location varying from 135 to 20 cm from the center of the participant's head. The sound velocity was $38.33 \text{ cm}\cdot\text{s}^{-1}$. 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 right-hand as quickly as possible each time a tactile stimulus was detected. They were asked to emphasize speed, but to refrain from anticipating. Percentage of detection and 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 at 300 ms from sound onset; T2 at 750 ms from sound onset; T3 at 1200 ms from sound onset; T4 at 1650 ms from sound onset; T5 at 2100 ms from sound onset, T6 at 2550 ms from sound onset and T7 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. 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 (see figure 8.2).

After a small training block aimed at getting the participants acquainted with the task, we checked by asking participants whether 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 18 conditions. The factors were: DELAY (nine levels: Tbefore, T1, T2, T3, T4, T5, T6, T7 and Tafter), HEMISPACE (two levels: left/right). In each session, there were a total of 36 trials with a tactile target, randomly intermingled with 4 catch trials. Thus for each session, trials were equally divided in 10 blocks of 40 trials, lasting about 4 min each. In total, on both sessions, every condition was repeated 40 times.

8.2.2 Results

Data processing

One participant was excluded from the analyses because he had a high rate of false alarms compared to the rest of the group (7.00 false alarms per bloc; group $M \pm SD = 2.44 \pm 1.80$), giving us reason to suspect that he did not correctly perform the task. The analyses were conducted on the remaining 9 participants. In order to exclude false alarms from the detection rates calculation, we excluded trials based on their RTs. Thus, we excluded trials with outlier 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. $\ln(\text{RTs})$ were considered outliers if they exceeded more than two standard deviations from the mean $\ln(\text{RTs})$ and trimmed from the analyses (2.04% of trials). The percentage of detection for each participant, for each HEMISPACE condition and each DELAY were calculated on the remaining data.

Effect of the sound on tactile detection rates

We then conducted an ANOVA on the mean percentage of detection with the within-subjects factors DELAY (9 levels: Tbefore, T1, T2, T3, T4, T5, T6, T7, 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 ($F_{(8,64)} = 9.80, p < .001, \eta_p^2 = .551$) suggesting that percentages of detection were influenced by the temporal delay of tactile stimulation delivery from sound onset (see figure 8.3 panel A). Detection in the unimodal trials Tbefore were significantly lower from all bimodal trials (T1, T2, T3, T4, T5, T6 and T7, Post-hoc Newman-Keuls' test: $p < .01$ in all cases). Detection in the unimodal trials at the delay Tafter ($M \pm SEM = 17.91 \pm 5.32$) were marginally lower than detection in the unimodal trials at the delay Tbefore ($M \pm SEM = 29.72 \pm 8.83$) (Post-hoc Newman-Keuls test: $p = .052$). However, given that RTs at Tafter were significantly slower than RTs at T5 ($M \pm SEM = 50.83 \pm 7.38$), T6 ($M \pm SEM = 56.39 \pm 6.19$) and T7 ($M \pm SEM = 60.83 \pm 8.83$) (Post-hoc Newman-Keuls' test: $p < 0.01$ in all cases), we can confirm that the irrelevant sound interacted with tactile processing.

Effects of sound delays and hemispace on detection rates

We then performed an ANOVA on the detection percentages measured in the bimodal trials only, with the within-subjects factors HEMISPAC (2 levels: Left/Right) and DELAY (7 levels: T1, T2, T3, T4, T5, T6, T7). The ANOVA revealed a significant main effect of DELAY ($F_{(8,64)} = 7.77, p < .001, \eta_p^2 = .551$), suggesting that percentages of detection were influenced by the temporal delay of tactile stimulation delivery from sound onset. No significant difference was found between tactile detection rates of two successive delays (T1 vs T2, T2 vs T3, ect...), thus we could not assess a limit of PPS boundary (all Post-hoc Newman-Keuls test $p > .16$).

No significant effect of HEMISPAC ($F_{(1,8)} = 1.23, p = .18, \eta_p^2 = .214$) or two-way interaction ($F_{(6,48)} = 1.35, p = .28, \eta_p^2 = .139$) were found. The observed power of the hemispace x delay interaction is $\alpha = .456$. The effect size is comparable to the effect size of the right-handers study in chapter 6 (with $\eta_p^2 = .168$). We can conclude that the same number of participants ($n=26$) would lead to a significant effect (observed power for RH experiment: $\alpha = 0.99$) (see figure 8.3 panel B).

