UNIVERSITÀ DEGLI STUDI DI TRENTO

Dipartimento di Scienze della Cognizione
e della Formazione

Doctoral School in Cognitive and Education Science

XXII cicle

Assessing audiotactile interactions: Spatiotemporal factors and role of visual experience

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Academic Year 2009/2010

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Thesis Overview

This thesis investigated the crossmodal interactions occurring between hearing and touch. Chapters 1 to 6 present the background to this topic and an introduction to the underlying mechanisms of crossmodal perception. Chapter 1 provides a historical overview on the pioneering studies in this issue, whereas in the successive ones the main behavioural evidence on is described. Specific aspects are presented across the chapters, with Chapter 2 presenting the studies using detection/discrimination tasks, intensity tasks, or investigating texture perception or crossmodal sensory illusions and pseudosynaesthetic correspondences. In the subsequent chapters, more specific aspects are taken into consideration, such as the temporal (Chapter 3) and the spatial (Chapter 4) constraints characterizing audiotactile interactions. In Chapter 5, special attention is given to the neural substrates of the audiotactile sensory interplay, in both humans and monkeys. Since there is considerable evidence showing that visual deprivation influences how touch and hearing interact, Chapter 6 will be devoted to explore this topic in more detail.

The following chapters present the experimental studies designed to empirically investigate different aspects of audiotactile interactions. Chapter 7 contains experimental studies examining the potential existence of a sensory dominance between hearing and touch, by investigating different portions of the peripersonal space and/or spatial arrangement of the stimuli. Chapter 8 is focused on evaluate the capability of humans in matching the frequency pattern of auditory, tactile and crossmodal stimuli. The spatial factors affecting audiotactile interactions will be explored in Chapter 9, by evaluating how the perception of apparent motion in one modality is biased by the presentation of apparent moving stream in the other modality. The investigation of crossmodal compatibility effects is the topic of Chapter 10. Since visual deprivation has been proved to influence how touch and hearing interact, the last chapter (Chapter 11) will be devoted to compare either spatial or temporal perception, as well as the construction of frames of reference for tactile processing - in relation with auditory stimulation- in blind and sighted individuals.

PART 1: Theoretical background

Chapter 1.

Multisensory integration and audiotactile interactions: an overview

1.1. Introduction

The aim of the present dissertation is to investigate - from both a theoretical and an empirical perspective - the crossmodal interactions occurring between hearing and touch.

Human individuals continuously interact with an environment providing a large amount of sensory information. Research has widely documented that the inputs delivered by the different sensory channels tend to be bound together by our brain. The process by which the human nervous system tends to merge together the available pieces of information in unique events is commonly known as ‘multisensory integration’ (see Calvert, Spence & Stein, 2004, for a review).

The process of combining sensory inputs is governed by specific principle at neuronal level, which will be described in more details in the Chapter 5, and determines benefits which are behaviourally observable. The most paradigmatic example is probably represented by the shortening of the interval between sensory encoding and motor-command formation, which in turn speeds sensory processing itself. The final outcome is that the response to multisensory events has a significantly shorter latency than the response to either of the unisensory components (cf. Miller, 1982). In addition to altering the salience of cross-modal events, multisensory integration involves the maintenance of the representation of unitary perceptual experiences. It thus follows that the process of integrating information from different senses must cope with two orders of complexities, those inherent each sensory modality, but also the fact that each modality has its own unique subjective impressions or ‘qualia’ (for example, the perception of hue is specific to the visual system, whereas tickle and itch are specific to the somatosensory system) which are not disrupted by the integrative process.

The process by which the brain overcomes these constraints to construct unitary percepts is still partially unknown. However, it is likely that this process is accomplished by first combining non-redundant information provided by different senses, thus leading to a temporary increase of the available information (i.e., ‘sensory combination’). In a later stage, ‘sensory integration’ reduces the uncertainty in the internal representation of the stimulus – supposedly in a statistically optimal way – which then improves the behavioural reaction (Ernst & Bülthoff, 2004).

Unlike audiovisual and visuotactile sensory pairings, the interactions occurring at both neuronal and behavioural level between hearing and touch have been much less explored (although see Kitagawa & Spence, 2006; Soto-Faraco & Deco, 2009, for reviews on this topic). This is somehow surprising, considering the wide range of everyday life situations in which we can experience – even though often in subtle and unconscious ways – the interplays occurring between these two sensory modalities (cf. Doel & Pai, 1996). Perceiving the voice and the steps of a person entering into our office making the floor to vibrate, while we are facing to the screen of the pc; perceiving the buzzing and the itchy sensation of an insect approaching the rear surface of our neck; reaching a mobile phones ringing and vibrating from the bottom of our bag or pressing the button to switch our laptop on and perceive that familiar click.

All these situations have in common the exclusive – or predominant – reliance on cue provided by senses other than vision. Besides these anecdotal reports, however, empirical evidence further support the existence of correlations between hearing and touch, thus justifying and corroborating additional investigations of this topic. In the Part I we will provide an overview of the studies investigating audiotactile interactions, both with behavioural (see Chapters 1-4 and Sections 6.1-6.3) and neuroimaging techniques (see Chapter 5 and Section 6.4). In the Part II (i.e., Chapters 7-11), the studies we have conducted will be described.

In the next section, in particular, seminal studies investigating the general similarities between hearing and touch will be presented.

1.2. Early studies on crossmodal interactions between hearing and touch

In his pioneering work, von Békésy drew some parallelisms between the senses of hearing and touch, which turned out to be so tight to lead him to consider the sense of touch as a reliable model for the study of functional features of audition (von Békésy, 1955, 1957, 1959). For instance, von Békésy noted that hearing and touch are analogous in regard to the level of the encoding mechanism at the respective receptor surfaces. Indeed, both the basilar membrane of the inner ear and mechanoreceptors in the skin respond to the same type of physical energy, namely the mechanical pressure endowed with specific vibratory rates (von Békésy, 1959; cf. Nicolson, 2005). Either touching the surface of the skin with a vibrating body and stimulating the stapes footplate of the ear determine the propagation of travelling waves. The analogies in the physiological mechanisms underlying tactile and auditory perception are likely to root into the common origins of these sensory systems (von Békésy, 1959). Studies on the ontogenetic brain development show that the order with which the sensory modality-specific neurons as well as multisensory neurons in the anterior ectosylvian sulcus emerge follows a precise time course, proceeding from tactile-responsive to auditory-responsive and finally to visually-responsive neurons (Wallace, Carriere, Perrault, Vaughan, & Stein, 2006). It can not be excluded, then, that the line of development of the different sensory systems would pervade the successive strength, direction and amount of reciprocal connections between them (Gregory, 1967; Katsuki, 1965). From this point of view, the evidence according to which the organ of Corti would gradually evolve from the skin tissue could be possibly informative of favoured links between hearing and touch (von Békésy, 1959).

This evidence parallels with the commonality of some physical properties, which according to von Békésy (1959), are shared across hearing and touch, such as pitch, loudness, volume, roughness, direction, distance, on-and-off effects, and rhythm. For instance, by adjusting the magnitude and the time pattern of either auditory clicks travelling along the skin of the forehead and spatially coincident air puffs, von Békésy succeeded in demonstrating that observers could hardly discriminate between auditory and tactile stimulations when they seemed to have the same directions. This results points to remarkable analogies – at least under specific conditions – between the two sensory modalities.

It should be noted, however, that von Békésy highlighted not only the physiological and functional analogies, but also some discrepancies featuring the relationship between hearing and touch. For instance, in touch the maximum of the vibration sensation can be detected in correspondence of the location where the object touches the skin, independently from the frequency of the stimulation delivered, whereas in hearing the place of maximal vibration changes as a function of the frequency of the tone. Similarly, the tactile pitch is coded by the periodicity of the travelling waves along the skin, differently from hearing, in which the place of maximal stimulation along the basilar membrane can be utilised as an additional cue (von Békésy, 1957). Moreover, von Békésy (1959) observed that the transduction time was lower in the ear than along the skin, giving rise to shorter latencies – and thus a better temporal resolution - in the encoding processes of tones as compared to vibrations presented on the skin.

These results have been partially replicated in a subsequent study (Gescheider, 1970), one of the first investigating the temporal acuity of the tactile and auditory modalities (cf. Hirsch & Sherrick, 1961). In his experiments, Gescheider (1970) investigated the temporal resolution threshold for stimuli presented to the ears and on the skin. Indeed, he found that the temporal acuity for both binaural and monoaural stimulation was significantly shorter than for cutaneous stimuli presented on the fingertips. For interstimulus intervals below 30 ms, the auditory stimuli were perceived as more separated in time than tactile stimuli separated by the same interval. However, for intervals exceeding the 30 ms, this crossmodal discrepancy in the temporal acuity was annulled. Thus, according to Gescheider, ears and skin differ in their temporal resolution only for stimuli separated by short time intervals. A more extensive argumentation on the temporal features of the audiotactile interactions will be the topic of the Chapter 3.

Gescheider also extended von Békésy's observations (1955) regarding the capability of ears and skin to localize sounds. In his experiments, von Békésy had studied the human capability to localize the sounds through the propagation of the waves along the membrane of a dimensional model of the mechanical parts of the human cochlea, placed in contact with the arm. This way, he had found that the skin can process both temporal-difference and intensive-difference cues – necessary for sound localization – as accurately as the ears. Over time, in fact, the participants were able to localize sounds even though the stimulation was exclusively provided by cutaneous cues delivered on the skin of forearms. Differently from what has been proposed by von Békésy (1955), however, who stated that ears and skin react identically to tiny time delays between the two stimuli, Gescheider demonstrated, by independently manipulating the intensity- and temporal-difference, that the auditory localization was influenced by both types of cues, whereas the cutaneous localization depended mainly on intensity differences. A more extensive and exhaustive discussion of the aspects risen by these early studies will be provided in the next chapter.

Chapter 2.

Audiotactile interactions in low-level behavioural tasks

2.1. Introduction

In this section, we will briefly described the experimental evidence observed in audiotactile tasks investigating low-level functions, such as detection/discrimination of auditory and tactile information (see Section 2.2), its intensity (see Section 2.3) or texture (see Section 2.4). Finally, we will review studies on audiotactile perceptual illusions (see Section 2.5) and synaesthetic and pseudosynaesthetic correspondences (see Section 2.6).

2.2. Detection/discrimination performance

The accidental observation that people who were involved in sensory (i.e., auditory and tactile) judgment tasks often reported that a tap on the fingertip resembled to a sound and, alternatively, that a click resembled to a tactile pulse led Gescheider and Niblette (1967) to reckon that the stimulation provided by one of these sensory modalities (i.e., touch or audition) could inhibit the perception of stimuli in the other sensory modality (i.e., audition or touch, respectively). In a series of experiments, these authors investigated the phenomenon of crossmodal audiotactile masking. The amount of inhibition induced by one sensory modality on the detection of stimuli presented in another (i.e., masking) is defined as the difference between the threshold measured in the presence and in absence of the masking stimulus (i.e., threshold increment). The results of their experiments showed an imbalance in the reciprocal masking effect occurring between touch and hearing, with stronger effects of the auditory masking stimulus on the perception (i.e., detection and temporal resolution) of tactile taps than the reverse condition (i.e., auditory targets and tactile masking stimuli). More specifically, the auditory clicks masked tactile perception by increasing tactile threshold, particularly when the auditory maskers were presented simultaneously with the tactile target and had higher intensities (see also Beauchamp, Yasar, Frye, & Ro, 2008; Weisenberger, 1994). Even though to a lesser extent than the previous condition, also the tactile pulses influenced the perception of the auditory targets, and again particularly when they were presented simultaneously with the targets. This evidence supports the idea that when the target and the masking stimuli are presented together, the intermodality inhibition is maximized, with a consequent decrease in the detectability of the targets.

In a subsequent experiment, Gescheider and coworkers (Gescheider, Barton, Bruce, Goldberg, & Greenspan, 1969) explored whether the auditory stimulation, which had been proved to be effective in masking the simultaneous tactile stimulation, could have reduced the detectability of the tactile stimulation or, rather, could have determined changes in observers' response criteria. Using signal-detection methodology, the authors showed that such auditory-tactile masking is the result of a reduction in signal detectability, together with a corresponding increase in the observers' criterion (i.e., response bias). Although tentatively, Gescheider put forward the argumentation that the neural mechanism potentially responsible for the crossmodal masking between hearing and touch can be identified with the reticular formation of the brainstem. This structure is the locus of convergence of neural impulses from all sensory modalities. According to Gescheider and colleagues, the activation of the reticular formation induced by the auditory stimulation could have resulted in inhibitory neural impulses along the tactile pathway from the periphery to the somatic cortex. Surprisingly, this pattern of results seemed to be partially disconfirmed by another study from the same laboratory (Gescheider, Kane, Sager, & Ruffolo, 1974). By applying a forced-choice procedure to a tactile detection task, these authors found that the detectability of the vibration was not adversely affected – but, on the contrary, was slightly facilitated - by the simultaneous presentation of a tone of the same frequency. However, the simultaneous tones induced changes in observers' response criteria, increasing both hit and false alarm rates. The authors interpreted their data by claiming that the tone could have possibly facilitated neural activity in the tactile sensory system, leading to an increase in both signal and noise level (see Lugo, Doti, Wittich, & Faubert, 2008a for recent evidence supporting the facilitatory role of auditory noise on the tactile detection performance). This resulted in an unchanged level of sensitivity, though accompanied by a reduction in the response criterion.

Some more recent studies contributed to resolve the above described debated interactions occurring between hearing and touch during detection tasks. For instance, Gillmeister and Eimer (2004; Experiment 1) investigated whether the presentation of task-irrelevant touch could influence the detection of simultaneous auditory stimuli presented near threshold in a two-interval forced choice task. Differently from what had been shown by Gescheider and Niblette (1967) and Gescheider (1970), in Gillmeister and Eimer's study the detection performance was significantly improved by the presentation of tactile stimuli. Similarly, Ro and coworkers (Ro, Hsu, Yasar, Caitlin Elmore, & Beauchamp, 2009) ran three experiments aimed to assess how task-irrelevant auditory stimuli can affect the detection rate of near-threshold tactile stimuli. When the stimuli were presented simultaneously from a central location (i.e., a centrally located loudspeaker was used to present the auditory distractors while the tactile targets were presented to the left index fingertip located in spatially correspondence with the loudspeaker; Experiment 1), the results showed that the task-irrelevant auditory stimuli increased sensitivity (i.e., increase of the detection rate of the somatosensory stimuli when they were accompanied by an auditory stimulus as compared to the baseline condition, where no auditory stimuli were presented). The experiment 2 showed that the enhancement of the somatosensory perception was spatially specific. Namely, only auditory stimuli presented on the same hemispace (i.e., right or left side of the body midline) as the somatosensory stimuli enhanced spatial discrimination of the somatosensry could influence the participants' detection performance. Interestingly, the effect of sounds on tactile stimulation varied as a function of the frequency similarity between the two. Specifically, the tactile discrimination increased when the sound had the same frequency as the tactile stimulus and decreased when the sounds were as a different frequency. Thus, despite the variety of the experimental paradigms used in Ro et al.'s experiments, they consistently showed that the auditory information influences touch perception in systematic ways. Their data seem to suggest that audiotactile multisensory enhancement effects are both spatially- and frequency-specific and could possibly be attributed to super-additive processing of the signals in brain areas coding for both these sensory modalities (e.g., the superior colliculus and the posterior parietal cortex).

As we will see in the next sections, not only the auditory stimuli influence the perception of tactile stimulation, but also the reverse holds, with touch influencing some aspects of auditory perception, thus rendering the crossmodal interplay between these sensory modalities even more complex and multi-faceted.

2.3. Intensity

As intensity is a common quality to various modalities, previous studies have investigated how this dimension can be differentially coded and compared across modalities. For instance, Marks repeatedly tried to quantify the perceptual similarity of intensity across sensory modalities and to what extent these cross-modal equivalences can be considered absolute (Marks, Szczesiul & Ohlott, 1986; Marks, 1988). On the basis of the above mentioned (see Section 1.2) similarities between hearing and touch highlighted by von Békésy, whose Marks and colleagues were perfectly aware, it turned out that the loudness and the vibration intensity are not only attributes non separable from the other features of the stimulus (i.e., pitch), but also that they depend primarily on the context (i.e., the particular array of auditory intensities presented).

In a subsequent study, Gillmeister and Eimer (2004; Experiment 2) tested whether the perception of the loudness of sounds could be affected by the presentation of tactile stimuli. Auditory intensity ratings systematically increased when tones were accompanied by tactile stimuli as compared to the baseline condition (i.e., where sounds were presented in isolation), especially for stimuli presented at a near-threshold level (i.e., inverse effectiveness rule; Cf. Diederich & Colonius, 2004). This enhancement of perceived auditory intensity by synchronous touch found by Gillmeister & Eimer (2004) mirrors the data observed in another study (Schürmann, Caetano, Jousmäki, & Hari, 2004). In Schürmann et al.'s study, the observers were asked to adjust a probe tone to sound equally loud as a reference tone. The results showed that the participants chose lower auditory intensities when touching a tube vibrating simultaneously with the probe tone (‘Hearing Hand Effect’). In contrast with these studies, which seem to suggest that the crossmodal enhancement of perceived auditory intensity could be ascribed to sensory-perceptual processes, as suggested by the selectivity of the effect as a function of the temporal arrangement of the stimuli, other evidence support a post-perceptual explanation of audio-tactile interactions (cf. Yarrow, Haggard, & Rothwell, 2008). Indeed, Yarrow and colleagues carried out three experiments to assess how a vibrotactile stimulus affects auditory perception of tones at the same frequency. Whereas in the Experiment 1, the effect reported by Schürmann and colleagues was substantially replicated (i.e., the presence of a vibrotactile stimulus induced an increase in the perceived loudness of auditory tones), in the following two experiments – using a 2-interval forced-choice procedure instead of a subjective paradigm - the performance was selectively biased when the vibrotactile stimulus was presented in one interval, but not when the vibrotactile stimulus was presented in both intervals (i.e., the performance was comparable to the condition when the auditory stimuli were presented in absence of vibrotactile stimuli). The fact that vibration can sometimes be ignored when judging the presence of an auditory tone indicates that the effect of the vibrotactile stimulus occurs after the perceptual processing of the auditory inputs. This speculation is supported by the evidence according to which a reliable effect of vibrotaction on auditory intensity was obtained only when using subjective methods (Gillmeister & Eimer, 2004; Experiment 2; Schürmann et al., 2004; Yarrow et al., 2009; Experiment 1), and not when using bias-free objective methods, such as two-alternative forced choice (Yarrow et al., 2009; Experiments 2 and 3). Thus, according to Yarrow et al., the interactions between vibrotaction and audition in intensity perception could possibly originate from a response bias or, at least, could only partially be explained on the basis of an exclusive early-sensory-based explanation. On the contrary, it is likely that these effects emerge post-perceptually, as a consequence of a combined audiotactile representation formed in secondary sensory areas (see Chapter 5 for a more exhaustive discussion on the neural substrate of audiotactile interactions).

2.4. Texture

One aspect of audiotactile multisensory perception that has been extensively investigated is the perception of textured surfaces (see Lederman, 1982, for a review). Indeed, tactual exploration of surfaces can be considered as a multisensory experience, since both tactile and auditory signals convey redundant information about texture, contributing to what has been defined as ‘textural timbre’ (Yau, Hollins, Bensmaia, 2009), but also, as recently demonstrated, information about the estimated speed and effort of haptic exploration (Hermes, Brouwer de Koning, & Geelen, 2009).

An earlier study conducted by Lederman (1979) investigated whether people is able to exclusively use touch-produced sounds to make judgments about the roughness of a surface, and if so, whether they would use them even when additional tactile information is available. The results obtained in those studies suggest that people can discriminate the sounds produced by rubbing the finger on different surfaces (e.g., sandpaper of different roughness) when they were presented in isolation. However, when congruent auditory and tactile texture cues were simultaneously provided, the latter tended to prevail in the estimation of the surface roughness (i.e., the sense of touch completely dominated the sense of audition). In more recent studies, the same topic has been investigated by asking the participants to touch the surfaces textures (i.e., sets of raised dots varying in inter-element spacing) not with their bare fingers, but by means of a rigid probe and asking them to assign any non-zero number that best described the magnitude of the perceived roughness of the stimulus (Lederman, Martin, Tong, & Klatzky, 2003; Lederman, Morgan, & Hamilton, 2002). Consistently with the prediction of the authors, the results showed that in this condition the observers used both tactual and auditory information to make their estimations. However, the relative weighting was still in favour of a predominant use of the tactile (vs. auditory) cues (i.e., 62% and 38%, respectively).

In a well-known paper, Jousmäki and Hari (1998) have showed that auditory cues can influence tactile judgments under certain conditions. Participants in their experiment were asked to rub their hands together while rating the sensation of the skin moistness/roughness. The sound of their hands being rubbed together was recorded via a microphone placed near the participants' hands and presented to the participants over headphones. The critical manipulation in that study consisted in the alteration of certain frequency bands of the acoustic feedback arising from the hand friction. Jousmäki and Hari reported that the perception of the palmar surface was significantly affected by the presentation of the modified sounds. Namely, the participants judged the skin of their hands as being 'smoother/drier' when either the overall sound level was increased, or if just the frequencies ranging between 2 and 20-kHz were amplified. Similarly, the participants judged their hands as "rougher/moister" when the sounds within this range were attenuated. This effect was labelled as 'parchment skin illusion'.

As successively pointed out (Guest, Catmur, Lloyd, & Spence, 2002), however, some methodological limitations (i.e., potential experimenter-expectancy effects and task demands, sample not randomly recruited, use of composite response scales) affecting the paradigm used by Jousmäki and Hari prevented from unequivocally disambiguate between the perceptual and the cognitive factors possibly contributing to the effect observed. In a successive study (Guest et al., 2002), more rigorous phychophysical testing conditions were applied in order to minimize any methodological confounds. Guest and al.'s results confirmed that the frequency content of the auditory feedback significantly modulated the tactile roughness perception of either abrasive surfaces (Experiment 1) and of the skin of the hands (Experiment 2), provided that the auditory feedback occurred simultaneously with the tactile stimulation (Experiment 3; see also Jousmäki and Hari, 1998). Taken together, these results turned out to be effective in replicating Jousmäki and

Hari’s observations, thus again demonstrating the dramatic effect that auditory frequency manipulation can have on the perceived tactile roughness.

A recent study (Suzuki, Gyoba, & Sakamoto, 2008) provided evidence in support of perceptual influences exerted by auditory inputs to the perception of texture roughness even when the auditory stimuli were not elicited by the movement of the observer (i.e., non touch-produced sounds)(Cf. Hermes et al., 2009). Participants were required to touch abrasive paper, synchronizing their touch with non informative sounds which could either consist of white noise bursts or pure tones. The results highlighted a selective effect of white noise auditory stimuli, but not of pure tones, on roughness perception. These results add to previous evidence (e.g., Kitagawa, Zampini, & Spence, 2005) showing that complex sounds - which include a wide range of frequency components – interfere with tactile stimulation at a greater extend than pure tones.

Thus, although previous studies (Lederman, 1979; Lederman et al., 2002, 2003)on this topic were in support of a prevalent reliance on tactile (vs. auditory) cues in texture perception, successive studies have somehow contradicted those results, suggesting that texture perception can be noticeably biased by auditory cues (Jousmäki & Hari, 1998; Guest et al., 2002). Moreover, these effects seem to be closely dependent on the auditory stimuli involved (Suzuki et al., 2008).

Whereas the inconsistence of the evidence aimed to determine the relative weight of auditory and tactile cues on texture perception points to the necessity of further investigations, the selectivity of the effects of white noise (vs. pure tones) on audiotactile interactions is, as will be discussed, well established. The importance of this specific aspect in the interactions occurring between hearing and touch is of great importance and deserve further and more extensive discussions (see Sections 4.3, 4.4 and Chapter 9).

2.5. Sensory illusions between hearing and touch

Besides the above described ‘parchment skin illusion’ (see Section 2.4), which is probably the most widely investigated audiotactile illusions, other illusions, whose we will now provide an overview, have been observed occurring in both these two sensory modalities.

The key aspect of the tactile funnelling illusion is the illusory perception of skin stimulation at a single central site of an actual array of multiple stimulation sites (e.g., Sherrick, 1964; von Békési, 1959, 1967). By presenting vibrotactile stimulation to the arm along the whole length of a rod lying on the skin surface, he found that resulting percept was the feeling of the rod vibrating only in correspondence of a section in the middle, and not along its full length. The lateral spread of this sensation depends on the frequency of the stimulus, its amplitude, as well as the density of the neural innervation of the skin section. For example, when an array of different frequencies but equal intensities is presented along the arm, only the frequency presented by the central vibrator is actually felt. Additionally, if one end of the rod is pressed against the skin, then the sensation is displaced toward the maximum of the stimulus amplitude. Decreasing the time delay between lateral stimuli leads to the fusion – to the ‘funneling’ - of the tactile sensations so that a single, more intense tactile sensation is perceived in correspondence of the central location (although no physical stimulus occurred at that site). Hence, the general impression is of a very much sharper and more centred sensation than the stimulus distribution that has been applied to the skin. The mislocalization and the sharpening effect of the sensation distribution along the surface of the skin is especially pronounced for stimuli with short presentation times and equalized in intensity. Under these conditions, only the sensation in the middle is felt with its corresponding frequency sensation. All the other tactile stimulations on both sides of the middle location are inhibited and disappear from the picture.

Neuroimaging studies have shown that the funnelling illusion is encoded in somatosensory cortex, with simultaneous stimulation of multiple skin sites leading to a single focal cortical activation between the individual activation regions, thus suggesting that not only perception of a tactile stimulus can happen where no physical stimulus actually occurred, but also that spatial perceptions in touch are strongly biased by central representations. Even though the inhibited stimuli are not perceived as separate entities, they do contribute to the overall intensity of the sensation that is heard or felt. (Chen, Friedman, & Roe, 2003; Gardner & Spencer, 1972).

Interestingly, when two auditory stimuli are presented binaurally and with no delay, the unified sensation is localized at a midpoint between the two ears, thus proving that a phenomenon analogous to the funnelling illusion can be observed in hearing as well (e.g., Watanabe, 1979). Moreover, Von Békésy (1959) found that the time delays necessary for the pattern of inhibition observed in the funnelling illusion were similar for hearing and touch.

The ‘cutaneous rabbit illusion’, firstly described by Geldard and Sherrick (1972), is a tactile illusion evoked by tapping two separate regions of the skin. Repetitive and rapid sequences of stimulation at two or more skin location can, under certain conditions, create the illusion of sequential taps at intervening locations along the arm, as if a rabbit hopped along it.

Related to the cutaneous rabbit illusion is the ‘saltation phenomenon’, in which an attractee stimulus is perceived as displaced towards a following attractant at a different location (Geldard, 1985). An analogous sensory saltation has been described in auditory spatial perception as well (e.g., Hari, 1995). Trains of eight binaural clicks at appropriate time interval so that the first four clicks were perceived as coming from the left and the click from five to eight as coming to the right were presented to the participants through headphones. At interstimulus interval of 30-90 ms, the participants perceived saltatory illusions, with clicks seeming to jump in discrete steps from left to right. No saltatory effects were reported for left-sided followed by right-sided monaural clicks.

Of interest in the present discussion is a recent study testing the existence of crossmodal tactile-auditory saltation (Trojan, Getzmann, Möller, Kleinböhl, & Hölzl, 2009). In that study, the tactile stimuli were presented to different locations on the forehead and spatially matched stereoscopic auditory stimuli were presented via headphones. After a reference stimulus at one of five spatial positions, the attractee was presented at a fixed position, followed by the attractant at a different fixed position with a delay of 81, 121, or 181 ms. The task was to rate whether the attractee was located left or right of the reference. The reference/attractee vs. attractant configuration could be uni- or crossmodal. At an attractee-attractant delay of 81 ms, saltation could be elicited unimodally as well as across modalities. Moreover, the tactile attractants had an overall stronger influence than auditory attractants. Although still tentative, this study succeeded in showing a crossmodal saltation between tactile and auditory stimuli, thus suggesting the existence of crossmodal interactions in this kind of paradigm.

Another sensory illusion occurring in the space close to the head has been described by Kitagawa and Igarashi (2005). In their experiment, they stroke the ear of a dummy head as if to tickle the ear, and recorded either the sound elicited via a microphone and the scene on videotape. The participants could be either presented with either the sound or with the video images of the ear ‘ticked’ (i.e., unimodal conditions) or both (i.e., crossmodal condition) for 30 s. The sound was presented either via headphones (Near condition) or via a loudspeaker placed 80 cm from the participant’s left ear (Far condition). Next, the participants were presented with a scale and asked to rate their agreement with each of a series of questionnaire statements (e.g., ‘I felt tickling my own ear’, ‘I felt as if my own ear was touched’, ‘I felt as if my ear was turning rubbery, ‘I felt as if my ear of the dummy head was my ear’). The participants in the ‘near’ condition responded more positively to statements 1, 2 and 4 (but not to the statement 3) than the participants in the ‘far’ or in the visual-only conditions. That is, sounds presented from close to the participants’ head induced more of a tickling impression, while sounds presented far from the participants’ head did not. Interestingly, the visual stimulation alone failed to influence the participants’ ratings. The surprising result of this study is the demonstration that a tickle sensation can be induced by presenting a sound delivered from close to their head.

Taken together, the evidence showing the existence of audiotactile illusions are useful in clarifying how physical attributes of the stimuli, their spatial arrangement, and their respective cerebral representations affect the perceptual accuracy behaviourally observable. The spatial selectivity based on the distance of the sound from the participants' own body will be further discussed in next sections (see Sections 4.1-4.8) and has been also experimentally investigated in one of our studies (see Chapter 7).