8.2.3 Discussion

The experiment validates the protocol at the tactile detection threshold. The calibration of individual tactile detection worked: participants did not detect all tactile stimulations or none. Crucially, tactile detection rates were modulated by the delay from the sound onset at which the tactile events arrived. Thus, tactile detection is

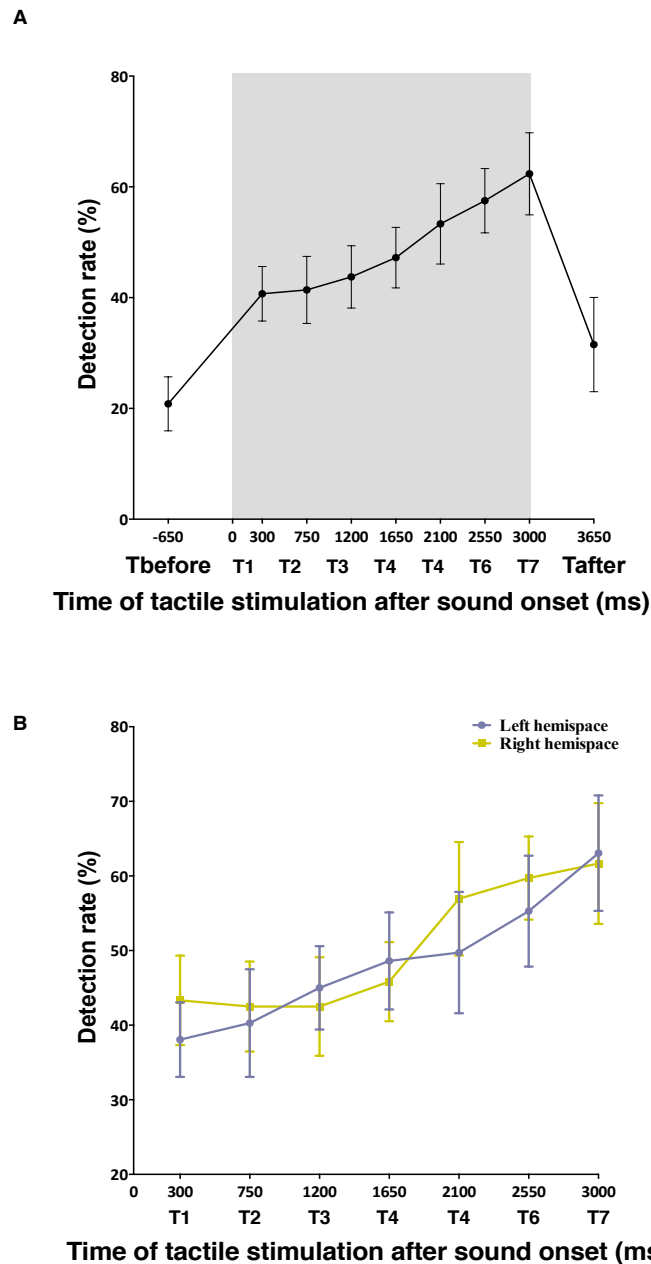


Figure 8.3: Impact of sound presence on tactile detection. Those figures report participants' mean detection rate ($\pm SE$) as a function of the time between the sound onset and the time at which tactile stimulation occurred (from the shortest time between tactile stimulation and sound onset T1, corresponding to the farther distance, to the longest time between tactile stimulation and sound onset T7, corresponding to the closest distance). A) It also represents detection rate in response to tactile stimulations presented without sound, before the sound onset (T_before) or after the sound offset (T_after). The shaded region indicates the duration of the sound. B) This figure depicts tactile detection rates for the two tested hemispaces separately

enhanced when a sound is located near the body. No critical distance marking the start of a boost was found, probably due to the low number of participants in this study. There was a marginal difference between unimodal trials detection presented before or after the sound. The reason of this effect is still unclear. A possibility is that tactile sensitivity is higher for the unimodal after the sound. The looming sound prime participants for a possible touch [Cléry et al., 2015a]. When the sound stopped near the body, the probability of being touched may stay high for some time, thus tactile sensitivity would be higher for tactile stimulation after the sound than before the sound.

We did not find a significant effect of the stimulated hemispace. However, the number of participants is low, thus the statistical power may be too low to reveal an effect. However, the size effect is not small and is comparable with the one found in the previous studies. This method has a main limitation. The protocol is heavier than one used before, as participants came for two sessions and had to performed the calibration task. This task also requires high attentional resources. The next step towards a new protocol could be to speed up the experiment, by shortening sounds duration. Furthermore, it would be interesting to test if possible expectancy effects impact detection rate.

8.3 PPS measured using shorts sounds

8.3.1 Description of the study

In this experiment, the variable of interest was still tactile detection rate with a tactile stimulus at the detection threshold. In order to significantly increase the number of trials in an experimental session, the length of trials was reduced from 7s to 2.5s. Five different sounds durations were used: from 1s to 1.2s by step of .05s. The tactile stimulation always arrived 200ms before the end of the sound. This fixed variability avoids response anticipation and at the same time gives a measure of expectation effects. Sounds started and stopped at variable distances to test the impact of sound proximity on tactile detection. All sounds moved at the same speed. We analyzed both RTs and detection rates as a function of the sound source distance and hemispace. We also looked at the effect of sound duration on RTs and detection rates, to understand if those variables are sensitive to expectancy.

8.3.2 Method

Participants

Eleven healthy individuals (9 females; age $M \pm SD = 23.90 \pm 4.50$) with normal hearing and touch participated in the study. As PPS is linked to handedness, participants' handedness was verified with a questionnaire measuring skilled hand preference (Flanders Handedness survey, FLANDERS) [Nicholls et al., 2013]. The questionnaire scores range from -10 for strong left-handed individuals to +10 for strong right-handed individuals. The participants' Flanders scores range from 8 to 10 ($M \pm SD = 9.64 \pm 0.81$). 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.

Procedure

As in the previous study, the first part of the experiment consisted in a measure of participants' tactile detection threshold. The second part consisted in the measure of PPS boundaries with an audiotactile task. During the whole experiment, a vibrator was fixated on the index finger of participants' left hand with a medical restraint file, to avoid movement of the vibrator during the test.

Tactile detection threshold determination

The same procedure as describes in the section 8.2.1 was used to determine the tactile detection threshold of participants.

Audiotactile detection task

An auditory stimulus was presented at each trial. The sound source approached from the frontal hemifield, either from the right (-60°) or from the left hemispace (60°). Tactile stimulation was administrated when sound was at different distances from the center of participants' head: at 245cm for D1, 215cm for D2, 185cm for D3, 155cm for D4, 125cm for D5, 95cm for D6, 65cm for D7 and 35cm for D8. Sounds velocity was 75 cm.s⁻¹(see figure 8.4 panel B) Five sound durations were used: Dur1: 1000ms, Dur2: 1050ms, Dur3: 1100ms, Dur4: 1150ms and Dur5: 1200ms. The auditory stimulus was preceded by a silence with a duration varying between 800ms

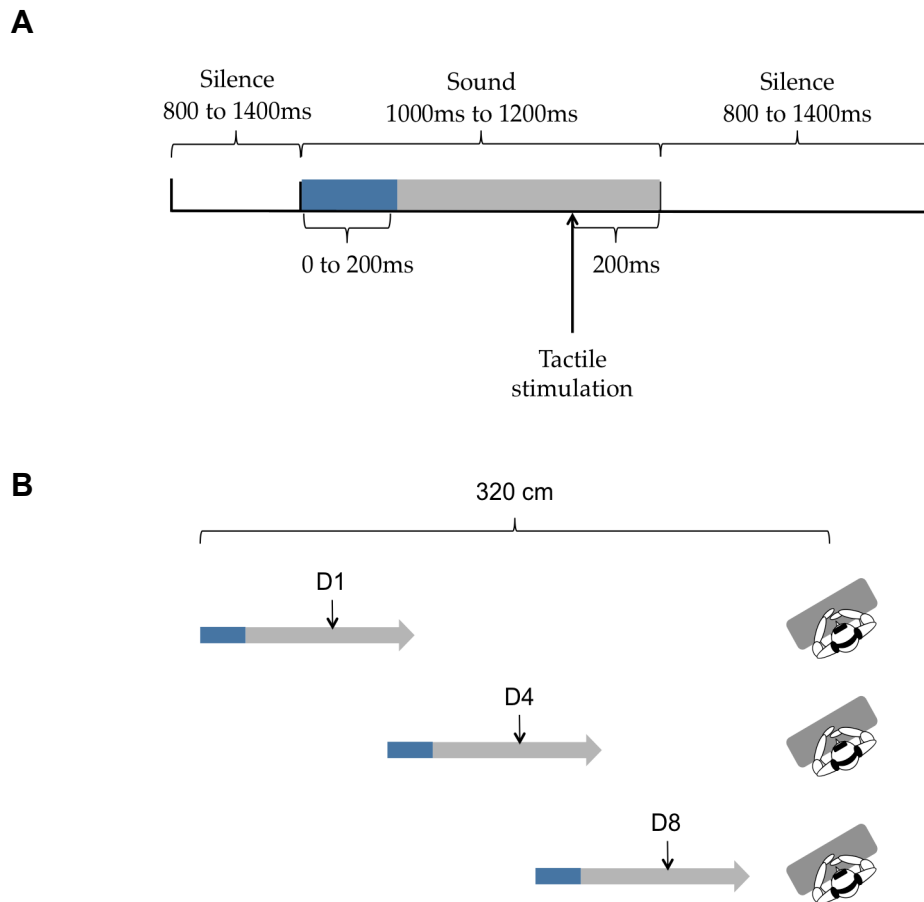


Figure 8.4: A) Description of a trial of the experiment measuring PPS using shorts sounds, described in section 8.3 B) This figure depicts example of sound position in space for three distances: D1, D4 and D8. Tactile stimulation was administered at different distances of participants' body. The arrows represent the trajectory of sounds in space. The blue part of the arrows represent the variable part of sounds depending on sound duration. The grey part of the arrows are the fixed portion of sounds, present whatever the sound duration.

and 1400ms. A period of silence, with a duration varying between 400ms and 1200ms, also occurred after the offset of the sound (see figure 8.4 panel A). Participants were instructed to ignore the auditory stimuli and to press a button with the index of their right-hand as quickly as possible each time a tactile stimulus was detected. They were asked to emphasize speed, but to refrain from anticipating. Percentage of detection and reaction times (RTs) were measured.