2.6. Synaesthetic and pseudosynaesthetic correspondences

In synaesthetic individuals, the presentation of a specific stimulus systematically evokes an additional sensory experience in either the same or a different sensory modality. However, it has been shown that multisensory interactions putatively reflecting the existence of associations between the attributes of stimuli presented in different sensory modalities also occur in the non-synaesthetic population (see Martino & Marks, 2001 for the distinction between 'strong' and 'weak' synaesthesia; see also Marks, 1983 for a review). Although investigated less frequently, the occurrence of synaesthetic interactions between vision and touch have also been documented, with participants preferentially matching black and white squares with low- and high-frequencies vibrotactile stimuli, respectively (Martino & Marks, 2000; see also Cinel, Humphrey, & Poli, 2002). Previous studies have suggested that the cognitive representation of auditory pitch in the human brain is spatial in nature, with higher-pitched frequencies being located in upper positions and lower-pitched frequencies being located in lower positions (Melara & Marks, 1990; see also Mudd, 1963; Pratt, 1930; Rusconi, Kwan, Giordano, Umiltà, & Butterworth, 2006). For instance, a significant congruency effect (intended as the speeding up in classifying stimuli containing corresponding (vs. non-corresponding) attributes (i.e., white/high or black/low vs. white/low or black/high; see Marks, 1987; see also Pomerantz, 1983) has been observed when people perform a speeded discrimination task regarding the visually-presented syllables "HI" and "LO" and of high- and low-pitched tones, with congruent stimulus attributes being classified more rapidly than incongruent stimulus attributes (Melara & Marks, 1990. See also Chapter 10 for the description of an analogous, not verbally-biased, correspondence between hearing and touch).

Synesthesia can be either developmental in origin (present throughout the life span, with a hereditary component) or, though less frequently, acquired. The case of developmental synaesthetic correspondences are extremely rare (although see Luria, 1968). Ro and colleagues, however, have documented a case of acquired synaesthesia between hearing and touch in a patient with a focal lesion in the right ventrolateral nucleus of the thalamus (Ro, Farné, Johnson, Van Wedeen, Chu, Wang, Hunter, & Beauchamp, 2007). She reported that many sounds produced intense tingling sensations on the upper part of the contralesional side of the body approximately 18 months after her stroke. Subsequent structural MRI and diffusion tensor imaging examinations revealed that in this patient the secondary somatosensory cortex was responsive to sounds (Beauchamp & Ro, 2008). The authors suggested that the lack of somatosensory thalamic input induced by the stroke might have allowed short-term masking of already existing crossmodal connections between adjacent auditory and somatosensory cortical regions (see also Ward, 2007). This speculation sheds light to the still largely unexplored role of thalamus in multisensory integration (Naumer & van den Bosch, 2009), which will be described more in detail in Section 4.8.

Chapter 3.

Audiotactile interactions in the temporal domain

3.1. Introduction

Whereas in the previous sections (Chapters 1 and 2) we have examined some general aspects of the crossmodal links between hearing and touch, in the present section we will examine more in detail the features of the audiotactile links in one of the most prominent aspect of the multisensory integration, the temporal perception.

3.2. Temporal resolution, synchrony and temporal order between hearing and touch

The discussion of temporal features characterizing the crossmodal interactions between hearing and touch can not - once again - leaves aside the seminal contributions of von Békésy (1959), the first to hypothesize that hearing and touch might differ in terms of temporal resolution (see Sections 1.2 and 2.2).

In some of the first empirical investigations on this topic, Gescheider (1966, 1967a, b) deepened into this topic and indeed confirmed the early intuition pointed out by von Békésy. Across multiple experiments, Gescheider showed that the skin and ear differ greatly in their ability to resolve successive stimuli (i.e., the temporal resolution thresholds for pairs of brief stimuli presented in rapid succession were found to be 5-10 times higher for cutaneous stimulation than for hearing). For instance, two stimuli of equal subjective intensity were perceived as temporally discrete if they were separated by ~ 2 ms for monaural and binaural stimulation, but ~ 10-12 ms for cutaneous stimulation in order to be perceptually resolved (Gescheider, 1966, 1967a). Moreover, pairs of auditory stimuli separated by less than 30 msec, were perceived as more disparate in time than pairs of cutaneous stimuli. However, when time intervals were greater than 30 ms, pairs of events in both modalities are perceived as equally successive (Gescheider, 1967b).

To the best of our knowledge, the very first study comparing people’s capability to judge to temporal order of pairs of stimuli presented either within and across different sensory modality was carried out by Hirsch and Sherrick (1961). Two surprising results to emerge from that study were that the temporal separation required for the judgment of perceived temporal order was of approximately 20 ms, independently from either the modality (i.e., vision, audition or touch; Experiments 1-3) and the stimulus pairing tested (e.g., audiovisual, visuotactile, and audiotactile; Experiment 4). Hirsch and Sherrick explained their results by saying that ‘whereas the time between successive stimuli that is necessary for the stimuli to be perceived as successive rather than simultaneous may depend upon the particular sense modality employed, the temporal separation that is required for the judgment of perceived temporal order is much longer and is independent of the sense modality employed’ (p. 432). As we will see, many subsequent studies have eventually disconfirmed that result (see, e.g., Fujisaki & Nishida, 2009; Spence et al., 2003; Zampini et al., 2003a, 2003b; Zampini, Brown, Shore, Maravita, Röder, & Spence, 2005).

A remarkable amount of successive studies has addressed the question of whether people’s perceptual simultaneity/successiveness sensitivity differs as a function of the stimulus modality pairings tested (Fujisaki & Nishida, 2009; Spence et al., 2003; Zampini et al., 2003a, 2003b, 2005; Laasonen , Service, Virsu, 2001). For instance, Fujisaki and Nishida (2009) have recently assessed whether there is a difference in temporal resolution of audiovisual, visuotactile, and audiotactile combinations of stimuli made by single pulses or repetitive-pulse trains. In that study, they used a set of paradigms, traditionally used to assess the temporal perception, such as a synchrony-asynchrony judgment task, a simultaneity judgment task and a temporal order judgment tasks. The results of the synchrony-asynchrony judgment task and of the simultaneity judgment tasks, and – although at a lesser extend – of the temporal order judgment task consistently showed that the temporal resolution of synchrony perception was significantly higher for the audiotactile stimulus pairing (i.e., more than 10 Hz for repetitive-pulses stimuli) than both audiovisual and visuotactile (i.e., more than 4 Hz). This striking result can reliably not to be attributed to within-modal artefacts, such as the specific set of the stimuli chosen. The fact that the audiotactile processing has a higher temporal resolution as compared to the other stimulus modality pairings can be ascribed, according to the authors, to two different reasons, not necessarily mutually exclusive. The first explanation takes into account the difference in temporal resolution existing among the sensory modalities. Since vision as known to have a worse temporal resolution than both auditory and tactile sensory modalities (Warren & Welch, 1980), then, whenever this modality is involved the performance decreases. The alternative explanation is that the higher audiotactile temporal resolution would reflect the more rapid operation of the comparator system for the audiotactile signals. The supposed higher degree of similarity in the temporal profile of the auditory and tactile input could possibly induce a facilitation in the comparison of their temporal characteristics as compared to when the matching between other sensory modalities is involved. As we will see, it is likely that this process is sub-served by tight cortical connections between these two sensory modalities (see Section 3.4 and Chapter 5).

Moreover, Ley and coworkers recently showed that humans are able to integrate auditory and vibrotactile temporal information in a statistically optimal manner by weighting each input by its normalized reciprocal variance (Ley, Haggard, & Yarrow, 2009). Another aspect to emerge from the experimental data is that audiotactile temporal order judgments seem to be unaffected by the spatial disparity from which the stimuli are presented. In a series of experiments, Zampini and coworkers (Zampini et al., 2005) asked the participants to perform a temporal order judgments task of pairs of stimuli, one presented in touch and the other in hearing, presented at varying stimulus onset asynchronies. The critical factor was that the stimuli could be presented from the same location (i.e., both on the right or the left side of the body midline) or from different locations (i.e., one on the right and one on the left side of the body midline). The results showed that, differently from what had been shown for audiovisual and visuotactile modality pairings (Spence et al., 2003; Zampini et al., 2003a, b), the audiotactile version of the TOJ task was unaffected by whether the stimuli were presented from the same or different locations. Indeed, in previous studies participants were more sensitive when the stimuli in the two modalities were presented from different spatial positions rather than from the same position. The null effect of relative spatial position reported in Zampini et al.'s study suggests that the audiotactile stimulus pairing may be somehow 'less spatial' than other multisensory pairings involving vision as one of the sensory modalities. These data add evidence to previous research documenting a reduced magnitude of spatial effects for this pair of modalities, as compared to audiovisual and visuotactile pairings, possibly suggesting a finer spatial resolution of vision as compared to the auditory and the tactile systems (Eimer, 2004; Lloyd, Merat, McGlone, & Spence, 2003; Murray et al., 2005. See Chapters 4 and 5 for a more exhaustive discussion of spatial links between hearing and touch).

Moving from the domain of the temporal order to the perceived asynchrony between pairs of stimuli, a certain amount of studies have addressed the question of whether the impression of temporal successiveness and whether the mechanisms of temporal recalibration/adaption between auditory and tactile stimuli differs from the audiovisual and visuotactile stimulus pairings.

It has been observed that inputs from different sensory modalities referred to the same external event reach the cortex at different times, due to differences in the speed of transmission of the signals through different sensory systems (King, 2005; Spence & Squire, 2003; Spence, Shore, & Klein, 2001). It follows that our perceptual system needs to be able to accommodate a certain degree of asynchrony between the information arriving through different channels. Two mechanisms are the candidates for this kind of process: a) the realignment of sensory neural signals in time, with the processing of one of the sensory modalities shifting in time toward the other; 2) widening of the temporal window for multisensory integration.

In their study, Navarra and collaborators (Navarra, Soto-Faraco, & Spence, 2007) investigated whether exposure to audiotactile asynchrony would induce some form of temporal recalibration between the processing of auditory and tactile stimuli. Participants had to perform an audiotactile TOJ before and after an exposure phase in which paired auditory and vibrotactile stimuli could either be presented simultaneously or with the sound leading the vibrations by 75 ms.

In the exposure, to ensure that participants attended to both auditory and tactile stimuli, they were asked to perform a control task, by detecting the stimuli which were longer than the standards.

The result showed that exposure to audiotactile asynchrony induces a temporal adaptation after effect affecting the temporal processing of the following auditory and tactile stimulation. More precisely, the minimal interval necessary to correctly judge the temporal order was larger after exposure to the desynchronized trains of stimuli (JND = 48 ms) than after exposure to the synchronous trains (JND = 36 ms). This suggests that the audiotactile temporal window is flexible and can be widened in order to compensate to the asynchronies occurring between these stimuli. This adaptation process takes place even after a relatively short exposure to asynchronies, probably because of the infrequence and the small magnitude of the asynchronies occurring between hearing and touch experienced in the everyday life. Contrasting results have been shown, however, in a recent study, which compared the changes in the perception of simultaneity in three stimulus combinations (i.e., audiotactile, audiovisual and visuotactile) as a function of the exposure to asynchronies, which were presented in each of the three stimulus combinations as well (Harrar & Harris, 2008). Differently from Navarra et al.'s results, no temporal adaptation was observed for the audiotactile pairings following exposure to any of the three stimulus combinations.

A series of studies aimed to assess people's perceptual sensitivity to simultaneity between successive haptic and auditory events used environments simulating realistic situations, such as a hammer or a drum tap followed by their auditory consequence (Adelstein, Begault, Anderson, & Wenzel, 2003; Levitin, MacLean, Mathews, & Chu, 1999). Even thought the results reported in those studies were inconsistent, being the Just Noticeable Difference for temporal asynchrony ~ 24 ms in Adelstein et al.'s study and ~ 42 ms in Levitin et al's study, in both cases these values were significantly different from zero. Even more interestingly, the variability of the performance of participants in Adelstein et al' study was very high (i.e., two participants were excluded from the analysis for their poor performance, whereas another reported a JND of 5-8 ms), as also replicated in a subsequent study (i.e., JND varying from 8 to 170 ms; Begault, Adelstein, McClain, &

Anderson, 2005). Although speculative, it can be proposed the hypothesis that the inconsistence of the results reported in other studies exploring temporal perception and recalibration (Navarra et al., 2007, Harrar & Harris, 2008) could be attributed to the high variability of the performance of humans within this perceptual domain. It remains to be addressed in future investigations what kind of factors could underlie this phenomenon.

Recently, a study investigated whether the adaptation to asynchrony has long-lasting effects and can generalize to ecologically normal environment (Virsu, Oksanen-Hennah, Vedenpää, Jaatinen, & Lahti-Nuuttila, 2008). In that study, the participants practiced simultaneity judgment tasks for trains of unimodal (i.e., visual, auditory and tactile) and crossmodal (i.e., audiovisual, visuotactile, audiotactile) stimuli and were re-tested seven months later in order to test potential practice effects. In all tasks, the participants showed an improvement in judging simultaneity, leaving unaffected the relative temporal resolution (Weber fraction, stating that the ratio of the increment threshold to the background intensity is a constant, Δs/s; Weber, 1834). Moreover, since the transfer of learning between practiced tasks was minimal, the results support the speculation that of simultaneity learning mechanisms are modality-specific. According to these data, thus, the sensitivity to asynchrony can develop through the interaction with environment like any other perceptual skill.

Despite the remarkable amount of evidence accumulated on this topic, its high inconsistence, as shown by the data here presented, seems to suggest that the temporal constraints occurring between hearing and touch are still debated and worth further investigations. A tentative attempt to better qualify these links will be presented in Sections 8.2 and 8.3.

3.3. Numerosity

In a typical temporal numerosity judgment task, a sequence of stimuli (i.e., flashes, beeps or taps) is presented and the observer’s task is to judge the number of stimuli presented (Cheatham & White, 1952, 1954; Taubman, 1950a, b).

The first study comparing the participants' ability in performing tactile, visual and auditory temporal numerosity discrimination of stimuli (i.e., two to nine pulses) presented to a single location at different rates (i.e., three to eight pulses per second). The results observed in this study showed that there was a generalized tendency toward the underestimation of the number of pulses, and the amount of errors in number assessment was more pronounced as the number of pulses and/or the rate of presentation increased. More interestingly in the current context is the finding that modality-specific differences were observed. In all the experimental conditions, the accuracy in the numerosity judgments was higher for audition than for both touch and vision.

A recent study investigated whether the combinations of trains of stimuli presented simultaneously in more than one modality could improve the numerosity estimation judgments (Philippi, van Erp, & Werkhoven, 2009). In contrast with other studies (e.g., Bresciani, Ernst, Drewing, Bouyer, Maury, & Kheddar, 2005; Bresciani & Ernst, 2007; Hötting & Röder, 2004; Shams, Kamitani, & Shimojo, 2000. See Section 3.3), which explored the interfering effect of incongruent sequence of stimuli, thus, in this study the goal was to explore the beneficial effect of the presentation of congruent sequence of stimuli on numerosity estimation judgments. Participants were presented with sequences (i.e., two to ten) of stimuli at interstimulus intervals varying from 20 to 320 ms and were overtly asked to use the multisensory redundant information to their advantage in performing the task. According to Philippi and colleagues, the presentation of stimuli in multiple sensory modalities could improve the estimation of the number of pulses of each train of stimuli. More specifically, the amount of underestimation (which has been consistently shown in previous unisensory numerosity estimation judgment studies; e.g., Lechelt, 1975; White & Cheatham, 1959), and possibly the variance in estimations, would be reduced as compared to the unisensory presentations. Overall, the results of unisensory conditions confirmed that participants' estimation of numerosity differed per modality. Although Philippi and colleagues' study confirmed that the judgments within vision were worse than the other two unisensory conditions (cf. Lechelt, 1975; White & Cheatham, 1959), the order of performance between touch and hearing was less consistent with previous evidence. Indeed, the judgments within touch were reported to be more accurate than the ones within audition, just as described by White and Cheatham (1959), but opposite to what found by Lechelt (1975). The overall results confirmed the experimental hypothesis, with the underestimation decreasing (for small ISIs) and variance decreasing (for large ISIs) in the multisensory as compared to the unisensory presentation conditions. However, the lack of an extensive comparisons between the different multisensory conditions prevent to know whether the advantages in temporal numerosity judgment differ as a function of the modality pairings tested. Of interest for the present purposes, Philippi and colleagues observed that the difference in the temporal numerosity estimation judgments between unimodal auditory or tactile conditions and bimodal audiotactile condition significantly differed only for short ISIs (i.e., 20 and 40 ms). Unfortunately, the authors did not further comment for any discrepancies between the audiotactile and visuotactile and/or audiovisual conditions.

As already mentioned, a large amount of previous studies investigated whether and to what extent the presentation of incongruent task-irrelevant multisensory pulse sequences can influence temporal numerosity judgments in the target modality. In the illusory flash paradigm, for instance, people are instructed to report the number of flashes presented with to-be-ignored incongruent sequences of beeps (Shams et al., 2000). The striking result of this study is that, when presented with a single flash and multiple auditory pulses, the observers perceive an illusory second flash. This illusory effect has been explained by taking into account the higher reliability of the auditory modality as compared to the visual modality in the time domain (cf. Shams, Ma, & Beierholm, 2005).

This effect, which has been shown to be a robust perceptual phenomenon, has also been replicated in the audiotactile domain (Bresciani et al., 2005; Bresciani & Ernst, 2007; Hötting & Röder, 2004). In one of their studies, Bresciani and Ernst (2005) presented series of beeps and taps and requested participants to report the number of tactile stimuli while ignoring the auditory distractors. The results showed that tactile perception can be modulated by task-irrelevant auditory stimuli, with participants' responses significantly depending on the number of delivered beeps. Such modulation occurred when the auditory and tactile stimuli were similar enough (i.e., had the same duration) and were presented simultaneously.

According to the maximum likelihood estimation model, the reliability of a sensory channel is related to the relative uncertainty of the information it conveys. The higher the relative variance of a sensory modality the weaker is its relative reliability (Ernst & Bülthoff, 2004). In order to investigate whether the auditory bias on tactile perception can be disrupted by manipulating the reliability of the auditory information, in a subsequent study, Bresciani and Ernst (2007) varied the intensity of the beeps. The auditory stimuli were presented at either 41 or at 74 dB (signal-to-noise ratio of, respectively, -30 and 3 dB). Bresciani and Ernst found that the participants were more sensitive (i.e., their estimates were less variable) in counting the number of the more intense (vs. less intense) beeps presented with irrelevant taps and, conversely, in counting the number of the taps presented with irrelevant less intense (vs. more intense) beeps (see also Wozny, Beierholm, & Shams, 2008). This pattern could be due to the fact that the decrease of the intensity of the auditory stimuli has reduced the relative reliability of the auditory modality, thus inducing differential interactions with touch as a function of the intensity level. Taken together, these results show that audition and touch reciprocally bias each other (when alternatively used as target or distractor), with the degree of evoked bias depending on the relative reliability of the two modalities (see also Bresciani, Dammeier, & Ernst, 2008).

3.4. Interactions based on frequency similarity

Perceptual interactions between hearing and touch are distinguishing amongst the associations occurring between other sensory modality pairings (Gescheider, 1970; Soto-Faraco & Deco, 2009; von Békésy; 1959; Zmigrod, Spapé, & Hommel, 2009; Experiment 2).

As already mentioned, auditory and vibrotactile stimuli are generated by the same physical mechanism, consisting of the mechanical stimulation of, respectively, the basilar membrane and the skin. Hence, both auditory and vibrotactile stimuli can be described according to their specific periodic patterns of stimulation (i.e., their frequency), defined as the number of repetitions of the sound waveforms (cf. Plack, 2004; Siebert, 1970) or of the tactile pulses (cf. Luna, Hernández, Brody, & Romo, 2005), respectively, per unit time.

In the somatosensory domain, the discrimination of vibrotactile stimuli differing in frequency has been investigated in monkeys (de Lafuente & Romo, 2005; Hernández, Salinas, García, & Romo, 1997; Mountcastle, LaMotte, & Carli, 1972; Mountcastle, Steinmetz, & Romo, 1990; Romo & Salinas, 2003; Werner & Mountcastle, 1965) as well as in humans (Bensmaïa, Hollins, & Yau, 2005; Horch, 1991; Iggo & Muir, 1969; LaMotte & Mountcastle, 1975; Mountcastle et al., 1972; Talbot, Darian-Smith, Kornhuber, & Mountcastle; 1968; Verrillo, 1985; Werner & Mountcastle, 1965. See also Harrington & Downs, 2001). In their seminal studies, Mountcastle and his coworkers investigated the capabilities of both humans and monkeys to discriminate between pairs of vibrotactile stimuli presented at different frequencies (e.g., LaMotte & Mountcastle, 1975; Mountcastle et al., 1972; Mountcastle, Talbot, Darian-Smith, & Kornhuber, 1967; Mountcastle, Talbot, Sakata, & Hyvärinen, 1969). The psychophysical investigations provided evidence that both monkeys and humans have nearly identical abilities in the discrimination of the vibrations in the sense of flutter (i.e., the difference limen for frequency discrimination overlapped nearly perfectly; see LaMotte & Mountcastle, 1975; Mountcastle et al., 1990; although see Imai, Kamping, Breitenstein, Pantev, Lütkenhöner, & Knecht, 2003).

On the basis of the above-mentioned evidence, it seems somehow surprising that the investigations of audiotactile interactions on the basis of their frequencies similarities has rarely been investigated thus far (although see Harris, Fucci, & Petrosino, 1986, 1991; Petrosino, 1989; Ro, Hsu, Yasar, Caitlin Elmore, & Beauchamp, 2009). Preliminary evidence from Nagarajan and colleagues (1998), however, has suggested that temporal information processing is governed by common mechanisms across the auditory and the tactile sensory systems. In their study, participants were presented with pairs of vibratory pulses and trained to discriminate the temporal interval separating them. The results not only suggested a decrease of threshold as a function of training, but also the generalization of the improved interval discrimination to the auditory modality. Even though the generalization was constrained to an auditory base interval similar to the one which had been trained in touch, these results are intriguing in suggesting that the coding of time intervals could be centrally represented (i.e., shared among modalities). Additionally, recent neurophysiological evidence in humans has shown that the discrimination of tactile stimuli with frequency properties (i.e. vibrotactile stimuli) was significantly improved in many of the participants undergoing the task by simply adding auditory feedback - with the same frequency - after the presentation of the tactile stimulation (Iguchi et al., 2007; see Ro et al., 2009, for evidence from a tactile detection task).

On the contrary, Yau and colleagues have clearly shown that auditory stimuli interfere with tactile frequency-discrimination. In their study, the participants performed a two-alternative forced choice task where they had to judge which of two vibrotactile stimulations (ranging from 100 to 300 Hz, steps of 40 Hz) had higher frequency. Crucially, the second vibrotactile stimulus was accompanied by an auditory stimulus presented at the same or different frequency as the tactile stimulus. The results showed a decrement in performing the task, but only for auditory distractors in the low frequency range.

Interestingly, since the same stimulus was ineffective in modulating an intensity judgment, and was restricted to the conditions where the tactile stimulus was at or near the same frequency this interfering effect is thought to be highly specific. Moreover, the perceived frequency of the tactile stimulus was pulled towards the frequency of the auditory stimulus.

It has been largely demonstrated that the ability of mammals to discriminate frequencies has been considered as reflecting the frequency resolution characterizing the auditory pathway at both the peripheral (i.e., the basilar membrane of the cochlea; Robles & Ruggero, 2001) and central (i.e., the primary auditory cortex; Langers, Backes, & van Dijk, 2007; Tramo, Cariani, Koh, Makris, & Braida, 2005) stages of auditory information processing. The systematic spatial mapping of frequency coding in the brain (known as tonotopy) and the filtering properties of auditory neurons and sensory receptors have been considered responsible for decoding the frequency of auditory stimulation (see Schreiner, Read, & Sutter, 2000, for a review; see also Elhilali, Ma, Micheyl, Oxenham, & Shamma, 2009; Romani, Williamson, & Kaufman, 1982; Schnupp & King, 2008). However, the tonotopic structure of the auditory system is not the only candidate for the representation of the temporal characteristics of the auditory stimuli. Indeed, the activity of neurons at different stages of the auditory pathway has been shown to change as a function of the repetition rates of the auditory events being processed (see Bendor & Wang, 2007, for a review). More specifically, acoustic signals within the flutter range are coded by neurons that synchronize their activity to the temporal profile of repetitive signals. These neurons have been observed both along the auditory-nerve fibres and in the inferior colliculus, the medial geniculate body, and in a specific neuronal population along the anterolateral border of the primary auditory cortex (AI; Dicke, Ewert, Dau, & Kollmeier, 2007; Oshurkova, Scheich, & Brosch, 2008; Wang, Lu, Bendor, & Bartlett, 2008). Other mechanisms regulate the activity of the neural population coding for auditory signals presented at higher repetition rates (i.e., above the perceptual flutter range). These neurons modify their discharge rates – not their spike timing – as a function of the frequency of the auditory events that are being processed (Oshurkova et al., 2008; Wang et al., 2008). Thus, the temporal profile of the auditory stimuli can be represented in AI by a dual process (i.e., stimulus-synchronized firing pattern and discharge rate), each involving specific sub-populations of neurons. The distinct neural encoding of auditory stimuli differing in frequency may also be responsible for the discrepancy in the perceptual impression conveyed by auditory stimuli. Indeed, when auditory events are presented at rates within the range 10-45 Hz (i.e., flutter) range, the resulting percepts tend to consist of sequential and discrete sounds (i.e., acoustic flutter; Bendor & Wang, 2007; see also Besser, 1967). According to Bendor and Wang, the discrete impression of the flutter percept could be considered as the direct outcome of the synchronized responses representing the event at different neural stages of the auditory pathway. On the other hand, the neurons encoding of stimuli with repetition rates beyond this range do not synchronize with the stimuli, thus failing to induce the impression of discrete sound events and instead giving rise to continuous-sounding percepts having a specific pitch (Bendor & Wang, 2007; Cariani, 1999; Hall, Edmondson-Jones, & Fridriksson, 2006; Tramo et al.,, 2005; Wang et al., 2008; Will & Berg, 2007; see also Deutscher, Kurt, Scheich, & Schulze, 2006).

In the tactile domain, the identification and the discrimination of tactile stimuli differing in frequency rely on the differential sensitivity of sensory vibrators and afferent nerve fibres supplying different portions of the skin (Johansson & Vallbo, 1979a, b; Morioka & Griffin, 2005). At the fingertips, the class of fibres classified as fast adapting (FA) fibres and the receptors known as Meissner corpuscles are responsible for the processing of low vibrotactile frequencies (i.e., 5-50), whereas the Pacinian (PC) fibres associated with the Pacinian receptors are more sensitive to higher vibration frequencies (i.e., higher than 40 Hz; Francis, Kelly, Bowtell, Dunseath, Folger, & McGlone, 2000; Iggo & Muir, 1969; Mahns, Perkins, Sahai, Robinson, & Rowe, 2006; Morley, Vickery, Stuart, & Turman, 2007; Talbot, Darian-Smith, Kornhuber, & Mountcastle, 1968; Verrillo, 1966). Animal studies suggest that one possible candidate for signalling information about the frequency of vibrotactile stimuli is an impulse pattern code, according to which the responses of rapidly adapting afferents are phase-locked to the periodicity of the vibrotactile stimulus. The strict correspondence between the temporal features of the vibrotactile stimuli and the impulse patterns have not only been observed in the periphery (i.e., along the sensory fibres), but also in neurons at higher levels along the ascending somatosensory pathway (Hérnandez et al., 2000; Mountcastle et al., 1990; Salinas et al., 2000).

Even though the encoding of the frequency pattern of vibrotactile stimuli involves all the stations along the somatosensory pathway, it is likely that more sophisticated processes, such as those involving the discrimination of different frequencies, occur more centrally. In primates performing a frequency discrimination task, the patterns of firing rates evoked in SI neurons by the comparison stimulus (i.e., usually presented as second in each pair) are independent from those elicited by the standard stimulus (i.e., the first stimulus of each pair). It thus seems that SI is a quite unlikely candidate for the encoding of the difference between the two stimuli (Romo & Salinas, 2003; Salinas et al., 2000). On the contrary, the fact that the response of neurons in the secondary somatosensory cortex (SII) to the second vibration is affected by the frequency of the first vibration suggests that these neurons contribute significantly to the coding of the frequency difference. Taken together, this experimental evidence suggests that in primates the perceptual comparison between different frequencies takes place in SII, with subsequent decisional processes involving the medial premotor cortex in the frontal lobe area, whose neuronal activity significantly covaried with monkeys' perceptual reports (de Lafuente, & Romo, 2005). The similarity of the performance shown by monkeys and humans in detecting and discriminating between stimuli differing in frequency suggests that the neural mechanisms investigated in monkeys may be analogous to those that exist in humans (Romo & Salinas, 2003; Salinas, Hernández, Zainos, & Romo, 2000; Talbot et al., 1968). In humans, just as in monkeys, frequency discrimination does not rely exclusively on SI, but also involves downstream areas, such as SII and some regions in the frontal cortex (Harris, Arabzadeh, Fairhall, Benito, & Diamond, 2006).

A recent fMRI study showed that the decreasing of hemodynamic activity during same vs. different vibrotactile stimuli could be observed in an extended region. Beyond the areas typically involved in this kind of task (i.e., SI and SII), other areas, such as the superior temporal gyrus, the precentral gyrus, ipsilateral insula, and supplementary motor area are involved (Li Hegner, Saur, Veit, Butts, Leiberg, Grodd, & Braun, 2007). Interestingly, the superior temporal gyrus is an area known for mediating the interactions between auditory and somatosensory stimuli, in both humans (Foxe, Wylie, Martinez, Schroeder, Javitt, Guilfoyle, Ritter, & Murray, 2002; Schroeder, Lindsley, Specht, Marcovici, Smiley, & Javitt, 2001) and monkey (Fu, Johnston, Shah, Arnold, Smiley, Hackett, Garraghty, & Schroeder, 2003; Kayser, Petkov, Augath, Logothetis, 2005). Neurons in the auditory belt areas not only respond to pulsed tactile stimulation, but also to vibratory stimuli, thus suggesting that the auditory association cortex acts as a cortical location of convergence between auditory and tactile inputs during the discrimination of tactile frequency (Iguchi, Hoshi, Nemoto, Taira, & Hashimoto, 2007; Li Hegner et al., 2007; Schürmann, Caetano, Hlushchuk, Jousmäki, & Hari, 2006; see also Caetano & Jousmäki, 2006; Golaszewski, Siedentopf, Koppelstaetter, Fend, Ischebeck, Gonzalez-Felipe, Haala, Struhal, Mottaghy, Gallasch, Felber, & Gerstenbrand, 2006). The evidence suggesting that the auditory areas involved in the processing of tactile stimuli are endowed by specific frequency temporal profiles and contribute to the vibrotactile frequency discrimination processes, raises the intriguing possibility of anatomo-functional similarities between cortical regions devoted to the processing of the periodicity in both vibrotaction and hearing. A study conducted by Bendor and Wang (2007) seems to suggest that this could be the case. These authors distinguished between two populations of neurons in the auditory cortex, known as "positive monotonic" and "negative monotonic", respectively. The first population typically increases the firing rate activity proportionally to the increase of the repetition rates of the auditory stimulus, whereas the second population showed the opposite pattern (see also Wang et al., 2008). Interestingly, neurons with positive and negative monotonic tuning to stimulus repetition rate have been observed not only in the auditory cortex, but also in the somatosensory cortex beyond SI (Bendor & Wang, 2007; Salinas et al., 2000). More specifically, in SII have been shown neurons whose spike rate can be positively or negatively related to the vibrotactile stimulus frequency (Luna et al., 2005; Salinas et al., 2000). The fact that neurons showing positive and negative monotonic tuning to stimulus repetition rate could be observed in both auditory and somatosensory cortices points to a communality in how these two sensory systems might encode variations in the temporal profile of, respectively, auditory and vibrotactile stimuli (Bendor & Wang, 2007; Wang et al., 2008. See also Soto-Faraco & Deco, 2009), pointing to a potential neural basis for the discrimination of frequencies delivered crossmodally (cf. Bendor et al., 2007).

Preliminary evidence by Nagarajan and colleagues (1998) suggest that this could be the case. In their study, the participants were presented with pairs of vibratory pulses and trained to discriminate the temporal interval separating them. The results of this study suggest that not only a decrease of the threshold as a function of the training, but also the generalization of the improved interval discrimination to the auditory modality. Even though the generalization was constrained to an auditory base interval similar to the one which had been trained in touch, these results are intriguing in suggesting that the coding of time intervals could be centrally represented (i.e., shared among modalities). Additionally, recent neurophysiological evidence on humans has shown that the discrimination of tactile stimuli with frequency properties (inaccurately discriminated in a vibrotactile stimuli discrimination task) was significantly improved in many of the participants undergoing the task by simply adding an auditory feedback after the presentation of the tactile stimulation (Iguchi, Hoshi, Nemoto, Taira, & Hashimoto, 2007). The investigation of the neural substrates of this effect led to the conclusion that the increase of the perceptual accuracy and the speeding up of the discrimination of the tactile frequencies were subserved by the co-activation of the SII and the supratemporal auditory cortices along with upper bank of the superior temporal sulcus. The data suggest that the auditory feedback could have induced a complementary processing of tactile information by means of an intervening acoustic imagery process. This study adds evidence to previous investigations showing considerable crossmodal convergence in the posterior auditory cortex of not only tactile stimulation (e.g., Foxe, Wylie, Martinez, Schroeder, Javitt, Guilfoyle, Ritter, & Murray, 2002; Kayser, Petkov, Augath, & Logothetis, 2005) but also of stimulation with frequency properties, in both hearing (e.g., Caetano and Jousmäki, 2006; Schürmann, Caetano, Hluschchuk, Jousmäki, & Hari, 2006) and deaf humans (Levänen & Hamdorf, 2001).

Although the amount of evidence on frequency discrimination is remarkable, a still unexplored issue regards the question of whether, and to what extent, people are able to match stimuli having comparable temporal rate features within touch, within audition, and especially crossmodally (i.e., an auditory stimulus and a tactile stimulus). We will specifically address this issue in the Chapter 8).

Chapter 4.

Audiotactile interactions in the spatial domain

4.1. Introduction

Touch is considered, along with taste, a contact sense, meaning that proximity or even contact between the skin surface and the object is a necessary requirement for sensations to be evoked. Since the body is directly involved in the emergence of the tactile perceptual sensations, it follows that interactions between audition and touch necessarily occur within the space close to the body, the portion of space commonly known as ‘peripersonal space’ (see Cardinali, Brozzoli, & Farné, 2009, for a review). This makes the audiotactile events somehow more salient than those consisting of, for instance, audiovisual components, mainly occurring in the distal space.

How touch and hearing interact in the spatial domain is still a debated topic, and studies on this topic have provided inconsistent evidence. Some studies (e.g., Lloyd et al., 2003; Murray et al., 2004; Zampini et al., 2005; Zampini et al., 2007) suggest that the links occurring between these two kinds of signals could be affected by spatial modulations to a lesser extent than other modality pairings, such as audiovisual (e.g., Spence & Driver, 1994, 1996) and visuotactile (e.g., Spence, Pavani, & Driver, 2000, 2004) stimulations, whereas others support the hypothesis that the spatial arrangement of the stimuli is effective in modulating people’s performance (e.g., Kitagawa, Zampini, & Spence, 2005; Tajadura, Kitagawa, Väljamäe, Zampini, Murray, & Spence, 2009).

In the next paragraphs, we will delve into this topic in more detail (see Sections 4.2-4.4); then, we will describe audiotactile interactions in the spatial audiotactile attention (see Sections 4.5 and 4.6), in the perception of motion (see Section 4.7)and, finally, and audiotactile interactions in the neurological population (see Section 4.8) will be explored.

4.2. Audiotactile crossmodal effects on stimulus localization

One of the first attempt to study differences and similarities between hearing and touch in the spatial domain dates back to the sixties, and adds to the body of research aimed to explore the potentialities of touch for the purpose of sound localization (e.g., von Békésy, 1955; 1959) and as a possible substitute channel for the completely deaf (e.g., Frost & Richardson, 1976; Richardson, Wuillemin, & Saunders, 1978).

Gescheider (1965) compared the capability of humans in localizing the sound sources when stimulation accuracy is delivered to the skin through a pair of vibrators or when the stimuli were presented through earphones, as a sort or artificial cochlea (see also von Békésy, 1955). In that experiment, the stimuli emitted by a speaker were collected by two microphones located at equal distances from the speaker, either along the vertical or horizontal axis. Acoustic stimuli produced by the speaker activated the two microphones, the signals from which were separately amplified and controlled by solid-state preamplifiers, amplifiers, and attenuators. The electrical signals were then transduced to mechanical energy by either a pair of vibrators or by earphones. The vibrators were used to deliver stimulation to the index fingertips of the two hands. Since each earphone or vibrator was driven by an independent microphone-preamplifier-amplifier system, when the sound-source location was varied, this arrangement permitted preservation between the two channels of temporal and intensive differences. By using these cochlear models, Gescheider independently varied the binaural time and binaural intensity differences – which are known to play an important role in auditory localization - at the two earphones and vibrators. The results reported in this study showed that for low tones the cutaneous localization was more precise than auditory localization, whereas for noise bursts the reverse held. Moreover, whereas auditory localization was found to mainly depend on both cues (i.e., intensity and temporal differences), cutaneous localization depended at a greater extent on intensity differences. Successive studies have extended these findings, showing that touch compared relatively well with audition in sound localization, but also in direction and distance judgments, thus possibly being considered as a suitable substitute for the ear, especially when the head movements were allowed as compared to when they were prevented (Frost & Richardson, 1976. Although see: Richardson et al., 1978).

Moving away from the unusual designs used in these pioneering studies, it can be observed that a remarkable part of the subsequent research has focused on how stimuli in one modality affect the localization of stimuli presented in the other.

For instance, Pick and colleagues (Pick, Warren, & Hay, 1969) introduced a spatial discrepancy between hearing and proprioception and asked the blindfolded participants to indicate the sources of stimulation. Participants wearing a ‘pseudophone’ which introduced a lateral displacement of the interaural axis were presented with auditory targets consisting of series of clicks delivered through a small speaker mounted on the top of a shelf. Participants were asked to point with their right hand under the shelf in four different locations: a) the locus of the displaced sound, b) the locus of their unseen finger, c) the felt position of their finger, which was touching the speaker producing the displaced sound, d) at the heard position of the sound coming from the speaker as it was being touched. The first two conditions were intended to provide a baseline measure of the performance to be compared to the discrepancy conditions, for proprioception affecting audition and audition affecting proprioception (i.e., c and d, respectively). The results showed that proprioception exerted a strong influence on auditory localization judgments, whereas auditory stimuli slightly affected proprioceptive judgments. Even though Pick and coworkers labelled the results of their study as ‘proprioceptive bias of audition’, it is unsure whether the participants’ auditory localization judgments in their study actually reflect a genuine bias induced by proprioceptive cues (i.e., perceived location of hand in space) or rather a bias induced by the arrangement of the experimental set-up (i.e., the felt position of the loudspeaker could have been confounded with the felt position of the limb *per se*).

Freedman and Wilson (1967), instead, studied whether the movement could be considered a prerequisite for compensation to audiotactile re-arrangement following exposure to auditory-tactile spatial discordance. During the exposure phase of that experiment, participants listened to the sound of a moving loudspeaker cone that sometimes touched their fingers. A conflict between the two signals was induced by using a ‘pseudophone’ (just as Pick et al. did in their experiment), with the auditory inputs displaced laterally. In the experimental phase, the participants showed a shift in pointing responses to auditory targets, thus suggesting that auditory and tactile inputs were integrated during the exposure phase to compensate for the induces spatial discrepancy. However, since the tactile stimuli delivered to the fingertips consisted in the contact with the loudspeaker, it can not be excluded - as in Pick et al.'s study - that the participants were using cues regarding the loudspeaker's location to recalibrate auditory maps.

More recently, a study (Caclin, Soto-Faraco, Kingstone, & Spence, 2002) tried to overcome these confounds by applying a more genuine measure of the magnitude of the auditory mislocalization induced by tactile inputs by adapting a procedure originally designed to study the audiovisual ventriloquism effect (Bertelson & Aschersleben, 1998). In Caclin et al.'s experiment, the participants were requested to make a left-right discrimination regarding the location of the presented sounds while task-irrelevant vibrotactile stimulation was simultaneously delivered from a central position in the frontal space. The location of the sounds was chosen using a psychophysical staircase procedure. The sounds were presented according to two intermingled staircases, each starting at the outermost right or left position, with the selection varying according to the participants' responses (i.e., location of the sound progressively converging toward the median location as a function of the accuracy of the performance). As with audiovisual stimuli (Bertelson & Aschersleben, 1998), Caclin and colleagues demonstrated, across four different experiments, that the vibrotactile stimuli biased the perceived location of concurrent sounds toward the central position. The reliability of the results was strengthened by the observation that the effect was shown only when the auditory and the tactile inputs were delivered synchronously, thus rendering the hypothesis that the effect could be attributed to the distracting interferences or to attentional bias exerted by the vibrotactile stimulators. Moreover, it must be noted that in that experiment the location of the tactile stimuli was not predictive of the location of the sounds (i.e., they were always delivered from the same location), thus ruling out a potential response bias account.

Taken together, these data suggest that the effect highlighted in their study could be considered as the first demonstration of a ventriloquism-like effect occurring between hearing and touch, reliably due to a genuine perceptual integration of audiotactile stimuli.

A recent study carried this evidence further, by addressing whether the audio-tactile ventriloquism effect operates in an external or body-centered coordinate system (Bruns & Röder, in press). To address this aim, the change in magnitude and in the direction of the audiotactile ventriloquism effect as a function of the hand posture was investigated. The participants were thus requested to report the perceived location of auditory stimuli presented from left, right and central locations, presented either alone or concurrently with tactile stimuli presented to the fingertips of the two hands. The participants placed their hands at the left or the right of the auditory array, and could either adopt, respectively, an uncrossed or a crossed posture. The manipulation of the hand posture allowed to assess whether the tactile mislocalization of the auditory stimuli was in the direction of the portion of external space where the tactile stimulus was presented or, rather, toward the side of the tactually stimulated hand. The results of this study not only confirmed the occurrence of a ventriloquism effect between auditory and tactile inputs, but also provided evidence that the tactile bias of the auditory localization was modulated by the change on hand posture. In the uncrossed posture, a larger absolute shift in sound localization was observed for large (vs. small) audiotactile spatial discrepancies and was primarily due to an increase of center responses. Crossing the hands determined a generalized reduction of the effect, which was, however, still significant for large spatial discrepancies. Even though the increase of the central responses could be due to a more pronounced uncertainty in performing the task as compared to the condition where the hands were kept in the uncrossed posture, the lack of any differences in the variability of the responses seems to make this speculation unlikely. More interestingly, in the crossed-hands condition, auditory localization was biased toward the external location of the tactile stimulus, rather than toward the side of the anatomical hand which was tactually stimulated. Overall, these data suggest that the audiotactile ventriloquism effect operates in an external rather than an anatomically-based coordinate system (cf. Sanabria, Soto-Faraco, & Spence, 2005. See also Section 11.3 and 11.4 for other evidence regarding the hand crossing effect).

4.3. The specificity of the space stimulated: Behavioural evidence

A large amount of experimental evidence suggest that the space in close proximity with the body (i.e., peripersonal space), and in particular of the space around and/or behind the head, have a particular degree of salience, in both primates (e.g., Fu et al., 2003; Graziano et al., 1999) and humans (e.g., Menning et al., 2005; Nguyen, Tran, Hoshiyama, Inui, & Kakigi, 2004; Sereno & Huang, 2006; Weinstein, 1968; Tajadura-Jiménez et al., 2009). As it will be more extensively described in the next sections (see Sections 4.3-4.4 and Chapter 5), it is likely that the privileged neural representation of the space surrounding the head and its multisensory nature respond to specific evolutive reasons, such as the vital necessity to protect from threads and perform flee reactions in dangerous circumstances.

The evidence not only supports the existence of brain areas specialized for the integration of multisensory information emanating from events occurring in the immediate vicinity of the body and whose activity is inversely proportional to the distance between the auditory (or visual) stimulus and the skin surface. Furthermore, the spatial modulation of auditory-somatosensory interactions greatly depends on the particular region of space in which the stimuli are presented (e.g., Fu et al., 2003; Ho, Santangelo, & Spence, 2009; Vitello & Ernst, 2007).

Indeed, previous behavioural studies support the assumption that audiotactile spatial interactions would be prevalent in particular in the region of space behind the head (i.e., in the part of space where visual cues are not available) than in front of it (Kitagawa, Zampini, & Spence, 2005; Zampini et al., 2005). Kitagawa and his coworkers conducted two experiments in order to investigate audiotactile interactions occurring in the space behind a participant’s head. In their first experiment, the participants had to judge the temporal order of presentation of pairs of auditory and tactile stimuli presented from loudspeakers or electrotactile stimulators attached to their earlobes, respectively. The stimuli could either be presented on the same side or from different sides. The results showed higher sensitivity (i.e., lower Just Noticeable Differences, JNDs, intended as the smallest detectable difference between a starting and secondary level of a particular sensory stimulus) for stimuli presented from different sides rather than from the same side. In Kitagawa et al.'s second experiment, a distractor interference task was used, with participants performing a tactile left/right discrimination task while auditory distractors were presented simultaneously from the same or opposite side. In this task, the participants responded more slowly (and less accurately) when the auditory distractors were presented on the opposite side from the tactile stimuli. Furthermore, this crossmodal interference effect significantly varied according to the complexity of the stimuli used. Whereas white noise bursts exerted a stronger interference when they were presented from close to the head (i.e., 20 cm) than when they were presented far from the head (i.e., 70 cm), when the auditory stimuli consisted in pure tones, the overall effect was lower and was not modulated by the distance from which the sounds were presented. As we will see in more detail in Section 4.4. and Chapter 5, this behavioural evidence mirrors neurophysiological data and it is likely to lie on specific evolutive reasons.

Kitagawa et al.'s results suggested that the spatial arrangement of stimuli delivered in the space behind the head affects participants' performance in both unspeeded temporal order judgment (Experiment 1) and speeded localization discrimination (Experiment 2) tasks. Thus, the suggestion that has emerged from this kind of research is that the absence of vision (or visual information) seems to be related to an improved ability to code spatial cues in the residual sensory modalities (i.e., audition and touch; Chen, Zhang, & Zhou, 2006; Collignon, Renier, Bruyer, Tranduy, & Veraart, 2006; Kitagawa et al., 2005; Röder, Kusmierek, Spence, & Schike, 2007; Röder & Rösler, 2004; Röder, Rösler, & Spence, 2004. See Chapter 6 for an extensive discussion of audiotactile interactions in visually deprived individuals).

A recent study reported three studies aimed to investigate the audiotactile spatial interactions in the space close to the head by means of a speeded detection task to unimodal auditory, somatosensory, or simultaneous auditory-somatosensory stimuli (Tajadura-Jiménez et al., 2009). Different variables, such as the distance of the auditory stimuli, the stimulated body surface and the spectral complexity of the sounds, were varied.

In Experiment 1, electrocutaneous stimuli were presented to either earlobe, while auditory stimuli were presented from the same vs. opposite sides, and from one of two distances (20 vs. 70 cm) from the participant's head. In Experiment 2, electrocutaneous stimuli were delivered to the hands, one placed on the side of their neck, (i.e., in proximity with the head), and the other outstretched to the side (i.e., far from the head), while the auditory stimuli were again presented at one of two distances. In Experiment 3, the experimental setup used in Experiment 1 was modified in a way that only the ‘near’ loudspeakers were used. The results showed a spatial modulation of auditory-somatosensory interactions in Experiment 1, with faster responses observed when the stimuli were presented from the same side (aligned), as compared to when they were presented from different sides (misaligned), of the participant’s head. Somehow surprisingly was the evidence that the spatial modulation was specific for the part of the body stimulated (i.e., head vs. hand) rather than for the region of space (i.e., around the head) where the stimuli were presented and was more pronounced for high- (vs. low) frequency sounds.

The results reported in Tajadura-Jiménez et al.’s study differ from previous studies investigating the redundant signals effect (RSE; i.e., the faster responding seen when pairs of multisensory stimuli, as compared to single unisensory stimuli, are presented; Miller, 1982) for auditory-somatosensory stimulus pairs (e.g., Murray et al., 2005; Zampini et al., 2007).

As just mentioned, previous studies had already investigated the RSE for auditory-somatosensory pairs (e.g., Murray et al., 2005; Zampini et al., 2007). Differently from Tajadura-Jiménez et al.’s study, however, the spatial modulation of audiotactile pairs was studied in the region surrounding the hands. For instance, in Murray and colleagues’ study (2005), participants were requested to make simple reaction time responses to stimuli presented in the following conditions: somatosensory stimuli alone, auditory stimuli alone, spatially ‘aligned’ auditory-somatosensory stimulation where stimuli were simultaneously presented to the same location (e.g. left hand and left-sided speaker), and spatially ‘misaligned’ AS stimulation presented to different locations (e.g. left hand and right-sided speaker). The behavioural data reported from that study demonstrated that the participants responded significantly faster to bimodal audiotactile stimuli than to unimodal (i.e., auditory or tactile) stimuli. However, differently from what had been shown in audiovisual and visuotactile speeded detection tasks (e.g., Forster, Cavina-Pratesi, Aglioti, & Berlucchi, 2002; Gondan, Niederhaus, Rösler, & Röder, 2005; Molholm, Ritter, Murray, Javitt, Schroeder, & Foxe, 2002), where the performance enhancement is reduced or even absent when a spatial separation is introduced between the stimuli, the magnitude of the reaction time facilitation did not vary as a function of the spatial configurations (i.e., same vs. different position) from which the stimuli were presented. These results led the authors to the conclusion that the audiotactile multisensory interactions might be ‘less spatial’ than those involving other combinations of stimulus modalities (see Section 4.4 for the description of the electrophysiological results).

In a subsequent study, the same experimental design was applied to investigate spatial audiotactile interactions for stimuli which could be presented in the frontal or in the rear space. More precisely, the participants placed one of their arms in front of them and the other behind their backs, while loudspeakers were placed close to each hand. Again, a significant facilitation of the reaction times, exceeding that predicted by probability summation, was observed for bimodal pairs, independently from their spatial arrangement and the region of space (i.e., frontal vs. rear) stimulated.

The equivalence of auditory-somatosensory spatial conditions reported in these studies, contrasts with other studies (see Sections 4.3 and 4.4), thus possibly suggesting differential spatial modulation on response latencies as a function of the part of the body (i.e., head or hand) and region of space stimulated (see also Chapter 8 on this point).

To conclude the discussion regarding the audiotactile interactions occurring in the region surrounding the hand, we will briefly describe two studies aimed to investigate the coding of auditory-tactile spatial compatibility (Merat, Spence, Lloyd, Withington, & McGlone, 1999; Simon, Hinrichs, & Craft, 1970. See also: Lloyd at al., 2003; Experiment 3). The label ‘Simon effect’ refers to the finding that, in speeded discrimination tasks, the level of performance, in terms of both response latencies and accuracy, is higher when the stimulus occurs in the same relative location as the response, even though the stimulus location is irrelevant for the task (e.g., Simon & Wolf, 1963). Simon, Hinrichs and Craft (1970) investigated whether this effect reflects the correspondence between the stimulus location and the effectors (i.e., the hands) or, rather, between the stimulus location and the response location. In order to disambiguate between these opposite hypotheses, the participants were asked to perform a pitch discrimination task of spatially lateralized auditory stimuli while keeping the hands in the uncrossed or crossed postures. The mapping rule between the pitch of the sounds (i.e., high or low) and the effector (i.e., right or left hand) was counterbalanced between participants. In the uncrossed condition, not surprisingly, a typical Simon effect was observed. The performance was better when the right-hand command was heard in the right ear than when it was heard in the left ear, and the converse pattern was observed for the left-hand command. The opposite pattern was reported in the crossed-hands condition, thus supporting a stimulus location -response location (vs. stimulus location-effector executing the response) account for the mapping of the stimulus-response correspondence underlying this effect. Even though Simon et al.’s results suggest a certain degree of dependence between the spatial coding of the auditory and tactile information, it must be noted that in their study the auditory stimulation did not occur in the peri-hand space, thus rendering the comparison between their data and those in previous studies hard to perform.

Merat and coworkers more specifically addressed this issue (Merat, Spence, Lloyd, Withington, & McGlone, 1999). In their study, the participants were asked to discriminate the elevation of vibrotactile target stimuli (upper vs. lower) presented to the left or right hand while trying to ignore auditory distractors that could independently be presented from upper or lower locations on either the same or the opposite side. Typically, when observers are asked to make speeded discriminations of a perceptual attribute in one modality, incongruent values of this attribute in the other modality determines an interfering effect (i.e., slower response latencies and lower accuracy) on the discrimination performance (i.e., crossmodal congruency effect; see Spence, Pavani, & Driver, 1998 for visuotactile pairs). The magnitude of this effect was compared between conditions where participants placed their two hands close together – in alignment with loudspeaker cones - and where they placed their hands far apart. Merat et al. reported that the crossmodal congruency effect was larger when the tactile targets and the auditory distractors were presented from the same side than when they were presented from the opposite side. However, it was not modulated by the relative position of the hands with respect to the loudspeakers presenting the auditory stimuli. These results, thus, seem, at least partially, to undermine the hypothesis put forward by Murray and colleagues (2005), according to which the interaction between auditory and tactile stimuli presented to and within the space surrounding the hand are not spatially modulated. As suggested by Zampini and colleagues (2007), it is likely that, whereas audiotactile simple RT tasks highlight general spatial constraints operating automatically, the spatial tasks reveal the operation of auditory-somatosensory interactions in the context of additional cognitive, attention- and task-related constraints.

4.4. Audiotactile integration in the peripersonal space: Neuroimaging studies

With the definition ‘peripersonal space’ is described the region immediately surrounding the body, modularly structured and represented through multisensory coding Namely, it is commonly decomposed in the personal space, occupied by the body itself and mainly coded through proprioceptive and tactile cues, the reaching space, defined by the distance at which an object can be reached by the subject, and based on the integration of tactile and visual information, and the extra-personal space, based on visual and auditory inputs coming from the distal space (Cardinali et al., 2009; Farnè, Demattè, & Làdavas, 2005).

Its properties render the peripersonal space highly suitable for the study of the functional interplay between the body and the proximal objects.

One of the first attempts to conceptualize the functional properties of the space surrounding – animals' – body was carried out by Hediger in the fifties (1955). On the basis of the observations of animals, he concluded that the most compelling requirement to survive is the possibility to detect threatening and potential dangerous events entering the space surrounding its body (the so-called 'flight zone') in order to promptly execute escape behaviours (cf. Graziano & Cooke, 2006).

As we will see in the course of the present section, the flight zone has been extensively investigated in primates (Graziano et al., 2002a, b; Graziano & Cooke, 2006) and served as a basis for the definition of peripersonal space in humans, which, analogously to the theorical context in animals, can be considered as a protective space region around the body (cf. Dosey & Meisels, 1969; Horowitz, Duff, Stratton, 1964; Felipe & Sommer, 1966; Neppi-Modona, Auclair, Sirigu, & Duhamel, 2004) toward which many attentional resources are directed (e.g., Farné & Làdavs, 2002; Làdavas, Pavani, & Farnè, 2001; Menning et al., 2005; Spence, Pavani, Maravita, & Holmes, 2004).

Whereas multisensory features of regions of space surrounding hands and feet have been already discussed, in the present section we will particularly focus on the peri-head space which is, for reasons which we will be discussed below, a rather distinguishing portion of space among those surrounding the different parts of the body.

The possibility of directly recording the neuronal response activity in monkeys offered the invaluable possibility to determine how the specific features of the space nearby the head are coded at neural level. Graziano and colleagues, for instance, found that about the 53% of neurons in the ventral premotor cortex (PMv) whose tactile receptive fields included the back of the monkey's head respond not only to visual (cf. Fogassi, Gallese, Fadiga, Luppino, Matelli, & Rizzolatti, 1996) but also to auditory stimuli (Graziano et al., 1999; Graziano & Gandhi, 2000). These trimodal neurons have receptive fields that extend to a limited distance from the head, being able to respond to contralateral visual and auditory stimuli presented within roughly 30 cm from the tactile receptive fields. This evidence makes these neurons the best candidates for the coding of multisensory characteristics of the space in close proximity with the body, within monkey's reach. Interestingly, the gradient of firing of this population of neurons was found to vary not only as a function of the distance of the auditory stimuli, but also as a function of their spectral complexity. Indeed, these neurons respond to auditory stimuli presented from close to the monkey's head (i.e., within 30 cm) and preferentially to complex sounds, with pure tones of different frequencies failing to elicit any response.

Subsequent investigations have confirmed that also in humans, stimuli of different complexity (i.e., pure tones vs. white noise bursts) induce distinct neural responses (Hall, Edmondson-Jones, & Fridriksson, 2006; Kitagawa & Spence, 2006; Schönwiesner, Rübsamen, & von Cramon, 2005; Schreiner, Read, & Sutter, 2000; Wessinger, VanMeter, Tian, Van Lare, Peckar, & Rauschecker, 2001), as well as qualitatively different behavioural responses – at least under certain conditions – in audiotactile tasks (see Farnè & Làdavas, 2002; and Kitagawa, Zampini, & Spence, 2005, for evidence from neurologically-impaired patients and intact people, respectively). Given the close similarity of monkeys and humans' data, one might hypothesize that the stronger interactions between somatosensory and complex auditory stimuli reflect evolutionary processes. It can be noted that in the natural environment the sounds are complex and thus more similar to white noise than to pure tones (Nelken, Rotman, & Yosef, 1999; Rauschecker, 1997). Therefore, neural substrates favouring the interplay between complex auditory stimuli and vibrotactile stimuli could result from the necessity of having to deal with the complexity of naturalistic auditory surroundings (cf. Farné & Làdavas, 2002).

Other regions which have been found to respond to trimodal stimulation (i.e., auditory, visual and tactile) in monkey's brain are a restricted zone in the precentral gyrus (polysensory zone, PZ; Graziano et al., 2002a, b) and ventral intraparietal area (VIP; Colby et al., 1993; Duhamel, Colby, & Goldberg, 1998; Graziano et al., 1999; Graziano & Cooke, 2006).

Similarly to the ventral premotor cortex, also this region has receptive fields located on the face, the arm or upper torso. The authors reported that the stimulation of the receptive fields near the left side head caused a squint or face grimace on the left side, a head turn and a thrusting of the left hand into the space near the left of the head (Graziano et al., 2002a, b) and centring eye movement (Cooke & Graziano, 2004). Interestingly, the activity of this area is strictly related to the supposed capacity of threatening of the object which falls into the space nearby the body. For instance, it has been observed that the neurons within this area are activated by the unfamiliar object – especially if real, three dimensional, and faster moving - approaching the skin surface, but not by the chair the primate is sitting on. This observation is consistent with the speculation that this area is part of a sensory and motor pathway which detects potentially threatening objects and plan defensive behaviours.

Taken together, the studies on body-centred receptive fields in VIP and PZ have highly contributed in defining the spatial extension and functional characteristics of a region – peripersonal space – which, by virtue of its features, is the best interface between the individual – spatially defined by his/her skin surface - and the surrounding – crossmodally characterized - environment.