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 hemisphere. On each trial, tactile stimulation was delivered at one among eleven possible delays from sound onset (T_{before}, T1, T2, T3, T4, T5, T6, T7, T8, T9, T_{after}). 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.

Vibratory tactile stimuli were delivered at 200ms before the end of the sound. With this procedure, tactile stimuli were processed when the sound source was perceived at varying distances from participants' bodies. Given that a looming auditory stimulus increases the detection rate of a tactile stimulus as long as it is perceived near the body, we considered the distance at which sounds started to boost tactile RTs as a proxy of PPS boundaries.

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 18 conditions. The factors were: DISTANCES (eight levels: D1, D2, D3, D4, D5, D6, D7 and D8), HEMISPHERE (two levels: left/right), and DURATION (5 levels: Dur1, Dur2, Dur3, Dur4, Dur5). In each session, there were a total of 800 trials equally divided in 10 blocks of 80 trials, lasting about 3 min each.

8.3.3 Results

Data processing

In order to exclude false alarms in the calculation of detection rates, we excluded trials with outlier 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 DISTANCE condition separately, we calculated the mean and the standard deviation of our transformed data. $\ln(\text{RTs})$ were considered outliers if they exceeded more than two standard deviations from the mean $\ln(\text{RTs})$ and trimmed from the analyses (3.87% of trials). The remaining data was analyzed separately for RTs and detection rates.

Effect of the sound duration on tactile detection rates

We analyzed if sound durations of the trial affected the rate of detection. For each participant and each DURATION condition separately, we calculated the rate of tactile detection. We then performed a one-way ANOVA on the hits percentage with the within-subjects factor DURATION (5 levels: Dur1, Dur2, Dur3, Dur4, Dur5). Sound duration had no significant impact on the tactile detection rate ($p=.91$).

Effect of the sound duration on RTs

We then looked at the effect of sound duration on RTs. For each participant and each DURATION condition separately, we calculated the mean of the RTs log transformed. The analyses were made on the means after being transformed back with the exponential function to obtain RTs back. First, we performed a one way ANOVA with the RTs with the within-subjects factor DURATION (5 levels: Dur1, Dur2, Dur3, Dur4, Dur5). The main effect of DURATION was significant ($F_{(4,40)} = 8.64, p < .001, \eta_p^2 = .463$) suggesting that RTs were influenced by the duration of sounds (see figure 8.5). RTs were significantly slower when the sound lasted 1s compared to the other durations (Post-hoc Newman-Keuls' test: $p < .05$ in all cases). RTs for Dur2 were similar to RTs for Dur3 (Post-hoc Newman-Keuls' test: $p = .76$). RTs at Dur3 were significantly slower than at Dur4 ($p=.050$), and significantly slower than at Dur5 ($p=.023$). RTs at D4 and D5 were not different statistically ($p=.94$). That result indicates that an effect of expectancy is modulating RTs in a non-linear way.

Effect of the sound distance and hemispace on tactile detection rates

We conducted an ANOVA on the mean percentage of detection with the within-subjects factors HEMISPACE (2 levels: Left/Right) and DISTANCE (eight levels: D1, D2, D3, D4, D5, D6, D7 and D8). The main effect of DISTANCE was significant ($F_{(7,70)} = 2.79, p = .013, \eta_p^2 = .218$), suggesting percentages of detection were influenced by the temporal delay of tactile stimulation delivery from sound onset. No significant difference was found between tactile detection rates of two successive delays (D1 vs D2, D2 vs D3, ect...), thus we could not assess a limit of PPS boundary (all Post-hoc Newman-Keuls test $p > .34$).