4.5. Audiotactile spatial attention: Behavioural studies

The events involving touch occur on or in close spatial proximity with the body surface, implying that the audiotactile interactions can be observed in the peripersonal space (see also Section 4.4 on this point). Since closer events are more likely to threaten and impact on our body, it is not surprising - as pointed out by some authors - that during the evolution a specialized attentional mechanism specific for the space near the body could have been possibly established. This attentional system has been extensively described in both monkeys (e.g., Cook & Mounsell, 2002; Graziano & Gross, 1998) and humans (e.g., di Pellegrino, Làdavas, & Farné, 1997; Halligan & Marshall, 1991; Pavani & Castiello, 2004) and it is devoted to the detection of signals from different sensory modalities approaching the skin surface, thus facilitating orienting behaviours and the implementation of defensive strategies (e.g., Graziano & Cooke, 2006).

It is not surprising, thus, that a noticeable amount of research on the audiotactile links has been devoted to investigate how these sensory modalities interact in the spatial attention mechanisms (e.g., Driver & Spence, 1998; Gainotti, 2009; Ho, Santangelo, & Spence, 2009; Lloyd, Merat, McGlone, & Spence, 2003; Spence, Nicholls, Gillespie, & Driver, 1998; See Section 4.6 for neuroimaging evidence), whereas far less numerous are the studies which addressed audiotactile attentional links in non-spatial domains (e.g., Dell’Acqua, Turatto, & Jolicoeur, 2001; Turatto, Galfano, Bridgeman, & Umiltà, 2004).

It is well known that attention is the cognitive process which allow us to select and successively process just those stimuli that may be particularly salient and of interest for us (Posner, 1980; Posner & Petersen, 1990). The most of the studies have focused on vision, revealing that people can focus their – visual – attention overtly (i.e., shifts of eyes and head toward the region of interest) or covertly (i.e., in absence of head or eye movements) on a particular location, and so facilitating the processing of stimuli occurring there (see, e.g., Posner, 1978, 1980). However, the observation that analogous mechanisms could also hold within both hearing (e.g., Buchtel, Butter, & Ayvasik, 1996; Mondor & Zatorre, 1995; Schröger & Eimer, 1997; Spence & Driver, 1994) and touch (Bradshaw, Howard, Pierson, Phillips, & Bradshaw, 1992; Driver & Grossenbacher, 1996; Kilgard & Merzenich, 1995; Sathian & Burton, 1991; Whang, Burton, & Shulman, 1991) led the researchers to explore the potential existence of crossmodal attentional links. Seminal studies, for instance, tested for any audiovisual (Buchtel & Butter, 1988) and visuotactile (Butter, Buchtel, & Santucci, 1989) links in spatial attention using a variant of the visual cuing paradigm (Posner, 1978), even though a far more extensive investigation on this topic has been carried out by Driver and collaborators (see Driver & Spence, 1998, for a review).

In this brief coverage of the topic, we will in particular focus on covert attentional mechanisms, on both endogenous (i.e., driven by expectancies) or exogenous (i.e., driven by salient peripheral cues) components, behaviourally and physiologically considered as distinct.

In one study, Spence and colleagues extensively investigated the crossmodal links in exogenous covert spatial orienting, in vision, audition and touch (Spence, Nicholls, Gillespie, & Driver, 1998). For the purposes of the present discussion, two of the three experiments reported, those exploring the audiotactile stimulus pairing, were of particular interest. In the Experiment 1, in particular, the possibility that the presentation of a spatially uninformative auditory cue on one side could induce a covert endogenous shift in the tactile attention to the cued side was assessed. The participants were requested to make a speeded discrimination for tactile targets (i.e., continous vs. pulsed), which were preceded by an auditory cue on the same or on the opposite side of the target (50% vs. 50% of the trials). The results showed that the presentation of a spatially uninformative auditory cue determined an advantage (in terms if reactions times and accuracy) in the discrimination of tactile stimuli presented from the same (vs. opposite) side of the body midline. These data clearly show that the peripheral presentation of an auditory cue results in the orienting of the attentional resources in another modality, the touch.

In the Experiment 3, the crossmodal audiotactile links in endogenous spatial attention have been studied by means of the orthogonal-cuing paradigm. In this task, participants make speeded discriminations regarding the elevation (up vs. down) of randomly presented visual and auditory stimuli presented from one of two vertical positions on each side of the midline. This time, the spatially uninformative cues consisted of lateralized tactile stimuli. Again, clear cuing effects were reported, with elevation judgments for both visual and auditory stimuli being faster and more accurate when the cues were presented from the same, rather than from different, side of the targets. These results show that the presentation of a peripheral tactile cue affects the exogenous orienting of both visual and auditory attention in the direction from where the cue was presented.

Taken together, the results of both experiments unambiguously demonstrated the existence of extensive crossmodal links between touch and audition (and vision) in exogenous covert orienting of the attentional resources.

A successive study contributed to the investigation of the topic by investigating the endogenous covert orienting between hearing and touch across three experiments (Lloyd, Merat, McGlone, & Spence, 2003. See also: Spence, Nicholls, & Driver, 2001). In the first experiment, an audiotactile version of the crossmodal congruency task (see Spence, Pavani, Maravita, & Holmes, 2008). The participants held a foam cube between the index and the thumb of each hand, keeping the fingertips in contact with vibrotactile stimulators embedded in the cube, and were requested to discriminated the elevation (up vs. down) of auditory and tactile targets presented to either the left or the right of fixation. The relative probability of occurrence of the stimuli in each modality was manipulated to encourage a prevalent focusing of the attentional resources toward the modality in which the stimuli were more frequently presented (73% vs. 27% of probability, respectively). The participants were also verbally prompted to focus on one of the two sides, where the stimuli in the primary modality were more likely to be presented. The results showed that the strong spatial expectancy about target location in one modality induced an endogenous spatial attentional shift selectively in the primary modality, but not in the other modality, thus suggesting that people are able to prevent a shift of attention in the secondary modality in the direction of a shift in the primary modality. In other words, people can selectively direct and sustain their spatial auditory or tactile attention to one side or the other with no effect on the spatial distribution of attention in the other modality.

In the second experiment, equally strong but opposite spatial expectancies within each modality were induced. The blocks alternated between targets expected on the same side (either left or right) for both audition and touch, and targets expected on different sides for each modality (i.e., audition on the left, touch on the right, or vice versa). No primary vs. secondary modality distinction was introduced. In some blocks of trials, both auditory and tactile targets were more likely (83% of all trials) to be on a common side (i.e., left or right, respectively) with the participants being verbally informed of these probabilities in advance. In other blocks of trials, tactile and auditory targets were both more likely (83% of all trials for each modality) to be on opposite sides (i.e., throughout a block tactile targets were more commonly on the left and auditory targets on the right, or vice versa).

The results of the experiment showed that people can shift and sustain both their auditory and tactile endogenous spatial attention in the same direction simultaneously and direct their attention in the two modalities to opposite side, provided that the stimulus probabilities and the instructions favour such a split of attention.

In their final experiment, Lloyd and coworkers manipulated the participants' posture in order to evaluate whether the crossmodal attentional links operate according to a representation that code for the current position of stimuli in the external space or, rather, they are refer to a spatial representation based on anatomical coordinates. The design was the same as the Experiment 2, with the sole exception that the task could have been performed in the uncrossed or in the crossed posture. The pattern of results reported suggested that the audiotactile representation of space refers to external locations, inducing a facilitation of the processing of sensory stimuli presented on the same region of space, independently from the part of body stimulated.

Taken together, the results of these experiments demonstrate that in the spatial domain, the endogenous links occurring between audition and touch are characterized by a higher degree of independence than what has been found for audiovisual (Driver, & Spence, 1994, Spence & Driver, 1996) and visuotactile (Spence, Pavani, & Driver, 2000) pairings. Indeed, people would be able to endogenously direct and sustain the auditory or tactile attention, with no effect on the spatial distribution of the attentional resources in the other modality. However, people would find harder to split their expectancies in the two modalities on different sides rather than direct them on the same side. According to Lloyd and colleagues, this pattern of results could be compatible with a 'separable-but-linked' view of crossmodal links in endogenous spatial attention, postulating the existence of separable attentional systems for audition and touch, which are though synergistically activated under certain circumstances.

Electrophysiological studies have extended the evidence by Lloyd and colleagues, providing clues about the differential distribution of the endogenous spatial attention resources across time (Eimer, van Velzen, & Driver, 2002; Hötting, Rösler, & Röder, 2003). Hötting and colleagues (2003), for instance, found that early processing stages are influenced by both spatial-selective and modality-selective attentional mechanisms, whereas during later stages the latter seem to prevail. However, the restraint of attentional resources to one sensory modality at later processing cognitive stages seems to affect the perceptual performance, provided, however, that the cognitive demands are high. For instance, Gescheider, Sager, & Ruffolo (1975) found that the distribution of attention between touch and audition significantly decreased the level of the performance when people were engaged in a simultaneous auditory and tactile perceptual task requiring a large amount of cognitive processing as compared to performance in each modality in isolation. These data show, thus, that when the level of difficulty of the task is increased – as for an auditory and a tactile task performed at the same time - people’s cognitive – but not perceptual – processing is disrupted. On the contrary, unimodal and bimodal perceptual tasks are performed at a same level of proficiency when cognitive demands were low (cf. Ho, Santangelo, & Spence, 2009; for differential capturing effect of audiotactile pairs of stimuli during high vs. low cognitively demanding visual tasks).

Despite the great amount of studies aimed to investigate how attention participates in the multisensory integration mechanisms, the issue of how attention processes information from different sensory modalities coming from the same spatial location has been far less investigated (Spence, Lloyd, McGlone, Nicholls, & Driver, 2000; Spence, 2002; Turatto, Benso, Galfano, & Umiltà, 2004).

In Turatto et al.’s study (2004), two stimuli, either presented in the same or in different modalities, were delivered from the same spatial location and were separated by a variable temporal gap, the task consisting in a speeded discrimination of the second stimulus of the pair (crossmodal exogenous cuing paradigm). Overall, the data showed that when the temporal lag between the two stimuli was very brief, the first, task-irrelevant, stimulus caught the attention to its modality, inducing a faster discrimination performance of the second stimulus presented when the two stimuli were ipsimodal as compared to when they were crossmodal. When tactile and auditory stimuli were involved and the modality of the first stimulus was uncorrelated with the modality of the second (i.e., the modality of the first stimulus was not predictive of the modality of the second stimulus; Experiments 1), a significant symmetrical modality-driven attentional capture was demonstrated at shorter intervals (i.e., smaller than 150). At longer temporal intervals (until 600 ms), however, the exogenous control of attention seemed to hold exclusively for audition, but not for touch (i.e., with an auditory stimulus affecting the processing of the subsequent tactile stimulus), suggesting a longer lasting crossmodal effect exerted by auditory stimuli as compared to tactile stimuli. In a successive experiment (Experiment 2), the participants' attention was induced to be fully focused on the modality of the second stimulus of the pair (i.e., the participants knew in advance that the modality would be kept constant throughout each block of trials). The results replicated the pattern observed in the previous study, with delayed latencies in discriminating the second stimulus of the pair when it was preceded by a crossmodal (vs. ipsimodal) stimulus. This evidence would suggest that, for relatively brief interstimulus intervals, the attentional allocation across modalities is highly automatic and driven by exogenous factors rather than the participants' expectancies. According to Turatto and collaborators, the selective facilitation of the performance in the conditions when the pair of stimuli consists in ipsimodal instead of crossmodal inputs would be consistent with the existence of a supramodal attentional mechanism. This speculation would parallel the findings of studies investigating the attentional blink phenomenon, showing that a central attentional limitation would occur when the first- and the second-target stimuli are presented in different sensory modalities (cf. Dell'Acqua et al., 2001). This theoretical frame would, however, contrast with Lloyd et al.'s observations, which are, as we have seen, more in support of a separate-but-linked different attentional systems model. However, as pointed out by the authors themselves, this discrepancy would be resolved by taking into account the difference of purposes between the studies, including their own one, investigating crossmodal attentional effects (Dell’Acqua et al., 2001; Spence et al., 2000; Turatto et al., 2004) and those mainly focused on the spatial features of attention (Spence, 2001). Since in the audiotactile domain attention seems to operate with different mechanisms according to the specific stage of information processing, it can not be excluded that attention selects incoming auditory and/or tactile information according to either a supramodal or a modality specific system depending on the stage of processing that is considered.

One last remark worth mentioning, given the consistency with which has been reported, is the recursive finding that people engaged in different typology of audiotactile attentional tasks often found particularly hard to shift their attentional resources away from touch (e.g., Eimer & Driver, 2000; Gondan, Lange, Rösler, & Röder, 2004; Hanson, Whitaker, & Heron, 2009; Lange & Röder, 2006; Roland, 1982; Spence, 2002; Spence, Nicholls, & Driver, 2001).

For instance, in Spence and coworkers’study (2001), participants were requested to make speeded spatial discrimination judgments (left vs. right) to an unpredictable sequence of auditory, visual and tactile stimuli targets. Crucially, whereas in some blocks of trials an equal number of targets was presented in each modality and participants were instructed to divide their attention equally between all three modalities, in other blocks, the majority (i.e., 75%) of the targets were presented in just one (to be expected) modality. Not surprisingly, the reactions times for targets in an unexpected modality were slower than when that modality was expected or no expectancy was applied. According to the authors, this effect of modality expectancy can be primarily as be interpreted as costs for the unexpected modality rather than benefits for the expected modality. Indeed, the latter can be considered as the consequence of the repetition of the stimulus in the same modality across the trials, rather than the effect of a purely endogenous expectancy mechanism (see also Gondan et al., 2004). The most intriguing finding here derived from the comparison between the latencies in response to the tactile (vs. auditory and visual) targets. The observation that the larger costs were associated with a violated tactile expectation indeed suggested a larger cost of shifting attention away from touch than from either audition or vision (cf. Spence, Kettenmann, Kobal, & McGlone, 2000). Comparable results have been obtained in a speeded detection task involving the presentation of visual, auditory and tactile targets, in conditions where attention could be either focused on a single modality or divided between multiple modalities (Hanson et al., 2009). The analysis showed that no significant differences were present in tactile reaction time in any conditions; however, both visual and auditory reaction times were slowed when observers were required to divide their attention between multiple sensory channels. The authors have advanced some explanations for this apparent difficulty in shifting attention away from the tactile modality by taking into account the philosophical conceptualization of touch (Martin, 1995) Differently from distal senses, such as vision and audition, touch can not be decoupled by the experience of our own body. This closer relation of touch with body representation renders the experience of a tactile sensation more distinctive, somehow more ‘urgent’ (Hanson et al., 2009) than the experience of either visual or auditory sensations. According to this view, the tactile sensations would be prioritized over visual or auditory events, and possibly even processed at a lower level, ‘pre-attentively’, as shown by the failing of any attempt to modulate tactile processing latencies (Hanson et al., 2009; Spence et al., 2001). These explanations, which to date have not found strong empirical support, is rather tentative and points to the necessity of further explore this primary issue.

4.6. Audiotactile spatial attention: Neuroimaging studies

The neuroimaging studies aimed to investigate the attentional links between hearing and touch have also mainly focused on the spatial domain (Eimer, Cockburn, Smedley, & Driver, 2001; Eimer & Driver, 2001; Eimer, van Velzen, & Driver, 2002; Hötting, Rösler, & Röder, 2003; Menning, Ackermann, Hertrich, & Klaus Mathiak 2005), with just a few exploring other domain, such as temporal perception (Lange & Röder, 2006).

As pointed out by Eimer & Driver (2001), the exclusive use of behavioural techniques does not allow disentangling whether the results observable behaviourally can be attributed to genuinely perceptual or rather to post- perceptual processes. In this regard, the event-related potentials (ERPs), allowing a recording of the neuronal activity with a high temporal resolution, provide a suitable insight into the differentiation of the different stages in the processing of visual, auditory, tactile stimulation in crossmodal attention tasks. Indeed, the successive ERP waveforms reflect different stages in the processing of the sensory events, with short-latency components – the ‘exogenous’ components - being sensory-specific (i.e., varying according to the physical features of the stimuli and being detectable in correspondence with specific brain areas) and longer-latency components – the ‘endogenous’ components - being related to post-perceptual processing stages (i.e., identification and categorization) and/or response selection/execution and being more spatially distributed. What is more, this technique provides measures useful to determine whether crossmodal attentional orienting processes are governed by a unique, supramodal, attentional system, or rather, consists of a network of interconnected modality-specific attentional systems.

In one of the first attempts to study crossmodal attentional mechanims, Eimer and colleagues (Eimer et al., 2001; Experiment 2) investigated the spatial coordinates of crossmodal links between hearing and touch. More specifically, these links could be reflected in the increase of activation of the contralateral hemisphere within one modality (i.e., touch) which could then affect the processing of the other modality (i.e., audition) within the same activate hemisphere. Alternatively, the crossmodal links can refer to a more abstract spatial frame of reference, referring to the location of stimuli from different modalities within external space. In this task, participants were asked to attend to the left or the right hand to detect infrequent tactile targets, while keeping the hands in uncrossed or crossed posture. Auditory stimuli served as task-irrelevant stimuli. According to the rationale of the experiment, if the audiotactile spatial links are based on an external frame of reference, an increase of the activity should be observed when both stimuli are presented on the same side of external space, irrespective with the posture. On the contrary, large activation should be observed for a stimulus on the same side as the attended hand in the uncrossed posture, and on the opposite side to the attended hand in the crossed posture. The results provide support to the hypothesis that crossmodal links in spatial attention are based on external spatial frames, rather than on initial hemispheric projections, with stimuli located in the same external portion of space as the attended hand causing an ERP enhancement, in both postures. Interestingly, even though the ERP results for the secondary modality did not show any modulation as a function of the posture, it strongly affected the ERP results consequent to tactile stimulation. In the uncrossed hand condition, spatial attention within touch was reflected in an enhancement of early somatosensory components at lateral central electrodes and sustained enhanced negativities at lateral central at midline sites. In contrast, in the crossed hand condition, the somatosensory ERP effects were reduced or eliminated, and sustained negativities were delayed and reduced in amplitude. It is likely that the conflict induced by crossing the hands has induced a reduction in the efficiency in processing tactile signals.

In another study, participants directed attention to the side indicated by a – visual, auditory, or tactile - cue to detect infrequent auditory or tactile targets at the cued side, with the relevant modality (i.e., audition or touch) being blocked (Eimer et al., 2002). The results showed that ERP modulations sensitive to the cued direction of an endogenous attentional shift were highly similar in the audition- and touch-relevant conditions. Namely, an anterior negativity contralateral to the cued side was followed by a contralateral positivity at posterior sites. Interestingly, these effects did not differ as a function of whether the cues signalled which side was relevant for audition or touch. However, contrarily to the effects of spatial attention on auditory ERPs in the touch-relevant condition, directing attention in the audition-relevant condition did not influence tactile ERPs. While reliable attentional modulations of somatosensory ERPs were observed when touch was relevant, no such effects were present in the audition-relevant condition. It thus seems that touch can be ‘decoupled’ when task-irrelevant from the spatial direction of attention in an auditory task, compatibly with a ‘separable-but-linked’ view of the crossmodal links between hearing and touch (cf. Lloyd et al., 2003. See Section 4.7).

Since the effects of tactually directed attention on auditory ERPs were similar to the auditory ERP modulation induced by visually guided attention (cf. Eimer, Schröger, 1998), the authors concluded that the spatial selection of a cued location is supramodal (Eimer, 2001; Eimer & Driver, 2001. Cf. Karns & Knight, 2009).

Whereas in Eimer and collaborators' studies the links between audition and touch were examined in a transient attention condition (i.e., the position to be attended was indicated by a cue at the beginning of each trial), Hötting et al. (2003) investigated whether attending stimuli in one modality modulates ERPs to stimuli presented in the other modality under conditions of sustained attention. In their study, stimuli of both modalities were presented randomly from the left and the right side and participants were asked to attend to one modality on one side and respond to infrequent deviant stimuli (i.e., double tones or double touches, respectively)of that modality and that side only. This design allowed to test unimodal and crossmodal spatial attention effects as well as intermodal attention effects and to assess the effects of crossmodal and intermodal attention on the processing of somatosensory and auditory stimuli. The analysis of the ERP data revealed that an endogenous shift of auditory attention to one side resulted in a significant enhancement of auditory ERPs at both early and late temporal windows, and that a shift of tactile spatial attention resulted in a significant enhancement of both early and late somatosensory ERPs to stimuli in the attended modality on the attended (vs. unattended) side. Moreover, when participants directed their attention to a spatial position, stimuli of the unattended modality presented at the attended position elicited more pronounced ERPs than when presented at an unattended position, thus giving evidence of the existence of crossmodal links in endogenous spatial attention between audition and touch. As can be inferred, some differences emerge from the comparison of audiotactile links between the sustained and transient forms of attentional orienting. Indeed, differently from Eimer et al. (2001), which found that although auditory ERPs were affected by a transient shift of tactile attention to one side or the other, there were no similar effects of a transient shift of auditory attention on ERPs to tactile stimuli, Hötting et al. found that a sustained shift of attention in either modality elicited a small but significant shift of attention in the other modality. This raises the opportunity of further investigations trying to determine more precisely the nature of the links in endogenous spatial attention between audition and touch.

Whereas in previous studies, stimulations were always delivered to or close to the hands, in a subsequent study aimed to investigate how audiotactile spatial attentional links differ as a function of the portion of peripersonal space stimulated, the tactile targets could be presented on the right or left side of the participant's face or to the right or left hand. In that study, the auditory primes were presented in the space surrounding the face and the hands, respectively (Menning et al., 2005). The results showed that when the tactile prime was presented to the participant's face, the N100 component evoked by the auditory stimuli was increased when the stimuli were presented from the same (vs. opposite) side (Menning et al., 2005). Similarly, the P50 component was more pronounced when the source of stimulation was proximal (i.e., presented from close to the participant's face). According to Menning et al., this evidence is consistent with the hypothesis that stimuli presented within close peripersonal space are more prominent in attracting attentional resources as compared to stimuli that are presented in more distant regions (see also Ho & Spence, in press).

Distinguishing from the studies above described is the study carried out by Lange and Röder (2006), which, investigated whether and how focusing attention on a point in time –not in space – influences the processing of auditory and tactile stimuli. In their study, participants were presented with short (600 msec) and long (1200 msec) empty intervals, marked by a tactile onset and an auditory or a tactile offset marker, and, on a block-basis, asked to attend one interval and one modality. Both the behavioural and electrophysiological data demonstrates that focusing attention to a point in time facilitates the processing of both auditory and tactile stimuli. More specifically, as shown by response latencies, stimuli at an attended point in time are processed faster than unattended stimuli, and irrespectively of which modality was task-relevant. Moreover, an enhancement of early negative deflections of the auditory and somatosensory ERPs (audition, 100–

140 msec; touch, 130–180 msec) were observed when audition or touch were task relevant, respectively. The effect of temporal attention on stimulus processing was also observed for task-irrelevant auditory stimuli when touch was task relevant (cf. Roland, 1982).

Taken together, these data show that in the audiotactile domain allocating attention in time does not only affect processing within a task-relevant modality but also in a task-irrelevant modality.

4.7. Crossmodal interactions in the perception of motion

A large body of empirical research has investigated how sensory modalities convey dynamic information (e.g., Gardner & Sklar, 1994; Getzmann & Lewald, 2007; Soto-Faraco & Kingstone, 2004; Sekuler, Watamaniuk, & Blake, 2002). In particular, many researchers have attempted to investigate how the senses (e.g., audition, vision, and touch) interact to provide a representation of dynamic perceptual events (e.g., Alais & Burr, 2004; Anstis, 1973; Bensmaïa, Killebrew, & Craig, 2006; Craig, 2006; Huddleston, Lewis, Phinney, & DeYoe, 2008; Lakatos & Shepard, 1997; Meyer & Wuerger, 2001; Senkowski, Saint-Amour, Kelly, & Foxe, 2007; see also Soto-Faraco & Kingstone, 2004, for a review). This issue is of particular interest given that multisensory integration is central to our perception of motion for many everyday objects and events (cf. Zihl, von Cramon, & Mai, 1983). For instance, information concerning the rapid-approach of a car is not only provided by visual cues (i.e., the rapid expansion of the retinal image) but also by auditory (i.e., the increasing sound emitted by the engine) and perhaps even tactile (i.e., the displacement of the air) cues.

Much research has also addressed the role of crossmodal processing in the perception of apparent motion (Soto-Faraco, Kingstone, & Spence, 2003, for a review). The impression of apparent movement is experienced when two stationary stimuli are displayed in rapid succession from two different spatial positions. Although no physical movement is present, the observer has the impression of a single object moving continuously through space from one position to the other.

Largely investigated in vision (e.g., Ramachandran & Anstis, 1986; Wertheimer, 1912; Yantis & Nakama, 1998), this phenomenon has also been shown to occur in the auditory (e.g., Strybel, Manligas, & Perrott, 1989; Griffiths, Bench, & Frackowiak, 1994) and tactile (e.g., Gardner & Sklar, 1994; Kirman, 1974; Olausson & Norrsell, 1993; Vitello & Ernst, 2007) modalities as well (see Kolers, 1972, for a review). The perception of apparent motion is modulated by the spatiotemporal relations between the displayed stimuli. According to the Korte's (1915) third law of apparent motion, the interstimulus interval required for optimal apparent motion is a function of the distance between stimulus positions provided that stimulus exposure duration and intensity are kept constant. These parameters, originally established for the case of visual apparent motion, also generalize to tactile and auditory apparent motion, thus suggesting that, at least to a certain extent, the spatiotemporal properties of apparent motion are shared across the sensory modalities (Lakatos & Shepard, 1997; although see Strybel, Manligas, Chan & Perrott, 1990).

One experimental paradigm that has frequently been used in recent years to investigate how sensory modalities interact in the perception of apparent motion is the "crossmodal dynamic capture" task (Soto-Faraco, Lyons, Gazzaniga, Spence, & Kingstone, 2002). In a typical study crossmodal dynamic capture task, two pairs of unimodal stimuli are presented from two different spatial locations at the appropriate temporal interval in order to give rise to the impression of one apparent motion stream in each sensory modality. Participants are instructed to determine the direction of motion in the target modality while simultaneously trying to ignore the apparent motion of the stimuli presented in the distractor modality. People are generally able to accurately judge the direction of the target motion when it is concurrently presented with spatially congruent distractor motion, when presented asynchronously with respect to the distractor motion, or else when presented in isolation (i.e., in the absence of any distractor stimuli). However, participants' performance is often dramatically impaired when they have to try and determine the direction of a target stream presented at the same time as a distractor stream moving in the opposite direction. The crossmodal dynamic capture effect has now been examined between various different pairs of sensory modalities, such as between vision and audition (Sanabria, Soto-Faraco, & Spence, 2004, 2007), between vision and touch (see Lyons, Sanabria, Vatakis, & Spence, 2006; Soto-Faraco, Spence, & Kingstone, 2004a), and between touch and audition (Sanabria, Soto-Faraco, & Spence, 2005; Soto-Faraco et al., 2004a).

The pattern of results reported in these studies suggests that the domain of apparent motion perception is characterized by specific asymmetries, as extensively documented in the multisensory integration of static stimuli (see Bertelson & Gelder, 2004; Caclin, et al., 2002). In particular, visual motion has been found to profoundly influence the perception of both auditory (Soto-Faraco et al., 2004b; Strybel & Vatakis, 2004) and tactile (Lyons et al., 2006) motion, with a capture effect occurring in approximately 50% and 40% of responses, respectively, while visual apparent motion tends not to be captured by stimuli presented in the other modalities.

In the audiotactile domain, contrary to what has been reported for those modality pairings involving vision, the dynamic capture effect occurs in both directions (Sanabria, Soto-Faraco, & Spence, 2005; Soto-Faraco et al., 2004a), with touch capturing audition and audition capturing touch. However, the effect has been shown to be stronger when the target motion is auditory and the distractors are tactile than when the target motion is tactile and the distractors are auditory (occurring in 35% and 15% of responses, respectively).

The nature of the crossmodal dynamic capture effect – i.e., whether it reflects a genuinely perceptual and/or a post-perceptual/decisional phenomenon – has been investigated recently (Soto-Faraco et al., 2005). Controlling for response-compatibility confounds (i.e., by making participants report whether the two streams moved in the same vs. different directions instead of discriminating between the right vs. left direction of the target stream) and for the use of response strategies (i.e., by presenting the streams at SOAs at which directional information is not consciously available to the observer), the authors found that the thresholds obtained for correct directional discrimination were higher when the two streams were presented together than when they were presented in isolation, thus supporting the account of a perceptual integration of the moving signals.

The perceptual nature of the capture effect (although note that some contribution of post-perceptual factors related to the decision making and/or the response execution cannot be rejected completely in all cases/studies; see Soto-Faraco et al., 2005) led Soto-Faraco and his colleagues to consider it as a genuine capture-like phenomenon, and not just simply the interference of one sensory modality on people’s ability to accurately process the direction in the other modality. This hypothesis is supported by the evidence according to which in the crossmodal block (as compared to the unimodal baseline block) there is a significant decrement of the d’ in the directionally incongruent trials, accompanied by a slight (albeit not significant) increase in perceptual sensitivity on directionally congruent trials (Sanabria, Spence, & Soto-Faraco, 2007).

In other words, under the appropriate spatiotemporal conditions, task-irrelevant (apparent) motion can significantly affect the direction in which the target (apparent) motion is perceived to occur. Indeed, in the audiovisual version of the dynamic capture task, it has been reported that the participants not only fail to report correctly the direction of the target stream but also report having perceived the auditory stimulus as moving in the same direction as the visual stimulus (Soto-Faraco, Spence, & Kingstone, 2004b; Soto-Faraco et al., 2005). Some tentative recent evidence has also suggested that a fusion of the signals also occurs in the case of the perception of motion presented in the auditory and tactile modalities (Ooshima, Hashimoto, Ando, Watanabe, & Kajimoto, 2008), possibly underlying the capture effect observed in the audiotactile version of the task (Sanabria, Soto-Faraco, & Spence, 2005; Soto-Faraco et al., 2004a).

Assessing whether the asymmetrical capture effect reported between audition and touch reflects inherent constraints in the organization of specific perceptual systems (and thus it is consistently replicable across different experimental conditions) or whether instead it reflects the specific set of stimulus parameters used in previous studies (and thus is liable to be affected by the changes of the experimental conditions) is specifically addressed in the experimental investigations reported in the Sections 9.2 and 9.3

4.8. Audiotactile spatial interactions in neurological populations

The studies presented so far all refer to neurologically intact participants. However, evidence in support of audiotactile interactions in the peripersonal space has been shown to assume singular features in neurological patients as well.

For instance, studies on extinction have shown remarkable interactions between sensory modalities (see Brozzoli, Demattè, Pavani, Frassinetti, & Farnè, 2006, for a review). Extinction is a clinical sign observed as a consequence of brain damage, whereby patients are able to detect a single stimulus presented either to the ipsi- or to the controlesional side of the body, but fail to report the contralesional stimulus when a concurrent stimulus is presented on the ipsilesional side. In the present context, we will focus on the crossmodal links in extinction which involve hearing and touch, even though similar phenomena have been also described between touch and vision (Làdavas, di Pellegrino, Farné, & Zeloni, 1998).

The influence of sounds on the performance of right brain-damaged patients affected by left tactile extinction has been explored in different studies (Làdavas, Pavani, & Farné, 2001; Farné & Làdavas, 2002). It has been shown that the concurrent presentation of sounds on the right side of the head while touches are delivered on the left side of the neck strongly interfered with the processing of the tactile stimuli (crossmodal auditory-tactile extinction). Interestingly, this interference varied as a function of the distance from which the auditory stimuli were presented, with a stronger interference occurring when the sounds were delivered near the head (i.e., within 20 cm) and a much weaker interference when they were presented far from the head (i.e., 70 cm). Furthermore, the magnitude of the crossmodal extinction significantly varied as a function of the complexity of the sounds used. Namely, pure tone exerted a weaker influence, which was restricted to the region of space behind patients' head. On the contrary, the extinction determined by white noise bursts was remarkable, in both frontal and rear space, and even comparable to the one obtained with touches (cf. Graziano et al., 1999).

These data clearly show that the competition between the signals is modulated by the distance in peripersonal space of the sound source, with extinction phenomena restricted to the peripersonal space surrounding the head. The observation that crossmodal interactions in extinction varies as a function of different parameters (e.g., distance between the stimuli and the body, spatial location of stimulation, auditory complexity) is consistent with a modular organization of the peripersonal space, which respond to the necessity of representing different aspects of the occurring stimulation and of pursuing multiple purposes (see Section 4.4 on this point).

As already mentioned, the cases of synaesthetic phenomena within the audiotactile domain are remarkably less numerous than those reported in other sensory domains (see Section 2.6). A recent neurological case of a patient suffering from stroke offered, however, the singular opportunity to observe a form of auditory-tactile synaesthesia, in which sounds produce somatosensory percepts. As a consequence of a right frontoparietal lesion, this patient developed alloesthesia, a clinical condition in which patients experience stimuli on the side opposite to the side of stimulation (Ortigue, Jabaudon, Landis, Michel, Maravita, & Blanke, 2005). In the case described by Ortigue and collaborators, when double bilateral stimuli were delivered,(i.e., left touch/left sound, left touch/right sound, right touch/left sound, right touch/right sound),the stimulus in the task-relevant modality (i.e., audition or touch, alternatively) was always reported. Interestingly, however, relevant left-sided stimuli were reported as delivered to the right side in the three fourth of the trials, with the localization of right-sided stimuli unaffected. Moreover, there was a trend for task-relevant touches delivered to different parts of the body (i.e., face, hand, foot) to be mainly mislocalized towards the face, whereas auditory task-relevant stimuli were significantly mislocalized when the touches were applied to the face or to the hand, but not when they were applied to the foot. The systematic mislocalization to the right side, which was specific for this modality pair, followed thus precise spatial rules, with mislocalization always occurring from left-sided lower body parts towards the right side of the face and differently affecting different parts of the body. Considering the specificity of the direction of the mislocalization (left to right), the authors interpreted this pattern of performance as an attentional disorder affecting the interhemispheric competition between the neural representations of sensory events during bilateral simultaneous stimulation. Moreover, since the mislocalization of tactile stimuli occurred to the homologous part of the body, it could not be excluded that the correct location of the stimulus was coded at a preattentive level, thus possibly suggesting an interpretation of this impairment as a preattentive modulation of multisensory integration within the peripersonal space.

In a subsequent neuroimaging investigation involving the same patient, the neural activations induced by, respectively, auditory and tactile stimuli were put in comparison with healthy controls (Beauchamp & Ro, 2008). The results showed a differential pattern of activations in the patient, as compared to the controls, in the secondary somatosensory cortex in the parietal operculum, a region adjacent to auditory association areas which show weak but consistent responses to auditory stimuli, in addition to somatosensory stimuli (Foxe et al., 2002; Ozcan et al., 2005; Schurmann et al., 2006). This area has been found to respond to sounds – especially to those more prone to evoke synaesthetic somatosensory percepts much more strongly in the patient than in the controls and, conversely, less to somatosensory stimuli in the patient compared to the controls. Moreover, the overall brain responses to touches were weaker than the ones observed in controls. This double dissociation of weaker responses to somatosensory stimuli and stronger responses to auditory stimuli in the secondary somatosensory area in the patient compared with normal controls suggests the possible functional reorganization intervening between the stroke and the time of the testing (i.e., six years after the event), with a progressive rewiring of auditory inputs into the deprived somatosensory cortex. According to the authors, the stroke-induced lack of somatosensory thalamic input might have allowed short-term unmasking of already existing connections between adjacent auditory and somatosensory cortex. Even though not extensively explored by the authors, their study raises the intriguing possibility that also the thalamus could play a significant role in multisensory integration processes (cf. Naumer & van den Bosch, 2009). The application of advanced imaging methods could possibly contribute in future investigations to a better definition of anatomical connections underlying the integration of sensory signals at neural level.

Chapter 5.

Neural substrates of audiotactile interactions

5.1. Introduction

Numerous studies using various techniques have contributed in delving into the neural substrates subserving audiotactile interactions behaviourally observable (see previous Sections). However, even though a large amount of evidence regarding both animals (e.g., rats: Barth, Kithas, & Di, 1993; cats: Clemo, Allman, Donlan, & Meredith, 2007; Dehner, Keniston, Clemo, & Meredith, 2004; gerbils: Budinger, Hess, & Scheich, 2006; ferrets: Keniston, Allman, Meredith, & Clemo, 2009; and monkeys: Kayser, Petkov, Augath, & Logothetis, 2005; Wallace, Ramachandran, & Stein, 2004) and humans (e.g., Caetano & Jousmäki, 2006; Foxe, Morocz, Murray, Higgins, Javitt, & Schroeder, 2000. Cf. Gobbelé, Schürmann, Forss, Juottonen, Buchner, & Hari, 2003; Lütkenhöner, Lammertmann, Simões, & Hari, 2002) are at present available, the pattern emerging from them look somehow mixed and deserving further investigations. For instance, there are evidence suggesting that the interactions occurring between touch and audition can be asymmetrical in nature when different parts of the body are put in comparison (e.g., hands vs. face: Fu et al., 2003; Menning, Ackermann, Hertrich, & Mathiak, 2005; hands vs. feet: Beauchamp, Yasar, Frye, & Ro, 2008; Kayser et al., 2005) and/or groups with different levels of expertise are involved (e.g., musicians vs. non-musicians; Pantev, Lappe, Herholz, Trainor, 2009; Schulz, Ross, & Pantev, 2003). Moreover, just as other sensory domain, also audiotactile interactions at neural level have been consistently proved to be prone to reorganization processes, such as ones occurring as a consequence of sensory deprivation (e.g., Auer, Bernstein, Sungkarat, & Singh, 2007; Levänen, Jousmäki, & Hari, 1998).

Recent studies have provided evidence for multisensory convergence not only in the typically defined ‘polisensory’ or ‘associative’ areas, but also at low level stages of the sensory cortical pathways, in areas traditionally considered as unisensory, in both monkeys (Foxe and Schroeder 2005; Kayser et al., 2005; Smiley & Falchier, 2009) and human participants (Foxe et al., 2002; Ozcan et al., 2005; Schürmann et al., 2006. See Kayser & Logothetis, 2007; Musacchia & Schroeder, 2009; Schroeder & Foxe, 2005 for reviews).

What is more, whereas somatosensory stimulations evoke activations in the auditory cortex (e.g., Fu et al., 2003; Hackett, Smiley, Ulbert, Karmos, Lakatos, de la Mothe, & Schroeder, 2007; Schroeder, Lindsley, Specht, Marcovici, Smiley, & Javitt, 2001; Schürmann, Caetano, Hlushchuk, Jousmäki, & Hari, 2006), no evidence of audiotactile multisensory integration occurring in the somatosensory cortex has been thus far observed in humans (see Meredith, 2009 for evidence in animals).

In the present chapter, we will provide an overview of the current state of art on this topic, by firstly reviewing the general principles ruling the multisensory integration processes at the neuronal level (see Section 5.2 and 5.3), then describing in more detail audiotactile integration mechanisms occurring, respectively, in monkeys (see Section 5.4) and humans (see Section 5.5).

5.2. General features of multisensory integration at neuronal level

The pioneering contribution to the understanding of the neural correlates of how signals coming from different sensory channels are merged together is owed to the studies in the superior colliculus performed by Stein and Meredith (1993).

This midbrain structure is characterized by a high proportion of neurons responding to stimuli from more than a single sense (i.e., multisensory neurons), thus leading Stein and Meredith to consider it a suitable model for the study of their properties (Stein & Stanford, 2008 for a review). The processes through which the inputs delivered by different sensory pathways (i.e., visual, auditory, and somatosensory) are fused together has been labelled ‘multisensory integration’ (e.g., Stein & Meredith, 1993; Calvert, Spence, & Stein, 2004. Multisensory integration is commonly assessed by considering the effectiveness of a crossmodal stimulus combination, in relation to that of its component stimuli, for evoking some responses from the organism. For instance, the magnitude of a response to an event that has both auditory and tactile components is compared with that for the auditory and the tactile stimuli alone. An operational principle has been derived in order to define multisensory integration at the level of a single neuron: the crossmodal combination of stimuli evokes number of impulses which is significantly higher than the number of impulses evoked by the most effective of these stimuli individually. Alternatively, it has been used the term of ‘multisensory convergence’ when a response elicited by one stimulus can be modulated (enhanced or depressed) by a stimulus from another modality (Beauchamp, 2005b. See also: Kayser & Logothetis, 2007). Multisensory neurons show this kind of multisensory convergence, as their responses can be affected by several sensory modalities. Based on the study of such neurons’ response properties, some principles for sensory integration have been formulated. The spatial principle is based on the evidence that each multisensory neuron has multiple receptive fields, one for each modality to which it is sensitive to. For multisensory neurons, the receptive fields of different modalities overlap. Only stimuli in spatial register (likely originating from the same external source), would fall within this overlap, thus inducing an enhanced response; on the contrary, stimuli from disparate locations would fall outside this area, failing to induce any enhancement or even causing a response depression if the second stimulus lies within an inhibitory area. A second principle claims that only stimuli which occur close in time cause response enhancement, whereas stimuli separated in time just induce responses comparable to the ones evoked by unisensory stimuli. Lastly, the strength of response modulation is inversely related to the effectiveness of individual signals to induce a response (principle of inverse effectiveness). As already mentioned (see Section 5.2), these principles suggest a functional link between neuronal activity and behavioural benefits of sensory integration. Furthermore, the operational definition of the properties of multisensory neurons allowed typifying the cortical regions and brain structures which have multisensory properties. In the next section, we will review the cortical regions which have been found to be capable of integrating crossmodal cues from the visual, auditory and somatosensory systems.

5.3. Multisensory areas

Several cortical areas have been identified on the basis of their multisensory properties, both in animals (Jiang, Jiang, & Stein, 2002; Keniston et al., 2009; Wallace & Stein, 1994) and in humans (e.g., Calvert, 2001; Calvert & Thesen, 2004). In the present context, we will focus on studies which have explored this topic in primates and humans. In the macaque monkey, important multisensory regions responding to somatosensory, auditory and visual stimuli have been detected in correspondence of the caudal part of the superior temporal sulcus (STS, also known as ‘superior temporal polysensory’; Bruce, Desimone, Gross, 1981; Hikosaka, Iwai, Saito, & Tanaka, 1988), the ventral intraparietal area (VIP; Colby, Duhamel, & Goldberg, 1993; Bremmer, 2005), and the frontal cortex (Chavis & Pandya, 1976; Matelli & Luppino, 2001), (see Ghazanfar & Schroeder, 2006 for a review. See also: Wallace et al., 2004b).

In particular, the ventral intraparietal region, located in the fundus of the intraparietal sulcus, has been shown to respond not only to visual, auditory and somatosensory stimuli (especially moving stimuli), but also to vestibular stimuli. In spatial proximity to VIP, the temporo-parietal area (Tpt), located in the posterior portion of the superior temporal plane and the superior temporal gyrus, has been found to contain trimodal neurons with receptive fields centred on head-neck region, thus possibly being involved in orienting head in space (Leinonen, Hyvärinen, & Sovijärvi, 1980).

Multisensory neurons responding to visual, auditory, and somatosensory inputs presented in proximity with the upper body - face, arm and upper torso - have also been found in a ‘polisensory zone’ located in the dorsal part of premotor cortex, and seem to be particularly involved in the production of defensive behaviours (Ghazanfar, Neuhoff, & Logothetis, 2002; Graziano, Alisharan, Hu, & Gross., 2002a; Graziano, Taylor, Moore, & Cooke, 2002b. See also Section 4.4).

Other studies on macaque have demonstrated the presence of neurons in the region of ventral premotor cortex which shows polymodal response properties to visual, tactile, and auditory stimulation (Graziano & Gross, 1998) with a somatotopic organization (Graziano et al., 1999; Graziano & Gandhi, 2000).

On the basis of the data collected on primates, a number of subsequent human studies have tried to determine whether the bank of human posterior STS (STSms) showed responses to visual, auditory and somatosensory stimuli, just as reported in monkeys. The data were, however, inconsistent (e.g., Bremmer et al., 2001; Beauchamp, Argall, Bodurka, Duyn, & Martin, 2004). A subsequent study contributed to clarify this issue (Beauchamp, Yasar, Frye, & Ro, 2008; see also Beauchamp, 2005a). Beauchamp and colleagues reported that neurons in STS responded more to multisensory auditory-visual stimuli than to unisensory auditory or visual stimuli, thus replicating previous evidence (e.g., Beauchamp et al., 2004). In addition, however, larger responses – albeit not super-additive - were also reported for multisensory auditory-tactile stimulus pairings than unisensory auditory or somatosensory signals. Differently from the measures recorded in monkeys, however, in humans the auditory-tactile integration did not follow the principle of inverse effectiveness, with weaker auditory stimuli eliciting stronger interactions with tactile stimuli. Interestingly, greater responses were recorded in the STSms to visual moving than to stationary stimuli, just as in monkeys (Bruce et al., 1981; Hikosaka et al., 1988). Furthermore, also the pattern of activation induced by auditory stimuli in human STSms paralleled the one in monkeys, with similar activity to very different kinds of sounds (i.e., animal, human, and mechanical sounds) and a higher preference for meaningful stimuli. In a very recent study, Tanaka and coworkers (Tanaka, Kida, Inui, & Kakigi, 2009) used MEG to investigate time-varying cortical processes responsive to unexpected unimodal changes during continuous multisensory (i.e., visual, auditory, and tactile) stimulation. The results showed multimodal activations in the temporo-parietal junction (TPJ) and inferior (IFG) and middle frontal gyri (MFG) in response to all unimodal changes occurring in different sensory modalities, accompanied by unimodal activations in other areas, such as middle occipital gyrus (responding to visual changes), superior temporal gyrus (responding to auditory changes), and secondary somatosensory area (responding to tactile changes). Whereas in STG, responses occurred to changes in both visual and auditory modalities, TPJ was found to respond similarly to all the unimodal changes occurring in more than one modality. This evidence is consistent with previous studies, demonstrating multimodal activations in the TPJ in response to novel and unexpected stimuli (e.g. Hikosaka et al., 1988) and abrupt changes of visual, auditory, and tactile stimuli during multisensory stimulation (e.g., Downar, Crawley, Mikulis, & Davis, 2000). It is likely that this region is part of the cortical network which includes MFG/IFG, regions known to underlie a wide variety of higher-order cognitive functions including voluntary and involuntary attention (e.g., Corbetta & Schulman, 2002) or executive control functions (Miller, 2000). It thus seems that activations of TPJ, as well as of MF/IFG could be part of neural system underlying the stimulus-driven, exogenous orienting of attention and the subsequent detection of changes in multisensory environments (cf. Tanaka, Inui, Kida, Miyazaki, Takeshima, & Kakigi, 2008).

Another area which has been found to be the centre of convergence of signals from different senses is the located in the depth of human intraparietal posterior sulcus (IPS; Bremmer et al., 2001). This area responds to polymodal motion stimuli and can be considered the human homologue of monkey area VIP.

5.4. Areas subserving audiotactile integration in monkeys

Early studies trying to typify the cortical areas involved in audiotactile integration in monkeys date back to the seventies, when Hyvärinen and Poranen (1974) by applying intracranial recordings identified posterior parietal cortex as candidate structures for the integration of auditory and somatosensory information. Subsequent studies have extended these findings, showing convergence of somatosensory and auditory inputs also in area Tpt, the parabelt region located in the posterior portion of the superior temporal plane (Leinonen & Nyman, 1979; Leinonen, Hyvärinen, & Sovijärvi, 1980), and the superior temporal sulcus (Hikosaka, Iwai, Saito, & Tanaka, 1988).

More recently, Lewis and van Essen (2000) injected tracers into defined areas of parietal and temporoparietal cortex in order to highlight the corticocortical connections implicated in visual and somatosensory integration. The network involving the ventral intraparietal area (VIP) is particularly interesting for the present context. Indeed, injections centred in that area revealed a complex pattern of inputs from numerous visual, somatosensory, motor, and polysensory areas, and from presumed vestibular- and auditory-related areas. These features lead the authors to consider VIP as a key area involved in a wide range of different functions, such as multisensory analysis of stimulus location and motion; the construction of a multisensory, head-centred representation of near extrapersonal space, and possibly an attention-related network.

In a subsequent study, awake monkeys were presented with binaural auditory stimuli (i.e., clicks, pure tones, and band-passed noise) via headphones and contralateral median nerve stimulation (Schroeder et al., 2001). This study demonstrated convergence of somatosensory and auditory inputs on the caudo-medial belt (CM) auditory cortex, which is just one synapse from primary auditory cortex and thus located at the second stage of the auditory hierarchy. Both auditory and somatosensory activation profiles had approximately the same latency and showed a feedforward pattern, with responses beginning in Lamina 4 and successively spreading to the extragranular layers. Furthermore, no activation of the higher cortical areas was observed, thus suggesting that the observed multisensory integration is a result of feed-forward processing and is not due to feed-back signals from higher areas. Although revealing, that study was still unable to define some aspects of the audiotactile convergence in CM, such as the proportion of neurons exhibiting excitatory somato-auditory convergence relative to those with unisensory excitatory inputs and the potential existence of a full body map within CM, which could serve as a demonstration of the involvement of CM in a network combining vestibular with other sensory inputs in the computation of the position of the head in space and/or in relation to the other parts of the body (Guldin & Gruesser, 1998).

These findings have been extended by Kayser and colleagues (Kayser et al., 2005), who used fMRI-BOLD measurements to assess the integration of auditory and tactile stimulations of hands and feet in anaesthetized monkeys. The results reported by Kayser et al. confirmed that the presentation of a tactile stimulus simultaneously with an auditory stimulus determined a supra-additive integration of the two signals in the caudomedial (CM) - but also in the caudolateral – belt areas of the auditory cortex. Moreover, the integration of auditory and tactile signals obeyed the principles of both temporal coincidence (i.e., integration was stronger for temporally coincident stimuli) and inverse effectiveness (i.e., a bigger enhancement of the response was observed for less effective stimuli). Two pieces of evidence support the automaticity of this process: namely, it occurs in an area which is located early along the auditory pathway; secondly, it occurs in anesthetized monkeys, thus ruling out the possibility that the observed effect can be affected by attentional and/or cognitive top-down factors.

Fu and coworkers (2003) used multi-neuron cluster recordings, along with a limited sample of single-unit recordings to better define the physiological features of CM. They found that, differently from primary auditory cortex, the majority of the auditory-responsive recording sites in CM were also responsive to some form of somatosensory stimulation, mainly to cutaneous stimulation of the head and hands and to lesser extent to stimulation with air puffs or von Frey hairs or deep pressure stimulation. A few sites responded to non-cutaneous somatosensory stimuli. In eight sites, for example, manipulation of the elbow joint or vibration produced neuronal responses. Thus, the bias of the cutaneous representation in CM toward the skin surfaces of the head and neck reported in Fu et al.’s study is consistent with the hypothesis that of such early multisensory integration in the posterior auditory cortex could play a functional role along “where” pathway in auditory processing, contributing in detecting and localizing objects in space (e.g., Rauschecker, Tian, Pons, & Mishkin, 1997).

Recent studies using injections of tracers into the belt areas of auditory cortex in monkeys allowed to typifying better the connections of these areas with cortical and subcortical areas

(Hackett et al., 2007; Smiley et al., 2007; Smiley & Falchier, 2009). CM and CL have proved to have connections, besides with primary auditory cortex, also with somatosensory (i.e., retroinsular cortex, Ri, and granular insula, Ig) and multisensory (i.e., temporal parietal occipital and temporal parieto-temporal) and visual (i.e., secondary visual area and prostriata) areas. Thalamic connections include the medial geniculate complex and several multisensory nuclei (supra-geniculate, posterior, limitans, medial pulvinar). The results suggest that Area CM is presumed to be a first-stage auditory association cortex, yet it has short-latency somatosensory responses especially after cutaneous stimulation of the head and upper body, receiving somatosensory input mainly from areas Ri and Ig, while multisensory regions of cortex and thalamus may also contribute.

Even though is generally accepted that sensory modalities converge on higher level areas through feedforward pathways, this assumption has been challenged by a certain number of recent studies, which have revealed that multisensory interactions can occur in unimodal areas, at very early levels of cortical processing. For instance, it has been shown that the neuronal activity of the primary auditory cortex, can be significantly modulated by somatosensory influences (e.g., Brosch, Selezneva, & Scheich, 2005). In monkeys performing an auditory categorization task, Brosch and colleagues found extensive crossmodal activation in the supratemporal plane and in near primary auditory cortex which was time-locked to the cue light and the touch of a bar - associated to the start of the tone sequence - during the behavioural procedure, possibly pointing to the representation in the auditory cortex to nonacoustic stimuli in addition to sound. According to the authors, the co-representation of non-acoustic events in the auditory cortex has emerged during the long training period the monkeys spent on the acquisition of the task as a strategy aimed to accelerate and improve participants’ performance.

An attempt to better outline the networks of heteromodal connections linking unimodal sensory areas was performed by Cappe and Barone (2005), who injected retrograde tracers in unimodal auditory, somatosensory and visual cortical areas of marmoset. Somatosensory projections to the auditory cortex were reported from the secondary somatosensory cortex (SII) and the anterior bank of the lateral sulcus. Furthermore, in a ventral somatosensory region including SII, parietal ventral (PV) and the ventral somatosensory area were found neurons responding to auditory stimuli, suggesting that these areas along with the posterior auditory fields belong to a larger cortical region involved in auditory and somatosensory integration. Furthermore, the short latencies of these multisensory connections support the existence of direct heteromodal connections, rather than connections from polymodal areas mediated through back projections.

A recent study analysed the physiological mechanisms underlying somatosensory-auditory interactions by recording current source densities and multi-unit activity in AI in awake macaque monkeys (Lakatos, Chen, O’Connell, Mills, & Schroeder, 2007). The authors succeeded in delineating the mechanism by which the somatosensory stimulus enhances auditory responses, founding that the somatosensory stimulus does not induce an increase in neuronal firing rates, but rather resets the phase of the ongoing local neuron oscillations. This phase resetting ensures that a simultaneous auditory stimulus arrives at the phase of optimal excitability, so that an auditory stimulus that is paired with a simultaneous somatosensory stimulus will elicit stronger neuronal responses than an auditory stimulus presented in isolation. This effect was spatially specific with respect to the hand receiving the somatosensory stimulus, and was more effective at moderate auditory stimulus intensities and when the stimuli were presented simultaneously, in agreement with the principles of multisensory integration. The ultimate aim of this process is allowing the matching of the temporal patterns (rhythms) of somatosensory and auditory inputs in phase as well as frequency, with the consequent enhancement of the auditory cortical response. Intriguingly, this effect occurs in the primary auditory cortex, a primary cortical structure widely viewed as exclusively auditory in function.

Differently from the somatosensory responses in CM, which are likely induced by feedforward connections (Schroeder et al., 2001), the somatosensory responses in AI are plausibly mediated by different anatomical mechanisms. The timing and laminar profile of the multisensory interactions in AI contribute in pointing to nonspecific thalamic afferents (Hackett et al., 1998) as the most plausible candidates of connections underlying the multisensory interactions in AI.

5.5. Areas subserving audiotactile integration in humans

Since some decades ago, an increasing amount of studies have addressed the question of whether interactions between auditory and somatosensory can be detected at neuronal level in humans (e.g., Hay & Davis, 1971; Davis, Osterhammel, Wier, & Gjerdingen, 1972; Greenwood & Goff, 1987; Huttunen, Hari, & Vanni, 1987). In one of these early attempts, Davis et al. studied the slow vertex potential and showed that a tactile stimulus reduced the auditory response by nearly the same factor as an auditory stimulus reduced the response to the tactile stimulus (by about 35%). Greenwood and Goff (1987) investigated how the somatosensory evoked potential in response to electrical stimulation of the right median nerve was changed by clicks delivered to the right ear, either simultaneously or with onset asynchronies between 20 ms and 2.5 s. Basically no effect was found for the primary somatosensory response N20-P30, but suppressive cross-modal interaction was observed with increasing latency, with the effect decreasing as a function of the increase of interstimulus intervals. Evidence of crossmodal interactions occurring in the late windows of sensory processing (i.e., 120 ms) was confirmed by Okajima et al. (1995) by simultaneously presenting tones and a painful electrical stimulus applied to the median nerve. In another study, Lam and colleagues reported that the activity considered to reflect activity of the ipsilateral secondary somatosensory cortex was suppressed by the continuous auditory (music) stimulation (Lam, Kakigi, Kaneoke, Naka, Maeda, & Suzuki, 1999). 1999). This brief overview shows that, except for the observation of Lam et al. (1999), a clear neural correlate of an interaction between auditory and somatosensory systems was until recently still far to be detected.

However, more recent studies have highly contributed in shedding light on this debated issue. For instance, a fMRI study where human participants listened to a sound that resembled sandpaper moving on a rough surface and/or felt the experimenter to rub their fingertips with sandpaper showed that the simultaneous stimulation in both auditory and tactile modalities resulted in significantly supraaddictive activity in the caudomedial (CM) belt area of auditory association cortex (Foxe et al., 2002. See also Ozcan et al., 2005). The close agreement between Foxe et al.'s data and studies on animals (Schroeder & Foxe, 2002; Schroeder et al., 2001. See Section 5.4) led the authors to label the region identified in their own study as the human homologue of monkey CM. This early finding has been confirmed and extended by a subsequent study using the same methodology (Schürmann et al., 2006), finding that tactile activation of auditory belt area can be induced by both vibrotactile (i.e., 200-Hz vibrations) and pulsed-tactile stimuli (i.e., tactile pressure pulses).

Partially consistent with these results are the ones reported in another study, which investigated the neural substrates of interactions occurring between binaural tones and tactile stimuli delivered to the right thumb using a whole-scalp magnetoencephalography (MEG)(Lütkenhöner et al., 2002). The results showed audiotactile interactions in the hemisphere contralateral to the side of the tactile stimulation, whereas an interaction was shown in the ipsilateral hemisphere in only three of eight subjects, likely those who showed strong SII activity to the tactile stimuli presented alone (cf. Lam et al., 1999. See above). The recording of the magnetic fields evoked by the audiotactile stimulation shows an outgoing flux at anterior scalp locations and a magnetic flux into the head at posterior locations. This pattern looks orthogonal to the one reported by Foxe et al. (2000), with extrema of opposite polarities over the vertex and the right central/postcentral scalp at 65 ms and, at 80 ms, a polarity reversal on the superior surface of the temporal lobe. However, since electrical potential and magnetic filed arising from a current dipole are oriented orthogonally to each other, sources observed in these two studies seem to be basically the same. Differently from what stated by Foxe et al., according to which the activity at 65 ms can be due to the somatosensory areas in the postcentral gyrus whereas the activity at 80 ms is attributable to auditory cortical areas, Lütkenhöner and colleagues consider the SII as a source of interaction field. However, it is likely that some methodological differences, such as the typology of tactile stimulation used, or the timing or spatial arrangement of the presentation of the stimuli, could have induced these discrepancies. Moreover, the time course of these activations showed major deflections of opposite polarities mainly arising from the SII region, thus possibly suggesting that the auditory stimulus resulted in a partial inhibition in SII.