No significant effect of HEMISPACE ($F_{(1,10)} = .074, p = .79, \eta_p^2 = .0074$) or two-way interaction between HEMISPACE and DISTANCE was found ($F_{(7,70)} =$

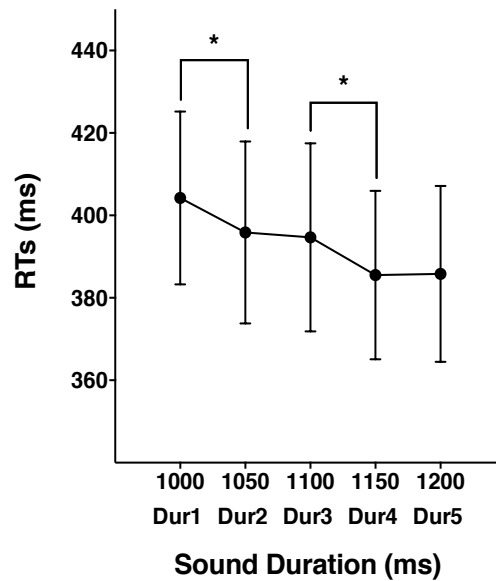


Figure 8.5: Impact of sound durations on RTs. This figure reports participants' RTs ($\pm SE$) as a function of the sound durations.

1.16, $p = .34$, $\eta_p^2 = .104$). The observed power of this interaction is $\alpha = .464$. The effect size is comparable to the effect of the right-handers of the experiment in chapter 6 ($\eta_p^2 = .168$) and to the effect of the previous experiment ($\eta_p^2 = .139$). We can take as a comparison the effect size of the factor HEMISPACE: $\eta_p^2 = .0074$.

Effect of the sound distance and hemispace on RTs

We conducted an ANOVA on the RTs with the within-subjects factors HEMISPACE (2 levels: Left/Right) and DISTANCES (eight levels: D1, D2, D3, D4, D5, D6, D7 and D8). The main effect of DISTANCE was not significant ($p = .14$, $\eta_p^2 = .142$, $\alpha = .638$), nor the main effect of HEMISPACE ($p = .12$, $\eta_p^2 = .23$, $\alpha = .343$) or the two-way interaction ($p = .90$, $\eta_p^2 = .038$, $\alpha = .164$).

8.3.4 Discussion

In this study, we investigated separately the impact of sounds distance and sounds duration on tactile detection. The intensity of tactile stimuli was fixed at participants' detection threshold. We analyzed the modulation of detection rates and RTs. We used looming sounds lasting between 1s and 1.2s, which is shorter than in the usual paradigm. Thus we also tested if short sounds were perceived in space and if their distances impact tactile processing.

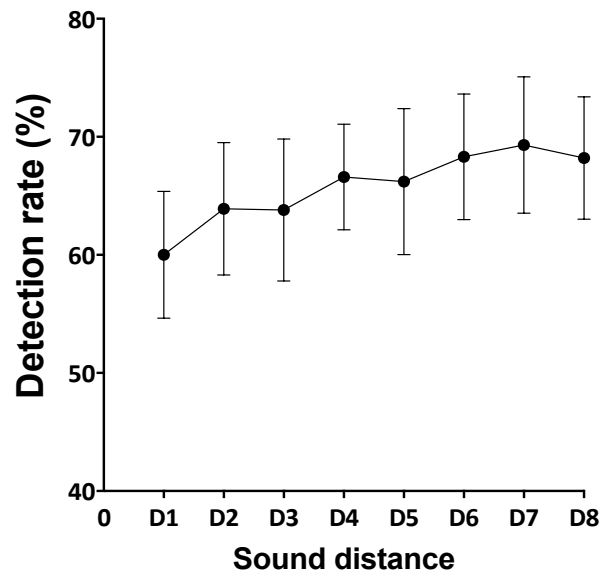


Figure 8.6: Impact of sound distances on tactile detection. This figure reports participants' mean detection rate ($\pm SE$) as a function of the sound distances when tactile stimulation occurred (from the further from the body D1, to the closer from the body D8).

First, we replicated the findings that sounds distances impacted tactile detection rates: tactile stimuli were detected more often when sounds were close to the body. Sound durations did not affect tactile detection rates. This confirms that tactile sensitivity increases when a sound is near the body. It also confirms that the experimental manipulation worked: one-second sounds were localized in space and their distance were taken into account for the audiotactile integration. Furthermore, we found that sounds duration did not impact tactile detection rates: this measure is not sensitive to expectancy. Taken together, those findings suggest that tactile detection rates could be an appropriate measure of PPS.

RTs were modulated by sounds duration. RTs were faster for longer sounds, thus for longer waiting times between sound onset and tactile stimulation. Expectancy effects on RTs have been widely described in the literature, [Kutas and Donchin, 1980, Mowbray, 1964, Niemi and Naatanen, 1981], and are due to motor preparation. Unlike our precedent studies, we found no significant effect of sound distance on RTs. This absence may be due to the higher variability of RTs induced by the manipulation of sounds duration, masking the effect of distance.

Overall, we disentangled the effects due to expectancy and due to multisensory integration on RTs and detection rates. Studying detection rates appears to be the best option to study PPS, as it is sensitive to sound distances but not to expectancy.

However, the protocole is not satisfying yet. We did not find a critical distance at which sound starts to boost tactile detection rates. This may be due to the small number of participants in the study (n=10). A more serious limitation is that the behavioral effects on this study are small. Mean detection rates increased from 60% at the furthest distance to 68% at the closest one. Further research is needed to improve this protocol.