The possibility, already raised by Fu et al. (2003), that CM could be part of a ‘where’ network involved in the localization of objects in space has been indeed recently confirmed in a human study (Renier, Anurova, De Volder, Carlson, VanMeter, & Rauschecker, 2009) which used fMRI technique to compare brain activations during the processing of spatial (i.e., localization) and nonspatial (i.e., identification) attributes of auditory and tactile stimuli, thus allowing the definition of the networks involved in ‘what’ and ‘where’ processing of comparable stimuli in the two modalities. The results showed a segregation between the two processing streams in, respectively, inferior-frontal and parietal regions, when comparing identification and localization conditions. To a lesser extent, also parts of the frontal cortex and of the parietal cortex contributed to the localization and to the identification tasks, respectively. Even more interestingly, it has been demonstrated that these two pathways are at least partially shared between hearing and touch. More specifically, areas in the right inferior frontal gyrus (IFG) and bilateral insula were more activated during the processing of stimulus identity in both audition and touch, whereas parts of the left and right inferior and superior parietal lobules (IPL and SPL), and additionally of caudal belt (cf. Smiley et al., 2007; Hackett et al., 2007), were recruited during the localization of both auditory and tactile stimuli.

An involvement of an auditory areas (i.e., superior temporal gyrus, STG) has also been demonstrated in the temporal processing of contralateral tactile stimuli, although not in tactile spatial processing (Bolognini, Papagno, Moroni, & Maravita, 2009). This area would operate in a later stage of temporal processing (i.e., 180 ms), whereas at an early processing stage the primary somatosensory cortex would be implied in both spatial (i.e., 60-120 ms) and temporal (i.e., 60 ms) processing of tactile information. The selective involvement of STG to the discrimination of temporal features of tactile information adds to previous evidence showing the crossmodal recruitment of contralateral auditory association cortex during the processing of tactile stimuli with frequency properties (Schurmann et al., 2006; Foxe et al., 2002. See also Section 3.4).

The spatiotemporal features of the integration processes occurring at neural level between auditory and somatosensory signals have been better defined by subsequent studies. For instance, in an EEG experiment, Murray and colleagues (2005) collected both behavioural and electrophysiological measures while participants performed a simple reaction time task in response to spatially aligned and misaligned audiotactile stimulus configurations. The participants were presented with somatosensory stimuli alone, auditory stimuli alone, pairs of stimuli simultaneously presented either to the same location (e.g., left hand and left-sided speaker) or to different locations (e.g., left hand and right-sided speaker), with left- and right-sided presentations being counterbalanced. Since the behavioural data have been already discussed elsewhere (see Section 4.3), here we will focused on the EEG data. Somehow surprisingly, these results revealed equivalent electrophysiological interactions at just 50-95 ms post-stimulus onset with both spatially aligned and misaligned stimuli. Source estimations of these interactions were localized to the auditory association cortices (i.e., posterior superior temporal plane. Cf. Foxe et al., 2000) in the hemisphere contralateral to the hand stimulated, regardless of the location of the auditory stimulus, possibly suggesting that CM of each hemisphere receives somatosensory inputs from the contralateral hand and auditory inputs from both the contralateral and ipsilateral portions of space (cf. Gulden & Grusser, 1998).

In another study, Gobbelé and colleagues (Gobbelé, Schürmann, Forss, Juottonen, Buchner, & Hari, 2003) conducted a MEG study on humans by recording cortical-evoked responses to unilateral auditory or tactile stimuli, or spatiotemporally coincident bimodal audiotactile stimuli, which could be presented either from the right or left side of the body midline. The analysis revealed that audiotactile integration occurs at two different temporal windows. A significant audiotactile integration activity was observed in the posterior parietal cortex (PPC) at an early processing stage (i.e., 75-85 ms) and in the contralateral temporoparietal areas at 105-130 ms. The effects were more pronounced in the left rather than in the right hemisphere, independently from the handedness of the participants tested, thus possibly suggesting a dominance of the left hemisphere for audiotactile interactions (cf. Renier et al., 2009). The observation that perceptual binding of stimuli presented simultaneously from a spatially coincident location occur in the posterior parietal cortex mirrors the data reported in previous studies (e.g., Bremmer et al., 2001), showing that an area depth of the intraparietal sulcus responds to spatially directed somatosensory, visual, vestibular and auditory stimuli. The multisensory integration activity observed later between the secondary somatosensory cortex (SII) and the auditory cortices was characterized by a closer similarity to responses to the tactile stimulation than to the auditory stimulation. This result could be plausibly attributed to the suppression of the responses to the auditory component of the audiotactile stimulus pairings. This speculation would be consistent with the participants' self reports that tactile inputs dominated during audiotactile stimulation. However, as pointed out by the authors themselves, this evidence could reflect the specific nature of the stimulation used rather than a genuine perceptual phenomenon, as the discrepancy between the data reported in Gobbelé et al.'s study and other data seems to suggest (cf. Lütkenhöner et al., 2002). Namely, when sounds were more salient than the tactile stimuli, as in Lütkenhöner et al.'s study, responses indicated partial inhibition in the SII region. Instead, pairs with more salient tactile than auditory stimuli (like the ones induced by electric stimulation; Gobbele´ et al., 2003) indicated suppression of the auditory responses (see also Kisley & Cornwell, 2006 on the issue of salience of auditory vs. somatosensory stimuli).

The issue of a sensory dominance between hearing and touch is a still controversial topic, we have already partially discussed (see Chapters 2. See also Chapter 7) and on which we will go back again in the course of the discussion. An additional interesting piece of information emerged from the subjective reports; namely, the participants reported perceiving simultaneous auditory and tactile stimuli from the same side as 'belonging together', pointing not only to the importance of spatial coincidence in the audiotactile integration processes, but also possibly stressing once more the high proneness of auditory and tactile signals to be automatically bound together (cf., Bresciani & Ernst, 2007).

The close relation between auditory and somatosensory signals has been further demonstrated by Caetano and Jousmäki (2006). In their study, the authors reported that a vibrotactile stimulation just above the individual tactile detection threshold delivered to the right-hand fingertips in absence of any auditory stimulation could elicit activations of SI, SII, but also, even more interestingly, a sustained activation in auditory cortices (Caetano & Jousmäki, 2006). The vibrotactile stimuli elicited vibrotactile evoked fields, with early responses, peaking around 60 ms, originating in the primary somatosensory cortex, followed (100-200 ms) by activations in the auditory cortices, and by activations in the second somatosensory cortex. Additional auditory sustained activation was identified in nine out of ten participants. This physiological evidence paralleled with the subjective reports of the participants, which declared to perceive a sound when touching the vibrating tube, and nothing when they were not (cf. Schürmann et al. for previous behavioural evidence). Complementary to these findings are those recently reported by Hötting, Friedrich & Röder (2008), which explored the neural correlates of the audiotactile version of the illusion first reported by Shams et al. (2000). In an oddball-paradigm tactile double stimuli together with two tones were presented as frequent standard stimuli and single tactile stimuli with two tones as rare deviant stimuli. Participants' task was to press a button whenever they perceived a single tactile stimulus and to ignore the tones. Once again (cf., e.g., Hötting & Röder, 2004), an effective auditory-tactile illusion was reported, with participants not responding to single tactile stimuli accompanied by two tones, thus proving that double touches had been perceived. The ERPs showed reduced tactile deviant processing when participants did not detect this single tactile deviant stimulus and thus perceived the auditory-tactile illusion. Interesting results were reported by observing the N2b ERP component, which peaks about 200-300 ms from the stimulus onset and is evoked when a stimulus is attentively detected as being different from the regular stimuli (Näätänen, Simpson, & Loveless, 1982). Interestingly, the amplitude of the tactile N2b was modulated by participants' subjective percept: the N2b was most pronounced when the actual number of touches was indeed perceived; it was significantly reduced when tones successfully altered the tactile percept and was lowest for standards that did not require an overt response. These results induce the authors to suggest the existence of a frontal brain system checking for potential discrepancy between co-occurring real stimuli and illusory percepts.

The fact that the activations observed were sensitive to the subjectivity of the perceptual processes add to a remarkable amount of evidence showing that audiotactile interactions are characterized by a high degree of interindividual variability (e.g., Adelstein et al., 2003; Begault et al., 2005; Lütkenhöner et al., 2002).

The occurrence of individual processing preferences and their influence on participants' performance in audiotactile tasks has been tentatively raised for the first time by Lütkenhöner and coworkers (2002). Considering the remarkable interindividual variability of the physiological responses observed across the whole study, Lütkenhöner and coworkers suggested that it could be the case that audiotactile multisensory integration operates in a flexible manner, and that it is to a certain extent tuned to the subjective perceptual individualities. This evidence would thus extend to the audiotactile interactions the evidence previously reported in the audiovisual domain, showing that there is a high inter-individual variability in the sensory modality that people preferentially rely on (attend to) when identifying stimuli (cf. Giard & Peronnet, 1999. See also: Mollon & Perkins, 1996; Stone, Hunkin, Porrill, Wood, Keeler, Beanland, Port, & Porter, 2001). In their study, Giard and Peronnet presented two objects, each defined by visual attributes alone, auditory attributes alone, or combined congruent attributes. The results showed that some participants were faster at identifying the objects on the basis of vision while others were better at identifying them on the basis of their auditory properties instead, thus leading the authors to categorize the participants as being either 'visually dominant' or 'auditory dominant'. This discrepancy in the preferential modality was observed both in the behavioural (i.e., shorter and more accurate responses) and electrophysiological data (i.e., an enhanced neural activity in the early stage of sensory analysis elicited in the cortex of the non-dominant sensory modality).

An issue which deserves a last remark is the still poorly investigated connections linking early, low-level multisensory interactions and behavioural indices of multisensory processing. Sperdin and coworkers (Sperdin, Cappe, Foxe, & Murray, 2009) have recently investigated this issue more in detail by recording behavioural and EEG data during a simple reaction time task in response to auditory, somatosensory or simultaneous auditory-somatosensory stimuli. The audiotactile stimulus pairing was chosen in accordance with previous evidence, showing that audiotactile stimulations evoke activations of auditory belt areas at relatively early latencies (cf., Caetano & Jousmäki, 2006; Foxe et al., 2000; Gobbelé et al., 2003; Lütkenhöner et al., 2002; Murray et al., 2005). This could reasonably induce to consider that the early effects within low-level cortices induced by the audiotactile stimulation are relatively unaffected by cognitive factors and reflect automatic processes. The study by Sperdin and colleagues elegantly provided good evidence of a strict link between the two orders of measures, with early-latency auditory-somatosensory interactions vary according to the later speed of the reaction times (RTs). By averaging the bimodal trials leading to fast and slow RTs for each experimental condition, the authors found that only trials producing faster RTs required the implication of neural response interactions, namely a facilitation of the reaction times in excess of probability summation. On the contrary, bimodal trials producing slower RTs did not exhibit such violation, but only the typically observed facilitation of mean RTs observed with respect to unisensory condition (cf. Miller, 1982).

Moreover, supra-additive neural response interactions were evident over the 40-84 ms post-stimulus period only when RTs were fast, whereas later effects (at 86-128 ms) were observed independently of RTs speed. Sources estimations localized these early non-linear effects to the posterior temporal cortex extending into the posterior insula, thus replicating previous results (e.g., Foxe et al., 2000, 2002; Fu et al., 2003; Kayser et al., 2005), but discovering that they were evident exclusively in trials producing faster RTs. Even though the individuation of mechanisms mediating the modulation of multisensory integration and RT speed is at the moment still speculative and deserve further investigations, the data reported by Sperdin and colleagues adduce interesting evidence in support of a strict connection between behavioural performance and early and low-level multisensory phenomena. Considering the interest raised by these preliminary data, it would be recommended to conduct future investigations to further explore the behavioural relevance of early and low-level multisensory phenomena.

Chapter 6.

Audiotactile interactions and visual experience

6.1. Introduction

An increasing amount of research has explored the consequences of long term visual deprivation in humans: the experimental evidence strongly suggests that the loss of vision determines perceptual and behavioural changes within the remaining sensory modalities (e.g., Cuevas, Plaza, Rombaux, De Volder, & Renier, 2009; Pascual-Leone & Hamilton, 2001; Theoret, Merabet, & Pascual-Leone, 2004). Reports investigating auditory skills support the notion that visual deprivation results in superior performances of blind as compared to sighted controls in tasks involving higher perceptual processing, such as auditory attention (Hugdahl, Ek, Takio, Rintee, Tuomainen, Haaral, & Hämäläinen, 2004) and memory (Röder, Rösler, & Neville, 2001) and temporal auditory resolution (Weaver & Stevens, 2006). More debated are the performances in intensity discrimination tasks, in which ambiguous results have been reported: contrasting with Starlinger & Niemeyer's results (1981), which documented a comparable performance between early blind and sighted individuals, Gougoux and colleagues (2004) found better pitch discrimination performances in the early blind compared to both sighted and late blind participants.

Moreover, the supposed superior capability of blind to localize sounds (Lessard, Paré, Lepore, & Lassonde, 1998) actually shows specific differences affecting different portions of the space: while blind individuals outperform sighted controls in spatial localizing sounds in peripheral space, no significant differences has been documented in central space (Fieger, Röder, Teder-Sälejärvi, Hillyard, & Neville, 2006; Röder, Teder-Sälejärvi, Sterr, Rösler, Hillyard, & Neville, 1999). These data demonstrate that the superior auditory capabilities showed by blind humans are based on a more strategic use of auditory features of sounds, such as spectral (Doucet, Guillemot Lassonde Gagné Leclerc, & Lepore, 2005) or echo cues (Dufour, Despré, & Candas, 2005), and a more efficient ability to relate proprioceptive cues to auditory spatial information (Lewald, 2002) rather than on supernormal auditory sensibility.

The study of tactile capabilities in blind has focused on measurement of tactile acuity (e.g. Goldreich & Kanics, 2003; Stevens, Foulke, & Patterson, 1996), using a variety of tactile tasks (e.g. Braille characters discrimination, grating orientation and discrimination). Overall, the pattern of results seem to show that no differences in sensory thresholds between blind and sighted subjects occur (Grant, Thiagarajah, & Sathian, 2000 experiment 2 and 3; Pascual Leone & Torres, 1993); when found (Grant et al, 2000 experiment 1; Stevens et al., 1996), these can be due to the increased practice induced by Braille reading or tactile recognition of objects rather than to an increased perceptual sensibility per se (Van Boven, Hamilton, Kauffman, Keenan, & Pascual-Leone, 2000. See also: Kauffman, Theoret, & Pascual-Leone, 2002).

This brief overview, however, makes perceive that, although the research on perceptual consequences of visual deprivation has extensively investigated both tactile and auditory domains (see Bavelier & Neville, 2002; Hötting & Röder, 2009; Röder & Rösler, 2004 for reviews), large part of these studies have focused on each of these modalities separately. However, far less research has been aimed to investigate whether, how, and to what extent, the crosstalk between these two senses is modifies as a consequence of blindness. This evidence is somehow surprising, considering the invaluable theoretical significance of this topic, as well as its value for possible application, for instance, into the technological devices in support to blind people (e.g., Minagawa, Ohnishi, & Sugie, 1996).

Since of interest in the context of the present discussion, we will focus exactly on the studies which have investigated the link between auditory and tactile functions with visual deprivation, by considering separately, similarly to the previous sections, the spatial domain (Section 6.2), attention (Section 6.3), the temporal domain (Section 6.4) and the neural substrates (Section 6.5).

6.2. Spatial aspects

As already extensively described (see Sections 4.3 and 4.4), the peripersonal space constitutes an appropriate frame to operatively evaluate the functional properties of audiotactile interactions. One of the most distinctive properties of the peripersonal space (see Sections 4.3-4.4) is its high plasticity, as it has been demonstrated in both primates (e.g., Iriki, Tanaka, & Iwamura, 1996; Povinelli, Reaux, & Frey, 2009) and humans (Farné, Iriki, & Làdavas, 2005; Holmes, Calvert, & Spence, 2007; Làdavas, 2002. See Làdavas & Serino, 2008; Maravita & Iriki, 2004; Maravita, Spence, & Driver, 2003, for reviews).

For instance, Iriki and colleagues (1996) found that the neuronal activity from the intraparietal sulcus, where somatosensory and visual information is integrated (cf. Duhamel et al., 1998), underwent a dramatic modification after five minutes of tool use. In particular, visual receptive field of bimodal neurons in this area, responding to both somatosensory information from a given body region, and to visual information from the space adjacent to it, expanded to include the entire length of the tool used to retrieve food located beyond animal's reaching space. Interestingly, this assimilation of the tool into the body schema was use-dependent (i.e. being exclusively observed after an active and strategic use of tool, and not after mere grasping by the hand) and limited in time (i.e., fading after some minutes after the end of the training). An analogous phenomenon has been shown in brain-damaged patients, whose visuotactile extinction extended from the space nearby the hand to the space around the tip of a rake after the patients had used a rake to retrieve tokens on a table in the far space (Farnè & Làdavas, 2000).

On the basis of this evidence, Serino and coworkers (Serino, Bassolino, Farnè, & Làdavas, 2007) recently evaluated whether the prolonged experience of cane by blind users could result in an expansion of the peri-hand space representation. In that study, both blind and sighted participants were asked to verbally identify an electrical stimulus (weak) presented in a sequence of strong electrical stimuli on the right index finger. A concurrent task-irrelevant auditory stimulus was presented either near the stimulated hand (i.e., peripersonal space) or on the floor at approximately the same distance of the tip of the cane (i.e., 125 cm; far space), thus far from the hand. Reaction times in response to the electrical target stimuli were compared between the two conditions, before and after 10 min of training consisting in using a cane to reach objects placed on the floor in the dark and in a follow-up session one day after the end of tool use. In order to test the specificity of the potential expansion of the peripersonal space, a control condition, where the blind participants perform the same task by holding a 14-cm-long, weight-matched handle, was run. The results nicely showed that, whereas in sighted people auditory peri-hand space which was limited to around the hand before tool use expanded after tool use and contracted back after a resting period, in blind participants the peri-hand space was immediately expanded when they held the cane and was limited to around the hand when they held a short handle. These results demonstrated that the auditory peri-hand space in sighted people can be dynamically extended by brief training to explore far space, as shown by the speeding up of the RTs to tactile stimuli associated with far sounds after tool use. This phenomenon has been shown to be highly reversible, as demonstrated by the re-emerging advantage in response latencies to target associated to near (vs. far) sounds after one day from the end of tool use. This evidence clearly shows that, similarly to what has been reported for visual receptive fields in monkeys (Farnè & Làdavas, 2000; Iriki et al., 1996), also the auditory peri-hand space is dynamic in nature and can be dramatically modified as a function of the experience. The fact that auditory stimuli coming from distal locations, in proximity with the tip of the cane, were processed as fast as those presented close to the hand support the hypothesis that tool use acted to enlarge the peri-hand space to include distal space surrounding the cane. Furthermore, the long-term and daily experience with a tool, resulted in a persistent elongation of the peri-hand space to include the length of the cane, as shown by faster RTs to tactile stimuli associated to far (vs. near) sounds. This effect, however, was specific for the cane, since, when holding a short handle, blind participants showed faster RTs to tactile stimuli associated with near (vs. far) sounds, just as for sighted participants. It thus seems that long-term experience with the cane induces a remapping of the far space as near space. This is consistent with the speculation that for blind people, the auditory peripersonal space, especially in proximity of the tip of the cane assumes a highly strategic importance during navigation, to detect stimuli along the path and to avoid collisions while walking. Thus, the plastic changes of the extension of the peripersonal space could likely reflect an adaptive facilitation of processes aimed to avoid potentially harmful stimuli in the external environment (cf. Graziano & Cooke, 2006).

The effects of visual deprivation on the construction of a common spatial framework for audiotactile stimulus integration have been more specifically address by Collignon and coworkers (Collignon, Charbonneau, Lassonde, & Lepore, 2009). In particular, the hypothesis that the exclusive use of an anatomically based frame of reference in people blind since birth (see also Sections 11.3 and 11.4) could impair their ability to integrate audiotactile information across postural changes was assessed through the RACE model inequality. To address this aim, early blind, late blind and sighted controls were asked to lateralize auditory, tactile and audiotactile stimuli while keeping their hands uncrossed or crossed over the body midline. The latter condition was used to introduce a conflict between anatomically- and visually-based frames of reference. One of the main findings of this study was that that the crossed-hand posture had an overall detrimental effect on performance in the auditory and tactile tasks, and selectively for late blind and control participants. In the auditory condition, this crossed-hand effect was attributed by the authors to the disruption of the spatial compatibility between the anatomical coordinates of the responding hand and the external sound coordinates (Röder, Kusmierek, Spence, & Schicke, 2007; Experiment 2). In the tactile condition, this is thought to be due to a conflict between somatotopic and external frames of references for coding the tactile stimulus location. According to recent studies, tactile stimuli are automatically remapped into external coordinates beyond an initial somatotopic representation stage (Azañon & Soto-Faraco, 2008; Röder, Rösler, & Spence, 2004; Yamamoto & Kitazawa, 2001). Interestingly, however, crossing the hands did not significantly impair the performance of early blind in tactile stimulus lateralization. This result mirrors the evidence reported in other experiments indicating that the remapping of tactile inputs into external coordinates occurs as a consequence of visual input during development (Röder et al., 2004; Röder, Föcker, Hötting, & Spence, 2008). The congenital or prolonged absence of visual cues, thus, not inducing any automatic external remapping of touch, is likely to have preserved this population from the detrimental effect of a conflict between internal and external coordinates in the crossed-hand posture, as also shown by their faster RTs. This also explains why the only condition where early blind did not outperform the other groups of participants is when auditory stimuli had to be lateralized with the hands crossed, which is indeed the only situation which requires an explicit matching of the external sound location with the anatomical coordinate of the responding hand to efficiently resolve the task (Röder et al., 2007). Not surprisingly, late blind demonstrated an intermediate pattern of performance between the scores obtained in controls and early blind in the detrimental crossed-hand effect and the overall performances the tasks (cf. Röder et al., 2004).

In the bimodal condition, an overall better performance was obtained as compared to unisensory conditions. More specifically, the probability distribution of the response latency to the bimodal target was less than what could be expected from a simple probability summation of the two unimodal conditions in both controls and late blind, and irrespectively of the hand posture. Whereas these two groups seem to process audiotactile signals in an integrative way, in early blind a race model violation with bimodal stimuli was obtained only in uncrossed-posture condition, suggesting audiotactile integration impairment in the crossed-hand posture. Because the auditory and tactile modalities initially code space in different reference systems (audition is external and touch is internal or body-centred), the alignment of the frames of reference for, respectively, distal (i.e., audition) and proximal (i.e., touch) senses is necessary for multisensory integration to be produced. Whereas this process is facilitated in sighted and late blind by the use of a common external spatial reference frame, in both hand postures. However, since early blind do not automatically remap touch into external spatial coordinates (Röder et al., 2004, 2008), have to deal with a conflict induced by a mismatch between auditory and tactile frames of reference, which may prevent efficient multisensory integration in the crossed hand posture.

6.3. Attention

The impact of visual deprivation on auditory and tactile spatial attention has been explored by an increasing amount of investigations (Collignon et al., 2006; Hötting, Röder, & Rösler, 2004; Kujala et al., 1995; Röder et al., 1996; Van Velzen et al., 2006; Weaver and Stevens, 2007).

For example, two EEG studies (Kujala et al., 1995; Röder et al., 1996) have employed tactile and auditory oddball tasks to compare performance of blind and sighted participants. In Röder et al.'s study, participants asked to count rare targets (i.e., tones of different frequency or tactile lines of different orientation) in a sequence of stimuli. A more posterior negativity (at 200 msec in the target condition and at 350 msec in the auditory condition) in response to rare targets ('N2b effect') was observed in blind, as compared to controls. Since the topographies evoked by tactile and auditory oddball targets were comparable, the authors concluded that occipital involvement in blind was not modality-specific.

This speculation has recently received support by an fMRI study by Weaver and Stevens (2007), which employed an oddball paradigm with auditory and tactile stimuli. Interestingly, that study identified several areas in occipital cortex of the early blind, and not in sighted controls, that responded to both auditory and tactile targets (i.e., calcarine sulcus, cuneus, lingual gyrus, and fusiform gyrus). Furthermore, the magnitude of BOLD responses was found to significantly vary as a function of the attentional demand of the task. The areas responding to both auditory and tactile target or distracter stimuli under unimodal conditions altered their responses under conditions of simultaneous presentation of auditory and tactile streams when subjects attended to one stream or the other. The BOLD activity observed in blind during auditory and tactile tasks supports the emergence of complex sensory-attentional interactions in occipital areas selectively after visual deprivation.

Successively, Hötting et al. (2004) compared the performance of sighted and congenitally blind participants in an attentional task, consisting in the random presentation of equally probable tactile stimuli and tones from the left and right side with respect to participants' body midline. In different experimental blocks, participants were asked to attend to stimuli of one sensory modality and one spatial position only to detect rare deviant stimuli within that modality and at that position (i.e., attend to tones on the right side only and respond to rare double tones presented from the right side; cf. Hötting et al., 2003). The data showed that sighted participants had a stronger influence of attended spatial location, with directing of attention to a position in space (i.e., audition or touch, alternatively) within one modality causing an attentional shift also in the other. However, this effect was more pronounced for the task-relevant (vs. task-irrelevant) modality, and later processing stages (at more than 200 msec) being modulated by spatial attention for the task-relevant modality only (see also Section 4.7). In congenitally blind, however, a different pattern of activation emerged. More specifically, differently from sight, blind participants did not show early crossmodal spatial attention effects. Moreover, ERPs after stimuli of the unattended modality, presented at the attended location, were more positive than ERPs to stimuli at the attended location in a later time window (around 200 msec). The results seem to suggest that blind people tend to direct attention on the basis of the sensory modality, and are able to split their attention for touch and audition to different spatial locations, whereas sighted tend to rely on both modality and spatial cues. In blind, no early spatial links between auditory and tactile focuses of attention could be observed, whereas at later stages crossmodal spatial attention effect (enhanced positivity to stimuli at the attended location) may reflect a suppression of task-irrelevant stimuli at the attended location. On the basis of this last piece of evidence, it can be speculated that early blind are more efficient at blocking the processing of an irrelevant modality, thus possibly suggesting a reduction of crossmodal exogenous orienting effects.

Enhanced attentional performance, independent from sensory influence, was also shown in a subsequent study, which compared blind and sighted participants in tactile and auditory selective spatial attention tasks, as well as in a bimodal divided spatial attention task (Collignon et al., 2006). In each attentional task, participants received four pairs of simultaneous auditory and tactile stimuli (i.e., left auditory and tactile stimuli, right auditory and tactile stimuli, left auditory and right tactile stimuli, right auditory and left tactile stimuli). In the auditory selective attention task, subjects had to detect, respectively, right- or left-sided sounds (auditory target), in the tactile selective attention task, respectively, left- or right-sided pulses (tactile target), and in the divided attention task, the combinations of a right-sided sound with a left-sided pulse (bimodal target). Opposite spatial location for auditory and tactile targets in the bimodal divided attention task was made to induce a real shift of attention. Collignon and colleagues reported faster RTs, accompanied by higher- though not significantly- level of accuracy, in early blind compared to sighted subjects in selective auditory and tactile spatial attention tasks as well as in a bimodal divided attention task (see also Kujala et al., 1995). Since the stimuli had been previously subjectively adjusted in intensity and given any absence of between-group differences in the simple reaction task, the faster reaction times observed for blind subjects in selective and divided attention tasks are unlikely related to differences in stimuli salience, nor from faster stimuli detection. The authors conclude that the latencies differences reported in both selective and divided attention tasks reflect a more efficient modulatory role of attention and a lesser sensitivity to the interfering effect of distractors in blind (vs. sighted) (cf. Hötting et al., 2004; Röder et al., 1996). These data seem to be in line with overcompensation of blind in sensory abilities within spared sensory modalities.

However, in a subsequent study, where blind and sighted participants – performing the task in a dark environment - had to shift attention to the left or right hand (as indicated by a preceding auditory cue presented at the start of each trial) in order to detect infrequent tactile targets delivered to this hand, no inter-group differences in the attentional modulations of somatosensory ERPs to tactile stimuli were found (Van Velzen et al., 2006). In both groups, an anterior directing attention negativity (ADAN) during cue-target interval was present, whereas at later processing stages, the posterior late attention negativity (LDAP) was absent. The dissociation between ADAN and LDAP components is in line with the hypothesis that these two components reflect separable attentional control mechanisms that differ in terms of their spatial reference frame. In particular, ADAN in early blind seems to suggest that this component is linked to attentional control processes within a somatotopically defined spatial reference frame. In contrast, the availability of visual spatial representations clearly plays a critical role for the posterior LDAP component, which is likely to reflect processes that guide attentional shifts towards task-relevant locations within visually defined coordinates of external space. The absence of this component also in the sighted sample can be explained by considering that the dark environment prevented sighted people to activate control processes that specify task-relevant external locations of tactile events in visually defined spatial coordinates (Eimer, Van Velze, Forster, & Driver, 2003).

Furthermore, the absence of earlier, or more pronounced attentional modulations of somatosensory ERP waveforms for early blind as compared to sighted participants supports the idea that, under conditions where attention is directed to one hand versus the other, the processes involved in the control of tactile attention shifts and the effects of tactile-spatial attention are very similar in the early blind and in sighted participants.

6.4. Temporal aspects

To our knowledge, one of the few studies investigating auditory and tactile temporal functions in congenitally blind people in comparison with sighted people was carried out by Hötting & Röder (2004). In their study, the authors used a modified version of an audiovisual illusion paradigm, first introduced by Shams and colleagues (see Section 3.3 for a description of the paradigm), in which the target stimuli consisted of tactile pulses presented to the right index finger and the task-irrelevant stimuli by tones. On each trial, one to four tactile stimuli were presented in a rapid sequence, accompanied by one to four task-irrelevant tones. The participants were asked to judge the number of tactile stimuli. If an illusion like the one demonstrated by Shams et al. would extend to the audiotactile domain, then the participants would report more than one perceived tactile stimulus whenever two or more tone were presented simultaneously with the tactile stimuli. Moreover, if the visual deprivation would have induced a higher efficiency in coding the temporal features of tactile information, then the sample formed by blind participants would show a weaker, if any, illusion. The results showed that both groups of participants were influenced by the tones although they were explicitly asked to ignore them. Namely, the mean perceived number of tactile stimuli was enhanced when one tactile stimulus was presented with two, three or, although at a lesser extent, four tones. Interestingly, however, the group of blind participants was significantly less deceived by tones as compared to the group of sighted participants, in particular when the discrepancy between the number of tones and the number of tactile stimuli was large, as in the condition where one tactile stimulus and four tones were presented. The fact that in that study the illusion was observed in both groups of participants is consistent with the modality appropriateness hypothesis, claiming that that perception is dominated by the modality that provides the most reliable information; for example, vision dominates in spatial tasks, haptic in texture perception, and hearing in temporal judgments (Welch & Warren, 1980). In that study, the dimension the participants had to judge was temporal in nature, thus an influence of the best suited modality for the temporal processing (i.e., audition) is in line with earlier findings (Shams et al., 2000). However, the reduced proneness of blind participants to be biased by the number of tones can be attributed, according to the authors, to their more precise tactile discrimination skills (it must be noted that all blind participants were professional Braille readers). This, in turn, would have determined a higher trust of blind (vs. sighted) in their tactile perception and a lower susceptibility to the interference played by task-irrelevant tones. From this point of view, the likelihood for multisensory integration might be lower in the blind than in the sighted because of their enhanced perceptual skills within the tactile and auditory modality. This speculation would be consistent with the inverse efficiency principle of multisensory integration stating that the likelihood of multisensory interactions is higher when the input of the single modalities is weak or of low reliability (Ernst and Banks, 2002; Stein and Meredith, 1993. Although see: Saito, Okada, Honda, Yonekura, & Sadato, 2006).

6.5. Neural substrates

Studies on both animals (Carriere, Royal, Perrault, Morrison, Vaughan, Stein, & Wallace, 2007; Rauschecker, 1995; Wallace, Perrault, Hairston, & Stein, 2004) and humans (Putzar, Goerendt, Lange, Rösler, & Röder, 2007) have largely demonstrated that the sensory experience received during postnatal life plays an important role in the development of sensory circuits in the cortex.

This conjecture is well supported by studies on cats that have been deprived of vision by means of binocular lid suture after birth (Rauschecker, 1995; Rauschecker & Korte, 1993) or that have been reared in total darkness (Carriere et al., 2007; Wallace et al., 2004). These procedures allow testing how the absence of visual inputs since birth alters the operation of the other sensory modalities, as well as the interplay between them, providing important insights into the influence of early visual inputs on the maturation of multisensory systems in the brain. Interestingly, the recording of neuronal responses in the superior colliculus in these animals showed that, although the neurons were responsive to visual, auditory and somatosensory inputs presented in isolation, no evidence of response enhancement to multisensory (vs. unisensory) stimuli was reported, not even for combinations of auditory-somatosensory stimuli. These results showed that visual deprivation had a dramatic impact on the integrative capabilities of multisensory neurons in areas traditionally known to underlie multisensory integration, such as anterior ectosylvian sulcus (AES) or temporo-parietal cortex (Carriere et al., 2007). Moreover, a sub-region of AES, an anterior ectosylvian visual area (AEV), which have purely visual responses in normal cats has been shown to respond to auditory and somatosensory inputs after visual deprivation (Rauschecker & Korte, 1993). It appears, therefore, that a region that normally represents visual activity can become driven by auditory or somatosensory activity of visual deprivation. These pioneering observations by Rauschecker in cats have been, however, largely confirmed by subsequent human neuroimaging studies, showing massive reorganizational processes in the occipital lobe in early-onset blind, which becomes involved in both auditory (e.g., Collignon, Lassonde, Lepore, Bastien, & Veraart, 2007;

De Volder, Toyama, Kimura, Kiyosawa, Nakano, Vanlierde, Wanet-Defalque, Mishina, Oda, Ishiwata, & Senda, 2001; Gougoux, Zatorre, Lassonde, Voss, & Lepore, 2005; Kujala, Palva, Salonen, Alku, Huotilainen, Järvinen, & Näätänen, 2005; Weeks, Horwitz, Aziz-Sultan, Tian, Wessinger, Cohen, Hallett, & Rauschecker, 2000) and tactile (e.g., Hamilton, Keenan, Catala, & Pascual-Leone, 2000; Melzer, Morgan, Pickens, Price, Wall, & Ebner, 2001; Merabet, Hamilton, Schlaug, Swisher, Kiriakopoulos, Pitskel, Kauffman, & Pascual-Leone, 2008; Ptito, Fumal, de Noordhout, Schoenen, & Kupers, 2008; Sadato, Okada, Kubota, Yonekura, 2004; Stilla, Hanna, Hu, Mariola, Deshpande, Sathian, & 2008) Tasks (see Amedi, Merabet, Bermpohl & Pascual-Leone, 2005; Sathian & Zangaladze, 2002; Théoret, Merabet, & Pascual-Leone, 2004 for reviews). It is likely that these mechanisms are probably due to the unmasking of already existing long-range cortico-cortical connections between early sensory cortices triggered by the lack of visual stimulation (Pascual-Leone & Hamilton, 2001).

However, somehow surprisingly, the changes that neural mechanism involved in intermodal plasticity in cerebral cortex undergo as a consequence of visual deprivation has been very rarely explored simultaneously in both tactile and auditory modalities (Hötting et al., 2004: Kujala, Alho, Kekoni, Hämäläinen, Reinikainen, Salonen, Standertskjöld-Nordenstam, & Näätänen, 1995; Röder, Rösler, Hennighausen, & Näcker, 1996; Van der Lubbe, Van Mierlo, & Postma, 2009; Weaver & Stevens, 2007).

Very recently, however, an EEG study was applied to compare the capability of sighted and blind people in discriminating the temporal duration of auditory and tactile stimuli (Van der Lubbe et al., 2009). Separate tactile and auditory duration discrimination tasks were conducted, with participants instructed to recognize targets of 100 or 175 ms, respectively, presented to the left o r the right. In order to test crossmodal exogenous orienting effects (Spence, 2002) and the supposed more efficient blocking of irrelevant stimuli in the early blind a compared to sighted (cf. Hötting & Röder, 2004), parts of the targets were preceded by to-be-ignored auditory cues of 100 msec to the same or different side as the targets (i.e., valid or invalid trials). In other subsets of trials, targets were presented in absence of auditory cues, or only auditory cues were presented. The results showed that blind people have superior duration discrimination abilities as compared to sighted controls, as shown by both speed and accuracy of their responses.

Moreover, the electrophysiological data suggest that their outperformance correlates with an enlarged posterior negativity for the blind (vs. sighted), in both tactile and auditory tasks, which was most significant from 320-340 ms (in the auditory task) and around 300 ms (in the tactile task). The source location analysis showed a temporal source for controls and an occipital source for blind, especially in the right hemisphere (cf. Weeks et al., 2000). Interestingly, in both conditions (i.e., auditory or tactile targets), increased posterior activity in the blind as compared to controls appears to be related to improved auditory duration discrimination. Furthermore, the examination of individual source locations along the anterior-posterior axis in the group of blind participants showed a significant correlation between the estimated source locations for both modalities. No reduced orienting effects induced by crossmodal cues were observed in blind, thus suggesting that changes in information processing in the early blind participants are not due to modifications in structures relevant for attentional orienting and alertness, but to a more advanced processing level. Taken together, these findings support the hypothesis that the enhanced performance and the pattern of activations observed in blind could reflect a modification at a later processing level instead of changes in early perceptual processes taken over by occipital cortex. Furthermore, these data are in line with a supramodal, rather than modality-specific, temporal perception process which involves occipital areas in blind.

These results add to the above mentioned evidence, demonstrating that the absence of visual afferences during development induces dramatic changes in areas engaged in visual processing. Until recently, the consequences of re-afferentation of visual inputs after a period of visual deprivation had never been explored. Testing patients born with dense binocular cataracts – which prevent from any visual stimulation – and successively (between 5th and 24th month of life) operated for its removal offered, however, the unique and intriguing possibility to test whether vision in postnatal period is necessary for multisensory function to emerge (Putzar et al., 2007). Although these patients showed a recovery of basic visual functions, auditory-visual interactions were reduced or absent even after 14 years from the operation. For instance, they showed less interference in an audio-visual capture paradigm and were not able to benefit from lip-reading in audio-visual speech perception, thus providing strong support to the hypothesis that normal vision and possibly multisensory inputs during early development is critical for the full deployment of cross-modal functions.

PART II: Experimental Studies

Chapter 7.

The sensory dominance between touch and audition

7.1. Introduction

One of the issues that has been widely explored in the field of multisensory integration research is the postulated asymmetric nature of the relationship between the senses (i.e., sensory dominance), which typically manifests itself under conditions of perceptual discrepancy (i.e., when the information provided by the different senses are incongruent; e.g., Welch & Warren, 1980).

One particularly impressive demonstration of the prevalence of one sensory modality over another has been provided by Colavita. In his seminal studies (Colavita, 1974; Colavita, Tomko & Weisberg, 1976¸ Colavita & Weisberg, 1979), participants were presented with auditory and visual stimuli and instructed to press rapidly one of two response keys depending on the modality in which the target was presented (i.e., speeded discrimination task). However, in Colavita’s earliest studies, the participants were unaware that bimodal audiovisual trials were also presented during the experimental session. The surprising result to emerge from these early studies was that, when both stimuli were presented, the participants tended to press the key associated with the visual stimulus significantly more frequently than the key associated with the auditory stimulus. The tendency for participants to preferentially report the visual component on the bimodal audiovisual trials in a speeded discrimination task, subsequently known as the “Colavita effect” (see Koppen & Spence, 2007a, for an operational definition), has been widely explored and replicated extensively for the audiovisual sensory pairing (Koppen & Spence, 2007a, b, c; Koppen, Alsius, & Spence, 2008; Sinnett, Soto-Faraco, & Spence, 2008; Sinnett, Spence, & Soto-Faraco, 2007).

Recently, Hartcher O’Brien, Gallace, Krings, Koppen, and Spence (2008) have shown that the Colavita effect also occurs between the vision and touch. Once again, a strong visual dominance effect was reported, with participants failing to respond to the tactile component of the bimodal visuotactile pairings of stimuli significantly more often than they failed to respond to the visual component (see also Hecht & Reiner, 2009, for similar results). Somewhat surprisingly, when the same paradigm was used with auditory and tactile stimuli recently, no Colavita effect was observed, thus suggesting the absence of any systematic pattern of dominance between touch and audition (Hecht & Reiner, 2009). These results add to previous studies on the interactions occurring between touch and audition, which turned out to be inconsistent in proving a clear pattern of sensory dominance between these two modalities (e.g., Bresciani & Ernst, 2005; Caclin, Soto-Faraco, Kingstone, & Spence, 2002; Soto-Faraco, Spence, & Kingstone, 2004).

A few studies have demonstrated that tactile cues can significantly affect the processing of simultaneously-presented auditory stimuli, resulting in a biasing of the perceived localization of auditory stimuli. For instance, Caclin and her colleagues (2002) demonstrated that auditory localization can be affected by the synchronous presentation of tactile stimuli (i.e., participants tended to mislocalize the perceived position of auditory stimuli toward the position of simultaneously-presented tactile stimuli), thus demonstrating the tactile ‘capture’ of audition.

On the other hand, other evidence supports the prevalence of audition over touch. In one perceptual illusion, known as the parchment skin illusion, participants rub their palms together in a back-and-forth motion and exposed to the recorded sound generated by performing this action (Jousmäki & Hari, 1998). The authors showed that manipulating the frequency of the sound that was presented modulated the perceived roughness/smoothness of the skin surface (crucially, no change in tactile sensitivity was reported, cf. Guest, Catmur, Lloyd, & Spence, 2002; see also Suzuki, Gyoba, & Sakamoto, 2008).

7.2. Experiment 1. The audiotactile Colavita effect in the frontal space

To date, however, the investigation of interactions taking place between hearing and touch has failed to provide any evidence of an audiotactile Colavita effect (cf. Hecht & Reiner, 2009). As in a typical study of the Colavita effect, the participants in that study had to make speeded detection responses to unimodal auditory, unimodal tactile, or bimodal audiotactile stimuli. The participants showed no preference for responding to either the auditory or the tactile stimuli on the bimodal target trials, thus suggesting the absence of any clear pattern of dominance between targets presented in these two modalities (Hecht & Reiner, 2009). It thus seems that auditory and tactile sensory inputs are more evenly matched, thus giving rise to an increase of the detection of each component. By extending previous tentative observations (Hecht & Reiner, 2009), in the present study it has been tested whether the null audiotactile Colavita effect is robust enough to resist the manipulation of either the physical features of the stimuli involved (Experiment 1) and/or the region of space from where the stimuli are presented (Experiment 2 and Experiment 3). Whereas in Experiment 1 the stimuli were presented from a single location in the frontal space (Experiment 1), in Experiments 2 and 3 the stimuli were presented from multiple locations (i.e., the tactile stimuli to the surface of the hands or of the cheeks; the auditory stimuli from headphones or frontal loudspeakers; Experiment 2). In Experiment 3, the stimuli were presented in the rear space (i.e., the tactile stimuli on the participants' neck; the auditory stimuli from headphones or from loudspeakers behind the participants' head. See Methods section for further details).

It is well-known that auditory stimuli of different complexity (i.e., pure tones vs. white noise bursts) can induce distinct neural responses in human (Hall, Edmondson-Jones, & Fridriksson, 2006; Kitagawa & Spence, 2006; Schönwiesner, Rübsamen, & von Cramon, 2005; Schreiner, Read, & Sutter, 2000; Wessinger, VanMeter, Tian, Van Lare, Peckar, & Rauschecker, 2001), as well as qualitatively different behavioural responses – at least under certain conditions – in audiotactile tasks (see Farnè & Làdavas, 2002; and Kitagawa, Zampini, & Spence, 2005, for evidence from neurologically-impaired patients and intact people, respectively). In Experiment 1, we tested the prediction that more complex auditory stimuli would interact more with tactile stimuli than pure tones, thus possibly resulting in a stronger binding of the auditory and tactile components of the bimodal targets. Such a pattern of results would parallel the extant evidence suggesting that tactile stimuli interact to a greater extent with complex auditory stimuli than with pure tones in the peripersonal space lying close to the hand (see also Fu, Johnston, Shah, Arnold, Smiley, Hackett, Garraghty, & Schroeder, 2003). Moreover, we introduced an additional condition, increasing the amplitude of the auditory stimuli. This manipulation has already been proved to be effective in modulating the crossmodal interactions between audition and touch in other studies (Bresciani & Ernst, 2007).

7.2.1. Method

Participants. Forty-five participants (24 females; mean age of 24 years; range from 18 to 34 years; 5 left-handed) took part in this experiment. The participants were randomly assigned to one of three groups: Group 1 (22 participants; 11 women; mean age of 25 years; range: 18-34 years; 19 right-handed), Group 2 (14 participants; 8 women; mean age of 24 years; 20-31 years; 13 right-handed), Group 3 (9 participants; 5 women; mean age of 24 years; 21-30 years; 8 right-handed). The experiment took approximately 30 minutes to complete.

Apparatus and stimuli. The participants sat in front of a table with the palm of their dominant hand resting on a foam cube positioned centrally on a table approximately 60 cm in front of them. An Oticon-A (100 Ohm, Oticon Inc., Somerset, NJ) bone conduction vibrator, with a vibrating surface 1.6 cm wide x 2.4 cm long, was secured in order to be in constant contact with the participant’s fingertip. One loudspeaker (Creative, Cambridge Soundwork, MA) was positioned directly behind the vibrotactile stimulator. In contrast to the car horn sound used in Hecht and Reiner’s (2009) study, the auditory stimuli used here consisted of the presentation of one of three sounds depending on the group: One group of participants was presented with pure tones (70dB(A) as measured from the participants’ head position); A second group of participants was presented with 70dB(A) white noise bursts; The third group was presented with 80dB(A) pure tones. It must be noted that a difference in intensity of 7 dB has been proved to be effective in modulating the magnitude of the interactions occurring between audition and touch in another study (see Section 9.3). The vibrotactile stimuli consisted of the activation of the bone-conduction vibrator that was driven by a pure tone generator. The auditory and tactile stimuli were both presented for 50 ms. White noise was presented at 60 dB(A) via headphones (Cordless Stereo Headphone SBC HC075, Philips) worn by the participant throughout the experiment in order to mask any noise made by the participant or elicited by the operation of the vibrotactile stimulator. Two footpedals were placed under the table in order to collect the participants' responses. The delivery of the stimuli and the recording of participants' responses were controlled by E-prime (Psychology Software Tools Inc.; www.pstnet.com/eprime).

Design. The participants were presented with 6 blocks of 100 trials, each consisting of 40 unimodal auditory trials, 40 unimodal tactile trials, and 20 bimodal audiotactile trials. These stimulus probabilities were chosen to match those used in previous studies (e.g., Colavita, 1974; Hartcher O'Brien et al., 2008; Koppen & Spence, 2007a). The order of presentation of the different trial types was randomized within each block of trials. A block of 30 practice trials was presented at the start of the experimental session in order to familiarize the participants with the task.

Procedure. The experiment was completed in a completely dark testing booth. On each trial, the participants were presented with a unimodal (i.e., auditory or tactile), or bimodal (i.e., audiotactile) targets. The targets were presented at the beginning of each trial, followed by a 1,450 ms response interval. The next trial began automatically at the end of the preceding trial. The participants had to release one footpedal (either the left or right) whenever they detected an auditory target and the other footpedal whenever they detected a tactile target. The stimulus-response footpedal mapping was counterbalanced across participants. The participants were instructed to release both footpedals whenever a bimodal target was presented (no specific instructions were given as to whether they should press the two response keys simultaneously or not). On each trial, the participants could make more than one response within the 1,450 ms response interval provided.

The participants were instructed to respond as accurately and rapidly as possible. No feedback about the correctness of a participant's responses was provided.

7.2.2. Results

Participants failed to respond on <3% of the trials, and these trials were not included in the subsequent data analysis.

Error data. A repeated measures analysis of variance (ANOVA) was performed on the error data with the within-participant factor of Trial Type (Unimodal auditory, Unimodal tactile, or Bimodal) and the between-participants factor of Sound Type (70dB Pure tone, 70dB White noise, 80dB Pure tone). Note that Bonferroni-corrected t-tests were used for all post-hoc comparisons reported in this study. The analysis revealed a significant main effect of Trial Type, F(2,84)=4.82; p=.02, with participants responding less accurately on the bimodal target trials (M=7.0% errors) than on either the unimodal auditory (M=3.4% errors; t(44)=2.43, p=.02) or unimodal tactile target trials (M=3.7% errors; t(44)=2.63, p=.01), but no less accurately on unimodal tactile than on unimodal auditory target trials (t(44)<1, n.s.). Neither the main effect of Sound Type, F(2,42)=1.05; n.s., nor the interaction between Trial Type and Sound Type, F(4,84)=1.58; n.s., reached significance.

We analysed the data from those bimodal trials in which the participants failed to report one of the two targets that had been presented, using a repeated measures ANOVA with the within-participants factors of Response (auditory-only vs. tactile-only) and the between-participants factor of Sound Type. Participants made approximately the same number of auditory-only and tactile-only responses (M=2.7% vs. 4.4%), and hence the main effect of response was not significant, F(1,42)=1.87; p=.18 (cf. Hecht & Reiner, 2009). The effect of Sound Type, F(2,42)=1.79; p=.18, and the interaction between the factors, F(2,42)<1; n.s., also failed to reach significance[1].

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[1] Even though non-significant effects (e.g., p>.05) are commonly considered as a proofs of absence of any effects, this conclusion is improper. Indeed, if the experimental results are non-significant, the null hypothesis fails to be rejected, but one can not draw the conclusion that the data are in support of the null hypothesis (“no evidence of effect is not proof of no effect”; Rouanet, 1996, p. 149. See also Lecoutre & Derzko, 2001). In Experiment, the absence of any – significant – evidence in support of an audiotactile Colavita effect prevents us from drawing the conclusion that no difference, even thought a *small* difference (cf. Rouanet, 1996) between the amount of the auditory-only and the tactile-only responses is present. Differently from other fields, such as physics and pharmacology, the statistical techniques aimed to asserting the smallness of effects have not so far been extensively used in experimental psychology. However, as pointed out by Gallistel (2009), the demonstration of null effects is in this field as important as the claims that some

RT data. The RT data from those trials in which the participants responded correctly were analysed using an ANOVA with the within-participants factors of Target Modality (auditory or tactile) and Target Type (unimodal or bimodal) and the between-participants factor of Sound Type. This analysis revealed a significant main effect of Target Type, F(1,42)=115.19; p<.001, attributable to participants responding significantly more rapidly on the unimodal (M=541 ms) than on the bimodal target trials (M=620 ms). The slowing of participants` responses on the bimodal trials replicates previous results (Hartcher O'Brien et al., 2008; Hecht & Reiner, 2009; Koppen & Spence, 2007a), and has been attributed to the costs associated with participants having to make two responses rather than just one (Sinnett et al., 2007). There was a significant interaction between Target Type and Sound Type, F(2,42)=4.24; p=.02, with a more pronounced difference in performance between the unimodal and bimodal target trials for the participants in the 70dB white noise condition than in either the 70dB pure tone or 80dB pure tone groups (110, 64, and 71 ms, respectively). There was no main effect of Target Modality, F(1,42)<1; n.s. In fact, the auditory and

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manipulations are effective in determining significant modulations of the effects investigated (e.g. Zampini, Brown, Shore, Maravita, Röder, & Spence, 2005).

In Experiment 1, all experimental manipulations introduced turned out to be ineffective in modulating the – null – audiotactile Colavita effect. In order to assess whether the present pattern of results can be considered as a support of a real equivalence between the two measures in exam, we performed an additional statistical analysis. According to the logic of the Null Hypothesis Significance Testing, the hypothesis to be demonstrated should be the alternative hypothesis. By contrast, the test procedure used here is based on the following assumptions (cf. Lecoutre & Derzko, 2001):

$\lambda = | \delta_{effec}|$

- H_1: $\lambda \subset [0, \Lambda)$ (i.e., "smallness of effect" hypothesis);
- H_0: $\lambda \subseteq [\Lambda, \infty)$ (i.e., to be rejected hypothesis)

where $\lambda = [0, \Lambda]$ defines a directional quantity used to specify the "smallness confidence interval" (i.e., SCI) for δ_{effect} between the compared. It is assumed that an SCI λ falling within the equivalence region $[0, \Lambda]$ can be considered as a statistical evidence in support of an "equivalence" between the two measures put in comparison. Otherwise, the effect size can not be considered as negligible.

We applied the procedure put forward by Lecoutre & Derzko (2009) to the error rate data reported in the bimodal trials. We chose the value of $\Lambda = 0.1$ as maximum interval bound, a value considered by Cohen as the half of a small effect (1988).

100(1-α)% smallness confidence interval for λ is calculated as:

$$\left[0, L\left(1+\frac{t_{v2;1-\alpha}}{\sqrt{v1F}}\right)\right]$$

L = observed Eta Squares; *v1* and *v2* = degrees of freedom of the F ratio.

We obtain the following values. For the Effect Modality (L = .043 and F[1,42] = 1.87, $t_{42;0.99} = 2.698$), the 99% SCI interval is [0, .0949]. For the Effect Sound Type (L = .79 and F[2,42] = 1.79, $t_{42;0.99} = 2.698$), the SCI is [0, 0.1484]. For the interaction Modality X Sound Type (L = .017 and F[2,42] =.37, $t_{42;0.99} = 2.698$), the SCI is [0, 0.0510]. From the results of this analysis it can be inferred that the SCI intervals relative to the effect of Modality and of the interaction Modality X Sound Type (of particular interest in the present experiment) are included in the region of equivalence. Thus, the hypothesis that the effect size of the factor Modality (Auditory-only vs. Tactile-only responses) and of the interaction Modality X Sound Type are greater than 0.1 can be rejected (p<.01).

tactile targets RTs were found to be identical (both M = 581 ms). None of the other terms in this analysis were significant.

	Pure Tone 70dB	White Noise 70dB	Pure Tone 80dB
Error rates (%)			
Unimodal Tactile	3.13 (0.5)	4.55 (2.2)	3.80 (1.0)
Unimodal Auditory	3.75 (1.3)	3.24 (0.5)	2.96 (0.5)
Bimodal			
Tactile-Only responses	3.30 (0.7)	7.18 (3.5)	2.8 (1.2)
Auditory-Only responses	2.31 (0.8)	3.87 (1.7)	1.7 (0.5)
Colavita effect	n.s.	n.s.	n.s.
RTs (ms)			
Unimodal Tactile	561 (26)	500 (24)	546 (43)
Unimodal Auditory	564 (30)	500 (29)	558 (41)
Bimodal			
Tactile responses	626 (28)	614 (33)	628 (48)
Auditory responses	626 (29)	606 (30)	618 (48)

Table 1. Mean error rates and reaction times (RTs) for the unimodal auditory, unimodal tactile and bimodal target stimuli in Experiment 1.

Previous studies have explored people’s performance in dual-tasks in which they had to make two responses to a feature of a single target. They found that people tended over time to select and initiate the two responses as a single responding act (e.g., Fagot & Pashler, 1992). In order to highlight any possible response coupling in the present study, an additional analysis was conducted on RT of participants’ correct responses to bimodal targets (cf. Koppen & Spence, 2007a). Thus, we calculated the correlation between the RTs to the auditory and the tactile component on each bimodal trial. The results (see Table 2 and Figure 1) revealed strong correlations between the RTs to the two components of participants' responses on the bimodal target trials. These results therefore support the hypothesis that on the majority of trials the participants tended to couple their responses to the auditory and the tactile components.

RT correlation values	**Experiment 1**		
	Group 1	**Group 2**	**Group 3**
	r(2441) =.895*	r(1445) = .827*	r(1020) = .900*

* indicates p < .01.

Table 2. Values of the correlations between the response latencies reported in Experiment 1.

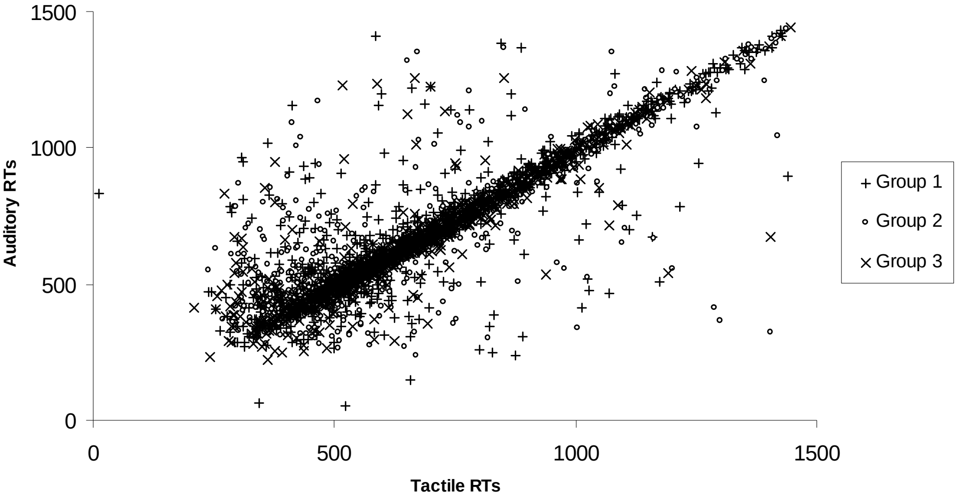

Figure 1. Scatterplots of the responses to the auditory and tactile components of the bimodal targets, for those trials in which participants made a correct response (Experiment 1). Each marker represents an individual trial from one participant.

The results of the analysis of the accuracy data from Experiment 1 show that participants did not respond preferentially to either the auditory or tactile stimuli when both were presented simultaneously. The null audiotactile Colavita effect has been replicated across a variety of different experimental conditions, and it has shown to be resistant to the manipulation of the complexity (i.e., pure tone or white noise) and intensity (70 or 80 dB(A)) of the auditory stimuli.

Thus, the results of Experiment 1 confirms that no Colavita dominance effect occurs between simultaneously-presented auditory and tactile stimuli when the stimuli are presented from a single location in frontal space, thus replicating the recent results reported by Hecht and Reiner (2009).

7.3. Experiment 2. The audiotactile Colavita effect: The effect of spatial factors and the part of body stimulated

Two major implications emerge from the results of Experiment 1: On the one hand, they suggest that the incoming sensory signals provided by the auditory and tactile channels are weakly competing (or competing in an evenly manner), at least as tested in the Colavita paradigm. On the other hand, one might argue that the Colavita effect can be uniquely considered as an expression of the dominance (or prepotency) that visual stimuli exert over stimuli presented in other sensory modalities (i.e., audition and touch), and can thus be considered as being a uniquely visual form of dominance effect (cf. Hecht & Reiner, 2009). It should be noted, however, that in the Experiment 1 the potential occurrence of a Colavita effect between touch and hearing involved the presentation of auditory and tactile stimuli from a central location in the space directly in front of the participant (cf. Hecht & Reiner, 2009). The tactile stimuli were presented on the fingertip of one hand and the auditory stimuli from loudspeaker(s) located within 60 cm of the participants in frontal space. In the next Experiment, we investigated whether the apparent sensory balance between audition and touch could be disrupted by presenting the auditory and tactile stimuli from different locations. In the Experiment 2, two different spatial locations were used to present the stimuli, both in touch (i.e., cheeks or hands) and in audition (i.e., external loudspeakers or headphones).