8.4 Towards a new protocole for PPS measurement?

These two studies validate the merits of the detection rates as a variable of interest to study PPS. Detection rates increase when sounds are closer to the body. Unlike RTs, tactile detection rates are not sensitive to expectancy effects. These results contribute to the literature arguing that sensory information near the body increases tactile sensitivity [Cléry et al., 2015a, Salomon et al., 2017]. The behavioral effect observed in both study is different. Detection rates for bimodal trials increased of 22% in the first study and 8% in the second study. The reasons of this difference are not obvious. It may be due to the difference in sounds durations.

Yet, we did not obtain an satisfying protocol to measure PPS. The paradigm of the first experiment seems to work properly but the protocol is costly in terms of time, it would not be efficient to test the effect of multiple factors. The second experiment has a faster protocol but the behavioral effects are smaller. Increasing the behavioral effects of multisensory integration could lead to an efficient protocol. Multisensory integration follows the inverse effectiveness principle: the multisensory gain is the largest when both unimodal stimulations are too weak to evoke a neural response by their own (see section 2.1.1). In the classical paradigm, both stimulations are strong and easy to detect. In this task, an asymmetry exists between both stimulations. Auditory information is strong whereas tactile stimulations are fixed at the detection threshold. To increase multisensory behavioral effect, we could lower the intensity of sounds stimulations.

Chapter 9

Discussion

The aim of this PhD was to study the perception of space around the body called PPS, and the flexibility and the adaptative function of this space representation. Space management in social situations is a well-studied area in social psychology, highlighting the complex influence of factors such as personality traits, hierarchical status or culture. In neuroscience studies investigated PPS coding in macaques. They found that this area is encoded by multisensory neurons in frontoparietal networks. However the study of the neural coding of PPS in humans, and of the factors modulating it is still at its beginning. We first conducted experiments on lateral PPS of isolated individuals that led us to question the links between PPS and handedness. We then studied the modulation of these lateral PPS boundaries in social contexts, contrasting collaborative context, competitive context and the mere presence of a non-active individual. We also questioned the methodological approach used to measure PPS, and investigated alternative experimental paradigms.

Links between PPS and handedness

In our first study, we found that lateral PPS was asymmetric for right handers, with a larger extent in the right than the left hemispace. For left handers, we found a symmetric lateral PPS. Those results suggest that the ability to act rapidly and precisely in space shapes the PPS size. Multiple studies in macaques and human highlight the fact that PPS is coded in motor terms for the purpose of voluntary actions. Studies investigating relations between motor capacities and PPS are based on the modification of motor possibilities, involving wrist weights or arms immobilization. Our study found a possible relation between intrinsic motor abilities and PPS. However, the observed differences could be linked to other functional variations

linked to hemispheric specialisation, such as an attentional bias. This result discloses the importance of looking at PPS boundaries not only in the front but also on all the three Euclidian dimensions. In particular, PPS in the back space has been rarely investigated. The human body is programmed to act in the front space and the coding of PPS in an area where no movement planning is done might well rest on different neural processes. Another question remains whether the differences observed in terms of multisensory integration near the body have more general behavioral effects. For example, do right-handers keep smaller distances with people seated on their right side than on their left side?

PPS in social contexts

Our second study revealed a social influence on PPS boundaries. Precisely, we found an asymmetric extension of PPS when a task was performed in a collaborative context. In comparison, no modulation was observed in a competitive context, nor in the presence of an inactive individual. The critical aspect of the study is that the extension of the right PPS boundary during collaborative task was observed whatever the position of the partner in space. Thus, the extension can not be explained as an inclusion of the other into one's own PPS. More research is needed to better understand this modulation. A step further would be to perform the same experiments but with left-handed participants, to test if we would observe a symmetric increase of PPS size in both hemispaces. Another possible variation would be to use the same paradigm but changing the position of participants in space, and placing them face to face or back to back. Those configurations could confirm that PPS modulation does not depend on the spatial position of the individual, nor on the possible action space of the partner, but on the binding ties imposed by social interaction.

Finally, studying the dependence between social bond and emotion might help to better understand the functional aspect of the modulation. Is the social modulation found in our study linked to a defensive function of PPS? Looming stimuli are thought to elicit defensive reactions, but we can not affirm that our method measures defensive space, especially as our sounds were emotionally neutral. A study found that the emotion impact of looming sounds was higher than receding ones only when the sound had a negative emotional value [Tajadura-Jiménez et al., 2010]. However, emotional arousal did not differ between looming and receding movements when sounds were neutral or pleasant. To study the functional aspect of PPS in social context, one approach could be to manipulate the emotional content of the sounds.

For example, we could examine the social modulation of PPS using frightening sounds that would potentially arouse the defensive function of PPS.

Methodological constraints

Our third study focused on the methodology of PPS measurement. We aimed to investigate and potentially overcome the limitations of Canzoneri's audiotactile method [Canzoneri et al., 2012]. Mainly we looked at a potential effect of expectancy, which is entangled with the target effect of sound distance. In two experiments, we tested the possibility of using detection rate instead of RTs as a variable of interest. We confirmed the efficiency of using this measure, as tactile detection rates increased with sound proximity. Critically, we also found that, in contrast to RTs, tactile detection rates were not sensitive to expectancy. Overall, detection rates appear as a promising alternative measure to study PPS.

An improvement of the method would be to find an appropriate model to fit behavioral data in function of the distance to the body, to extract the relevant parameters describing PPS morphometry. PPS is usually depicted as a bubble around the body, with increased multisensory integration within its boundary. Thus, studies have tried to model data with a sigmoidal function, which is a function taking as parameters an upper bound, a lower bound, a threshold (at which data value attain the middle between the two bounds) and a slope of variation. Studies on audio-tactile integration in space found sigmoid fitting as a good representation of RTs modulation [Canzoneri et al., 2012, Ferri et al., 2015, Bassolino et al., 2014], but recent studies on visuotactile integration found that the linear model was the best [Salomon et al., 2017, de Haan et al., 2016]. The line bisection task also relies on linear fitting [Lourenco et al., 2011]. In our studies in chapters 6 and 7, we took as a measure of PPS boundaries the farther distances at which sound started to boost tactile detection. In the left hemispace, we found that multisensory integration continues to evolve within PPS boundaries, with different distances of RTs boost. Overall, there is no consensus on the appropriate model reflecting PPS characteristics. The dynamics of multisensory integration within PPS boundaries remains unexplored, and its study could provide a better approach of PPS morphometry.

PPS as a proxy of social affiliation?

We found that PPS is modulated in social contexts, in cooperative situations but not in competitive ones. PPS modulation in positive social contexts only has been

described previously [Teneggi et al., 2013, Pellencin et al., 2017]. PPS extension in social contexts seems to be linked to prosocial effects. In cognitive neurosciences, positive effects of social interactions are not easy to study, and few methods are available to provide robust measures. Methods generally measure social affiliation with economical games and questionnaires. If we would find an efficient way to measure PPS through a reliable index of multisensory enhancement, it could provide a psychophysical measure of prosocial effects.

Towards a clarification of PPS definition

The large number and variety of methods used to study PPS highlight the fact that PPS in humans is still defined according to different criteria across investigations. However, the links between those methods are unclear. We can not affirm that the behavioral observations have the same underlying neural processes. Comparisons between the different PPS measurements methods, and analysis of their neural basis would allow a clarification on space perception phenomenon in humans.

Motor coding of space during collective actions

We found that PPS boundaries are modulated during a collaborative task, this modulation does not depend on the position of the partner in space. This would argue for a specific space perception for collective action. Studies on joint action argue that people automatically represent other's actions [Knoblich and Sebanz, 2012]. The question here is to know if this action representation is embedded in space, if individual's motor space changes depending on others' actions. If we look at crowded social situations like concerts, protests or in the subway, the possible actions of one individual are highly dependent on the possible actions of the people around. Individual own motor abilities would not be enough to represent the possible actions. Further research is needed to better understand the links between motor action, social contexts and space perception.

Altogether, the present research brings new information about multisensory integration in space and suggests that motor and social factors are important variables to take into account in the investigation of space monitoring. Further studies on factor coding PPS might help us to better understand spatial behaviors. In 1966,

Hall described proxemics to evaluate how humans use space and handle distance from their fellows. In order to come closer to the original approach of proxemics, as done in anthropology, we could use sensory stimuli with a biological relevance to study the links between social context and the multisensory coding of space. The use of looming human sounds (vocalization or steps sounds) would represent a paradigm closer to the ecological situations in which we handle distance from our fellows. Future research on PPS aiming at increasing the ecological validity of social interactions in experimental paradigms will lead to an integrative view of spatial behaviors from low-level multisensory coding of space to space management in society.

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ANNEXES

Flanders handedness questionnaires

Flinders Handedness Survey (FLANDERS)

Surname: _____ ..First name: _____ .

Date of birth: _____ .Sex (m/f) _____ .

The ten questions below ask which hand you prefer to use in a number of different situations. Please tick one box for each question, indicating whether you prefer to use the left-hand, either-hand, or the right-hand for that task. Only tick the 'either' box if one hand is truly no better than the other. Please answer all questions, and even if you have had little experience in a particular task, try imagining doing that task and select a response.

		Left	Either	Right
1	With which hand do you write?			
2	In which hand do you prefer to use a spoon when eating?			
3	In which hand do you prefer to hold a toothbrush when cleaning your teeth?			
4	In which hand do you hold a match when you strike it?			
5	In which hand do you prefer to hold the rubber when erasing a pencil mark?			
6	In which hand do you hold the needle when you are sewing?			
7	When buttering bread, which hand holds the knife?			
8	In which hand do you hold a hammer?			
9	In which hand do you hold the peeler when peeling an apple?			
10	Which hand do you use to draw?			

Handedness score (please don't fill this out)	
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Résumé

L'homme ne perçoit pas l'espace de manière homogène : le cerveau code l'espace proche du corps différemment de l'espace lointain. Cette distinction joue un rôle primordial dans notre comportement social : l'espace proche du corps, appelé espace péripersonnel (EPP), serait une zone de protection du corps, si la présence d'un individu est perçue comme une menace. L'EPP a été initialement décrit par la psychologie sociale et l'anthropologie, comme un facteur de la communication humaine. L'EPP a été plus tard décrit chez le singe par des études de neurophysiologie comme un espace codé par des neurones multisensoriels. Ces neurones déchargent uniquement en réponse à des événements sensoriels situés à une distance limitée du corps du singe (qu'ils soient tactiles, visuels ou auditifs). L'ensemble de ces neurones multisensoriels code ainsi l'EPP tout autour du corps. Ce codage exclusif de l'EPP est crucial pour interagir avec le monde extérieur, car c'est dans cet espace que sont réalisées les actions visant à protéger le corps ou visant à atteindre des objets autour de soi. Le codage multisensoriel de l'EPP pendant des interactions sociales est à ce jour peu étudié. Dans ce travail de recherche, nous avons réalisé plusieurs études en vue d'identifier des facteurs contribuant à la perméabilité de l'EPP et ses aspects adaptatifs.

Une première étude a examiné les frontières latérales de l'EPP chez des individus seuls, en mesurant l'interaction d'une source sonore dynamique s'approchant du corps avec le temps de détection de stimulations tactiles. Cette étude a montré des différences dans la taille de l'EPP entre les deux héli-espaces, qui seraient liées à la latéralité manuelle. Une seconde étude a exploré les modulations de l'EPP dans des contextes sociaux. Elle a montré que l'EPP est modifié lorsque des individus réalisent une tâche en collaboration. La troisième étude est une recherche méthodologique qui vise à dépasser les limitations des paradigmes comportementaux utilisés actuellement pour mesurer l'EPP. Elle propose de nouvelles pistes pour évaluer comment les stimuli approchant le corps sont intégrés en fonction de leur distance et du contexte multisensoriel dans lequel ils sont traités.

L'ensemble de ces travaux montre l'intérêt d'étudier l'intégration multisensorielle autour du corps dans l'espace 3D pour comprendre pleinement l'EPP, et les impacts potentiels de facteurs sociaux sur les processus multisensoriels de bas-niveaux. De plus, ces études soulignent l'importance pour les neurosciences sociales de développer des protocoles expérimentaux réellement sociaux, à plusieurs participants.

Mots clés: Espace péripersonnel, intégration audio-tactile, cognition sociale, latéralité manuelle, perception de l'espace

Abstract

The space near the body, called peripersonal space (PPS), was originally studied in social psychology and anthropology as an important factor in interpersonal communication. It was later described by neurophysiological studies in monkeys as a space mapped with multisensory neurons. Those neurons discharge only when events are occurring near the body (be it tactile, visual or audio information), delineating the space that people consider as belonging to them. The human brain also codes events that are near the body differently from those that are farther away. This dedicated brain function is critical to interact satisfactorily with the external world, be it for defending oneself or to reach objects of interest. However, little is known about how this function is impacted by real social interactions. In this work, we have conducted several studies aiming at understanding the factors that contribute to the permeability and adaptive aspects of PPS.

A first study examined lateral PPS for individuals in isolation, by measuring reaction time to tactile stimuli when an irrelevant sound is looming towards the body of the individual. It revealed an anisotropy of reaction time across hemispaces, that we could link to handedness. A second study explored the modulations of PPS in social contexts. It was found that minimal social instructions could influence the shape of peripersonal space, with a complex modification of behaviors in collaborative tasks that outreaches the handedness effect. The third study is a methodological investigation attempting to go beyond the limitations of the behavioral methods measuring PPS, and proposing a new direction to assess how stimuli coming towards the body are integrated according to their distance and the multisensory context in which they are processed.

Taken together, our work emphasizes the importance of investigating multisensory integration in 3D space around the body to fully capture PPS mechanisms, and the potential impacts of social factors on low-level multisensory processes. Moreover, this research provides evidence that neurocognitive social investigations, in particular on space perception, benefit from going beyond the traditional isolated individual protocols towards actual live social interactive paradigms.

Keywords: Peripersonal space, audio-tactile integration, social cognition, handedness, space perception