There are evidence suggesting that the interactions occurring between touch and audition can be asymmetrical in nature when different parts of the body are put in comparison (e.g., hands vs. face: Fu et al., 2003; Menning, Ackermann, Hertrich, & Mathiak, 2005; hands vs. feet: Beauchamp, Yasar, Frye, & Ro, 2008; Kayser et al., 2005). Even though evidence concerning the cortical organization of the somatosensory cortex for the different parts of the face are equivocal (Eickhoff, Grefkes, Fink, & Zilles, 2008; Iannetti, Porro, Pantano, Romanelli, Galeotti, & Cruccu, 2003), it is well-known that the representation of the face is of great importance in terms of the cerebral representation of the body (Nguyen, Tran, Hoshiyama, Inui, & Kakigi, 2004; Sereno & Huang, 2006; Weinstein, 1968; see also Menning, Ackermann, Hertrich, & Mathiak, 2005). Moreover, the evidence showing greater cortical convergence in the auditory cortex for somatosensory inputs originating from the face (vs. hand) surface (Fu et al., 2003) further supports the assumption that the stimuli presented close to the face are treated by the brain as being particularly relevant (e.g., Làdavas, Zeloni, & Farné, 1998; Serino, Padiglioni, Haggard, & Làdavas, 2008a; Serino, Pizzoferrato, & Làdavas, 2008b; Tipper, Phillips, Dancer, Lloyd, Howard, & McGlone, 2001; Tsakiris, 2008; see also Blakemore, Bristow, Bird, Frith, & Ward, 2005). It might thus be expected that the stimulation of the face could possibly induce a facilitatory effect (in terms of accuracy and response latencies) in the processing of the tactile stimuli as compared to when the stimuli are presented to the hand.

In a Colavita task, where the participants typically have to respond to the modality of the targets (though see Koppen et al., 2008), an interference effect is commonly shown, with participants responding more slowly in the bimodal (vs. unimodal) trials. This contrasts with the multisensory facilitation effect observed in speeded detection tasks, where no such discrimination is required (Sinnett, Soto-Faraco, & Spence, 2008). Thus, if we assume that the spatial manipulation introduced here would make the auditory and the tactile stimuli to compete for central processing capacity, then it can be inferred that the outcomes emerging from our study would be analogous to the results obtained in previous studies of the Colavita effect. One might expect that the number of errors in the bimodal trials would be higher than in the unimodal trials (where no such competition occurs). Crucially, in the bimodal trials, participants would respond preferentially to the dominant sensory modality, failing to report the stimulus presented in the other sensory modality on a certain proportion of the trials, thus giving rise (for the first time) to an audiotactile Colavita effect.

If, on the other hand, audiotactile interactions reflect a more evenly balanced match between the senses, the simultaneous presentation of stimuli in both sensory modalities (note that in the typical study of the Colavita effect, the sensory components in bimodal trials are presented simultaneously; though see Koppen & Spence, 2007d) should facilitate their detection (i.e., with the number of errors reported in the bimodal trials not significantly differing from the errors reported in unimodal trials).

Regarding the spatial manipulation introduced here, the facilitation resulting from the simultaneous presentation of signals in both sensory modalities should be increased when they are presented in close spatial proximity (cf. Tajadura-Jiménez, Kitagawa, Väljamäe, Zampini, Murray, & Spence, 2009). In one of his audiovisual studies, Colavita (1982) advanced an alternative conjecture regarding the modulatory effect of spatial factors on the visual dominance effect that now bears his name. The first investigations conducted by Colavita on the visual dominance effect that now bears his name were conducted with the visual and auditory stimuli presented from different positions in frontal space (Colavita, Tomko, & Weisberg, 1976; Colavita & Weisberg, 1979). In one of the studies conducted later, the auditory stimuli were presented via headphones, whereas the visual stimuli were presented from a central position in frontal space. Colavita hypothesized that the use of the headphones might possibly have served to free the participants from directing the attention towards two locations in space (i.e., representing the sound and light source), thus resulting in a reduction or even the abolishment of the visual dominance effect. The results of Colavita's study (1982) showed that the use of headphones resulted in a reduced visual dominance effect, which was nevertheless observable and considerable, with participants failing to respond to the sound on 85% of the bimodal trials. Even though the two proposed accounts differ in terms of the key underlying mechanism (i.e., spatial in our hypothesis and attentional in the hypothesis forwarded by Colavita), both are rooted in the assumption that the facilitation of the sensory processing should reduce the dominance among the components.

7.3.1. Method

Participants. Ten participants (8 females; mean age of 25 years; range from 20 to 33 years; one left-handed) took part in this experiment. Three participants had taken part in Experiment 1 as well. The experiment took approximately 60 minutes to complete.

Apparatus and stimuli. The experimental situation was similar to that used in Experiment 1 except for the following differences. The participants rested their hands on the table 40 cm to either side of their body midline. Two bone conduction vibrators were used to present the tactile stimuli to the hands (i.e., the right stimulator to the to the right index finger; the left to the left index finger). Two loudspeaker cones were positioned directly behind the vibrotactile stimulators. Identical vibrotactile stimulators were attached to the participant's cheeks. The auditory stimuli (i.e., 50 ms pure tones at 80dB(A) as measured from the participant's head position) could be delivered either from the loudspeakers or via headphones worn by the participant, and they originated from either the right (A_R) or left (A_L) side. The vibrotactile were presented on the right (T_R) or left (T_L). White noise was presented at 70 dB(A) from a central loudspeaker throughout the experiment in order to mask any noise made by the participant or elicited by the operation of the vibrotactile stimulators.

Design and procedure. The participants were presented with four blocks of trials, each consisting of 120 trials. A 2x2 factorial design was used, with auditory location (i.e., loudspeakers vs. headphones) and tactually-stimulated body-part (i.e., face vs. hand) as the factors. The order in which the four blocks (i.e., loudspeakers/face, loudspeaker/hand, headphones/face, headphones/face) were conducted was counterbalanced across participants. Auditory and tactile stimuli could either be presented simultaneously (AT multisensory stimulus pair) or as unimodal (A or T) target events. A total of eight different stimulus conditions were presented in a random order: T_L, T_R, A_L, A_R, A_LT_L, A_RT_R, A_RT_L, A_LT_R. Each unimodal target condition (i.e., T_L, T_R, A_L, A_T)

consisted of 18 trials, whereas each bimodal target condition (i.e., A_LT_L, A_RT_R, A_RT_L, A_LT_R) consisted of 12 trials. In addition, participants performed 28 (i.e., 6 unimodal auditory, 6 unimodal tactile, 16 bimodal audiotactile) practice trials before each block of experimental trials. The experiment took about 60 minutes to complete. The procedure was exactly the same as in Experiment 1.

7.3.2. Results

The participants failed to make any response on 2% of the trials, and these trials were not included in the subsequent data analysis.

Error data: Since preliminary t-test comparisons conducted on the data confirmed that no statistical differences were present between T_L and T_R, A_L and A_R, A_LT_L and A_RT_R, and A_RT_L and A_LT_R trials, the accuracy scores reported for these stimulus pairings were collapsed. A repeated measures analysis of variance (ANOVA) was then performed on the resulting error data with the within-participant factors of Body-Part (Hand vs. Face), Sound Location (Loudspeakers vs. Headphones) and Trial Type (Unimodal Auditory, Unimodal Tactile, Bimodal Same Side, and Bimodal Different Sides). The analysis failed to reveal any significant terms.

Next, we analysed the data from the bimodal error trials (i.e., from those bimodal trials in which the participants failed to report one of the two target modalities that had been presented; 7.6% of the trials), using a repeated measures ANOVA with the factors of Body-Part (Hand vs. Face), Sound Location (Loudspeaker vs. Headphones), Side (Same vs. Different), and Modality (Tactile-only vs. Auditory-only response). The analysis revealed a significant main effect of Modality (i.e., Colavita effect), F(1,9)=6.67; p=.03, with participants making significantly more auditory-only than tactile-only responses (M= 5.2% vs. 2.4%, respectively). The main effect of Side also reached significance, F(1,9)=16.71; p=.003, with participants making more errors when the stimuli were presented from the same side than when they were presented from different sides on the bimodal target trials (M=4.7% vs. 2.8%, respectively). There was a borderline-significant interaction between Body-Part and Side (F(1,9)=5.10; p=.05), with a more pronounced difference between same and different side stimulation when the face rather than the hand was tactually stimulated (mean difference of 2.6% and 1.3%, respectively; see Figure 2).

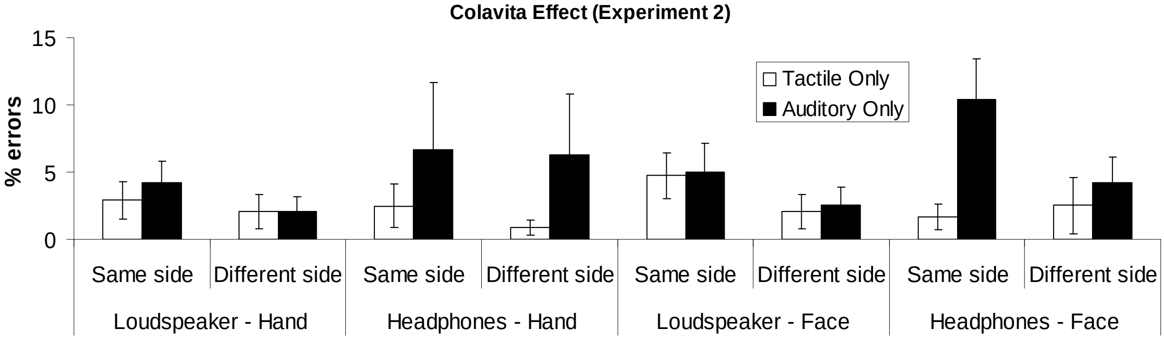

Figure 2. Percentages of errors in the bimodal trials for each of the four spatial conditions tested in Experiment 2.

RT data: The RT data from those trials in which the participants responded correctly were analysed using an ANOVA with the within-participants factors of Body-Part (Hand vs. Face), Sound Location (Loudspeaker vs. Headphones), Trial Type (Unimodal vs. Same Side vs. Different Sides) and Modality (Tactile vs. Auditory). The analysis did not reveal any significant terms. In order to determine whether there was any evidence of response coupling in the bimodal RT data, we ran an additional data analysis designed to look for a correlation between participants' correct responses to the two elements of the bimodal targets. The results (see Table 3 and Figure 3) revealed strong correlations between the RTs to the two components of participants' responses on the bimodal target trials. These results therefore support the hypothesis that on the majority of trials in which the participants responded correctly to both stimuli, their tactile and auditory responses were coupled.

RT correlation values	**Same Position**		**Different Positions**	
	Headphones	**Loudspeaker**	**Headphones**	**Loudspeaker**
Hand	r(222) = .748*	r(215) = .899*	r(226) = .936*	r(220) = .986*
Face	r(203) = .899*	r(215) = .949*	r(217) = .984*	r(221) = .907*

* indicates p < .01.

Table 3. Values of the correlations between the response latencies reported in Experiment 2.

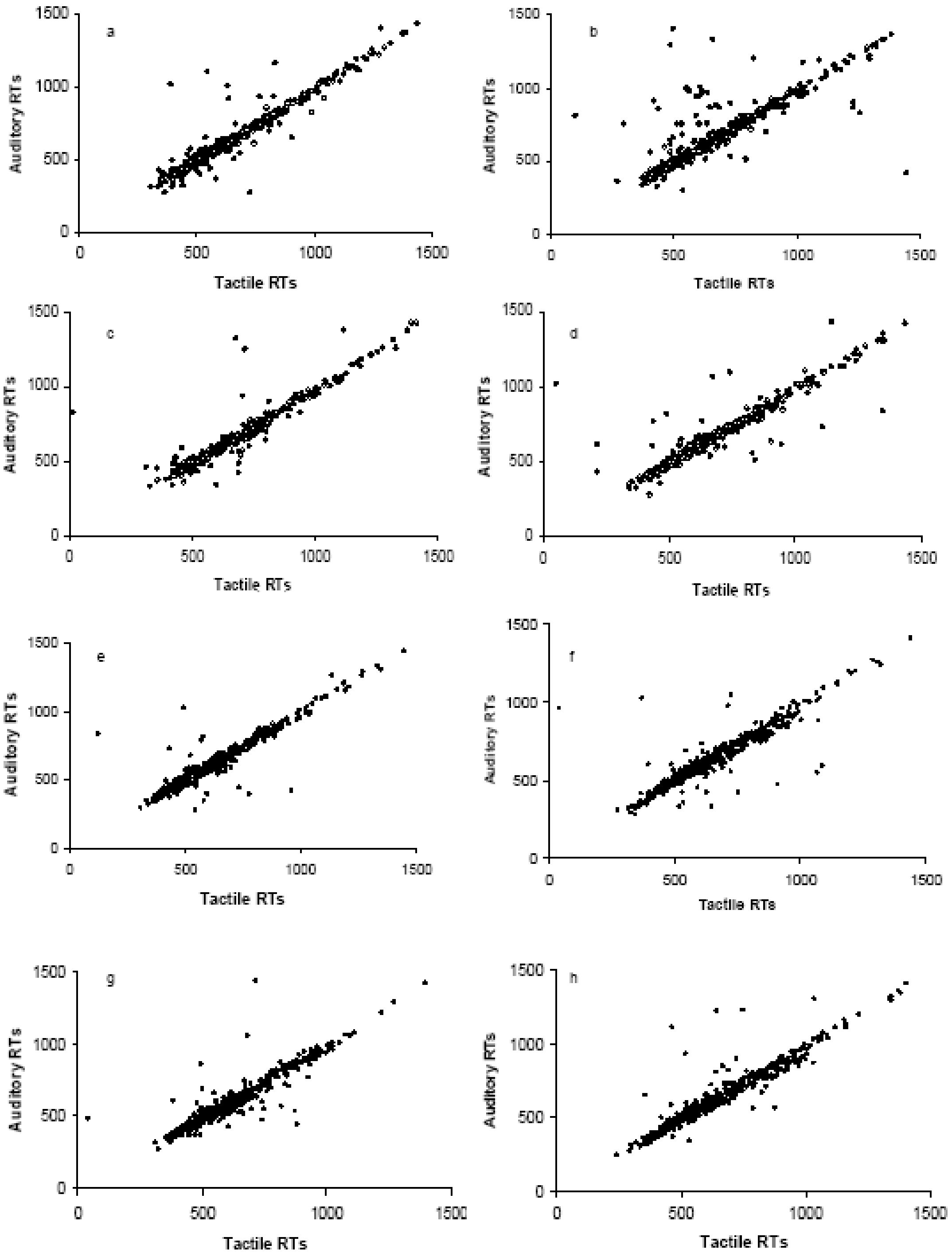

Figure 3. Scatterplots of the responses to the auditory and tactile components of the bimodal targets, for those trials in which participants made a correct response. Each graph represents one of the four blocks: (a) Face-Headphones; (b) Hand-Headphones; (c) Hand-Loudspeakers; (d) Face-Loudspeakers (Experiment 1); (e) Headphones-White Noise; (f) Loudspeakers-White Noise; (g) Headphones-Pure Tone; and (h) Loudspeakers-Pure Tone (Experiment 2). Each dot represents an individual trial from one participant (filled markers for the “same side” trials, empty markers for the “different sides” trials).

Conclusions

Three key results emerged from the analysis of the data reported in Experiment 2: First, a significant audiotactile Colavita effect was demonstrated for the very first time, with participants preferentially reporting the auditory (rather than the tactile) target on the bimodal target trials (M= 5.2% vs. 2.4%, respectively; see General Discussion on this point). Second, this effect was spatially modulated, with participants making more errors when the bimodal target stimuli were presented from the same position than when they were presented from different sides of fixation (M=4.7% vs. 2.8%). This result is consistent with the data reported previously in the audiovisual (Koppen & Spence, 2007b) and the visuotactile (Hartcher O'Brien et al., 2008) versions of the Colavita effect. In both of these earlier studies, participants tended to make more errors when the stimuli were presented in close spatial proximity (i.e., when the auditory and visual stimuli were presented from the same eccentricity; Koppen & Spence, 2007b; and when the tactile stimuli were presented on the hand and visual stimuli illuminating its surface; Hartcher O'Brien et al., 2008; Experiment 3).

Note that the spatial modulation of the audiotactile Colavita effect reported here contrasts with previous evidence showing lateralized facilitatory effects of auditory stimuli on somatosensory perception (i.e., from studies showing that sounds presented on the same side as tactile stimuli improve tactile spatial discrimination performance; Ro, Hsu, Yasar, Caitlin, Elmore, & Beauchamp, 2009; Spence, Nicholls, Gillespie, & Driver, 1998) and that people find it easier to shift and maintain their attention on touch and hearing on the same side than on different sides (see Eimer, Cockburn, Smedley, & Driver, 2001; Lloyd, Merat, McGlone, & Spence, 2003). The evidence currently supports the existence of crossmodal links in spatial attention between audition and touch, even though, as pointed out by Lloyd et al., the systems responsible for controlling the focusing of the attentional resources toward touch or audition (at least for the case of endogenous attention) have a certain degree of independence (cf. the "separable-but-linked" account of crossmodal links in endogenous attention; Spence & Driver, 1996, 2004).

The spatial modulation of the Colavita effect reported here tended to vary as a function of the part of the body whose surface and surrounding space were stimulated. More specifically, there was a trend toward the effect of the spatial arrangement (same vs. different side) being more pronounced when the tactile stimuli were presented to a participant’s face than when they were presented to their hands instead (mean difference of 2.6% and 1.3%, respectively; see the General Discussion on this point).

7.4. Experiment 3. The audiotactile Colavita effect in the rear space

Previous behavioural studies support the assumption that audiotactile spatial interactions are more prevalent in the region of space behind the head (i.e., in the part of space where visual cues are not available) than in front of it (Kitagawa, Zampini, & Spence, 2005; Zampini, Brown, Shore, Maravita, Röder, & Spence, 2005). Kitagawa and his coworkers conducted two experiments in order to investigate audiotactile interactions occurring in the space behind a participant’s head. In their first experiment, the participants had to judge the temporal order of presentation of pairs of auditory and tactile stimuli presented from loudspeakers or electrotactile stimulators attached to their earlobes, respectively. The stimuli could either be presented on the same side or from different sides. The results showed higher sensitivity (i.e., lower JNDs) for stimuli presented from different sides rather than from the same side. In Kitagawa et al.’s second experiment, a distractor interference task was used, with participants performing a tactile left/right discrimination task while auditory distractors were presented simultaneously from the same or opposite side. In this task, the participants responded more slowly (and less accurately) when the auditory distractors were presented on the opposite side from the tactile stimuli. Kitagawa et al.’s results suggested that the spatial arrangement of stimuli delivered in the space behind the head affects participants’ performance in both unspeeded temporal order judgment (Experiment 1) and speeded localization discrimination (Experiment 2) tasks. Thus, the suggestion that has emerged from this kind of research is that the absence of vision (or visual information) seems to be related to an improved ability to code spatial cues in the residual sensory modalities (i.e., audition and touch; Chen, Zhang, & Zhou, 2006; Collignon, Renier, Bruyer, Tranduy, & Veraart, 2006; Kitagawa et al., 2005; Röder, Kusmierek, Spence, & Schike, 2007; Röder & Rösler, 2004; Röder, Rösler, & Spence, 2004). Given these results suggesting important behavioural differences in terms of audiotactile interactions in front versus rear space, we investigated whether a more pronounced audiotactile Colavita effect could be highlighted by presenting the stimuli in rear space In Experiment 2. As in the Experiment 1, in the bimodal trials, the temporally co-occurring stimuli could either be presented from the same or from different sides. We expected to observe the preferential processing of the spatial cues and, thus, a facilitation of target detection when the auditory and tactile signals were presented from different sides of space (see Experiment 1).

There is considerable evidence to show that auditory stimuli differing in complexity are not only processed by differentiated cortical areas (e.g., Hall, Edmondson-Jones, & Fridriksson, 2006; Schönwiesner, Rübsamen, & von Cramon, 2005), but also that they interact differentially with tactile stimuli, thus generating various behavioural outcomes (Farnè & Làdavas, 2002; Kitagawa et al., 2005; Suzuki, Gyoba, & Sakamoto, 2008). Specifically, more pronounced audiotactile interactions have been observed for complex auditory stimuli than for pure tones (e.g., Farnè & Làdavas, 2002; Kitagawa et al., 2005; Suzuki et al., 2008). In order to test for the potential effect of sound type on audiotactile spatial interactions, the auditory stimuli used in our second experiment either consisted of white noise or pure tones (cf. Kitagawa et al., 2005; Experiment 2).

7.4.1. Method

Participants. Twelve participants (4 females; mean age of 25 years; range from 19 to 31 years of age; one left-handed) took part in this experiment. Two of the participants had taken part in Experiment 2.

Apparatus and stimuli. The experimental situation was similar to that used in Experiment 2 except for two differences. Two loudspeakers were now placed close to the back of the participant's neck. They were positioned on a shelf at ear-level, 60 cm from the participant's ears, and situated

40 cm to either side of the body midline. The auditory stimuli consisted of either pure tones or white noise bursts. Two bone conduction vibrators were placed on the rear of the participant's neck, one on each side of the body midline. White noise was presented at 70 dB(A) from a central loudspeaker cone throughout the experiment in order to mask any noise made by the participant or elicited by the operation of the vibrotactile stimulators.

Design and procedure. The experiment was completed in a completely dark testing booth. Four blocks of trials, each consisting of 120 trials, were presented. A 2x2 factorial design was used, with auditory location (i.e., loudspeakers vs. headphones) and auditory type (i.e., pure tone vs. white noise) as the factors. The order of presentation of the blocks was counterbalanced across participants. The conditions and the number of trials per condition were exactly the same as in Experiment 2.

7.4.2. Results

The participants failed to respond on 1.3% of the trials, and these trials were not included in the subsequent data analysis.

Error data: A repeated measures ANOVA was performed on the error data with the within-participant factors of Sound Location (Loudspeaker vs. Headphones), Sound Type (White Noise vs. Pure Tone) and Trial Type (Unimodal Auditory, Unimodal Tactile, Bimodal Same Side or Bimodal Different Sides). The analysis revealed a significant main effect of Trial Type, F(3,33)=3.77; p=.045, indicating that participants made significantly more errors in the same side condition than in the different sides condition (M=11.7% vs. 4.6%, respectively).

Next, we analysed the data from the bimodal error trials (i.e., from those bimodal trials in which the participants failed to report one of the two target modalities; 8.3% of the trials), using a repeated measures ANOVA with the factors of Sound Location (Loudspeaker vs. Headphones), Sound Type (Pure Tone vs. White Noise), Side (Same vs. Different) and Modality (Tactile vs. Auditory). The analysis revealed a significant main effect of Modality, F(1,11)=11.76; p=.006, with participants making more auditory-only than tactile-only errors (M=7.7% vs. 1.2%, respectively). In other words, a significant Colavita effect was demonstrated once again. The main effect of Side was also significant, F(1,11)=10.54; p=.008, with participants making more errors in the same side condition than in the different sides condition (M=6.3% vs. 2.5%, respectively). There was also a significant interaction between Side and Modality, F(1,11)=6.46; p=.027, with the significant Colavita effect being reported in the same side condition, t(11)=-4.03; p=.002, while the effect in the different sides condition was only borderline significant, t(11)=-2.03; p=.068.

The three-way interaction between Sound Location, Sound Type, and Side was significant, F(1,11)=10.87; p=.007. The four-way interaction between Sound Location, Sound Type, Side, and Modality was also significant, F(1,11)=6.15; p=.031. In order to understand the meaning of these terms more clearly, separate ANOVAs were performed for each level of the Sound Type factor (White Noise and Pure Tone). The analysis of those trials in which the auditory stimuli consisted of pure tones revealed a borderline-significant effect of Modality, F(1,11)=4.72; p=.053, revealing a tendency for participants to make more auditory-only than tactile-only errors (M=8.2% vs. M=1.0%, respectively). Participants made more errors in the same side than in different sides condition (M=5.8% vs. 3.3%, respectively). However, this difference (i.e., the main effect of Side) only approached significance, F(1,11)=3.73; p=.08.

The analysis of those trials in which the auditory stimuli consisted of white noise bursts revealed a significant main effect of Modality, F(1,11)=13.91; p=.003, with participants making more auditory-only than tactile-only errors (M=7.2% vs. 1.5%, respectively). The main effect of Side was also significant, F(1,11)=10.64; p=.008, with participants making more errors in the same side than in the different sides condition (M=6.9% vs. 1.8%, respectively). There was a significant interaction between Sound Location and Side, F(1,11)=8.52; p=.014, showing that the difference between the same and different side conditions was more pronounced when the auditory stimuli were presented over headphones, t(11)=3.51; p=.005, than when they were presented via loudspeakers, t(11)=2.28; p=.043 (mean difference of 7.1% vs. 3.0%, respectively). A significant audiotactile Colavita effect was reported when the stimuli were presented from the same side, t(11)=3.56; p=.004, while the effect was only borderline-significant in the different sides condition, t(11)=2.07; p=.063 (M=8.6% vs. 2.6%, respectively; see Figure 4).

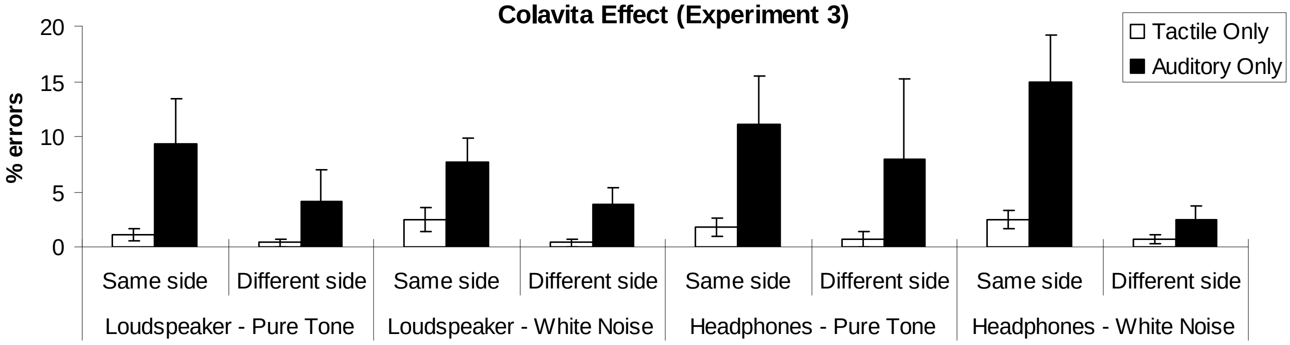

Figure 4. Percentages of errors in the bimodal trials for each of the four conditions tested in Experiment 3.

RT data: The RT data from those trials in which the participants responded correctly were analysed using an ANOVA with the within-participants factors of Sound Location (Close vs. Far), Sound Type (White Noise vs. Pure Tone), Trial Type (Unimodal, Same Side vs. Different Side), and Target Modality (Tactile vs. Auditory). The analysis revealed a significant main effect of Target Modality, F(1,11)=17.98; p=.001, with participants responding more slowly to tactile than to auditory targets (M=622 vs. 603 ms, respectively). The spatial arrangement of the stimuli affected performance, as shown by the significance of the main effect of Trial Type, F(2,22)=19.97; p<.001. Participants responded significantly more slowly in the same side condition than in both the unimodal, t(11)=-3.97; p=.002, and the different sides condition, t(11)=5.72; p<.001. The comparison between the unimodal and the different sides conditions was borderline-significant, t(11)=2.03; p=.067. The complexity of the sounds modulated the latency of participants' responses, as indicated by the borderline-significant interaction between Sound Type and Target Modality, F(1,11)=4.76; p=.052. The difference between auditory and tactile RTs was more pronounced when the auditory stimuli consisted of pure tones than when they consisted of white noise bursts (M=24 vs. 15 ms, respectively).

The four-way interaction between Sound Position, Sound Type, Trial Type, and Target Modality was also significant, F(2,22)=5.01; p=.034. To better understand the meaning of this term, separate ANOVAs were conducted for each sound type. When the auditory stimuli consisted of white noise bursts, the discrimination of the target modality was slower when the target consisted of both components coming from the same side (M=642 ms) than when they were presented in isolation (M=593 ms), t(11)=-3.58; p=.004, or from different sides (M=584 ms), t(11)=4.40; p=.001. There was no difference between the unimodal and different sides conditions, t(11)<1; n.s. Thus, the spatial modulation of response latency gave rise to a significant main effect of Trial Type, F(1,11)=6.03; p=.032.

The main effect of Modality was also significant, F(1,11)=6.01; p=.032, with participants responding more slowly to the tactile than to the auditory stimuli (M=614 vs. 601 ms, respectively). When the stimuli consisted of pure tones, there was a significant main effect of Trial Type, F(2,22)=13.28; p<.001. As for the auditory white noise burst stimuli, the participants responded more slowly in the same side condition (M=644 ms) than in either the unimodal conditions (M=614 ms), t(11)=-3.22; p=.008, or the different sides condition (M=597 ms), t(11)=5.77; p<.001. There was no difference between the latter conditions, t(11)=1.66; p=.13. The main effect of Target Modality was also significant, F(1,11)=42.62; p<.001, with participants responding more rapidly to auditory than to tactile stimuli (M=606 vs. 631 ms, respectively). For auditory pure tone stimuli, the difference in response latencies was modulated by the spatial proximity of the tactile and auditory stimuli, giving rise to a significant interaction between Sound Position and Target Modality, F(1,11)=5.42; p=.04. A significant difference in the RTs could be observed when the auditory stimuli were presented over headphones (M=33 ms), t(10)=6.09; p<.001, but not when they were presented from the loudspeakers (M=14 ms), t(10)=1.89; p=.09 (cf. Tajadura-Jiménez et al., 2009).

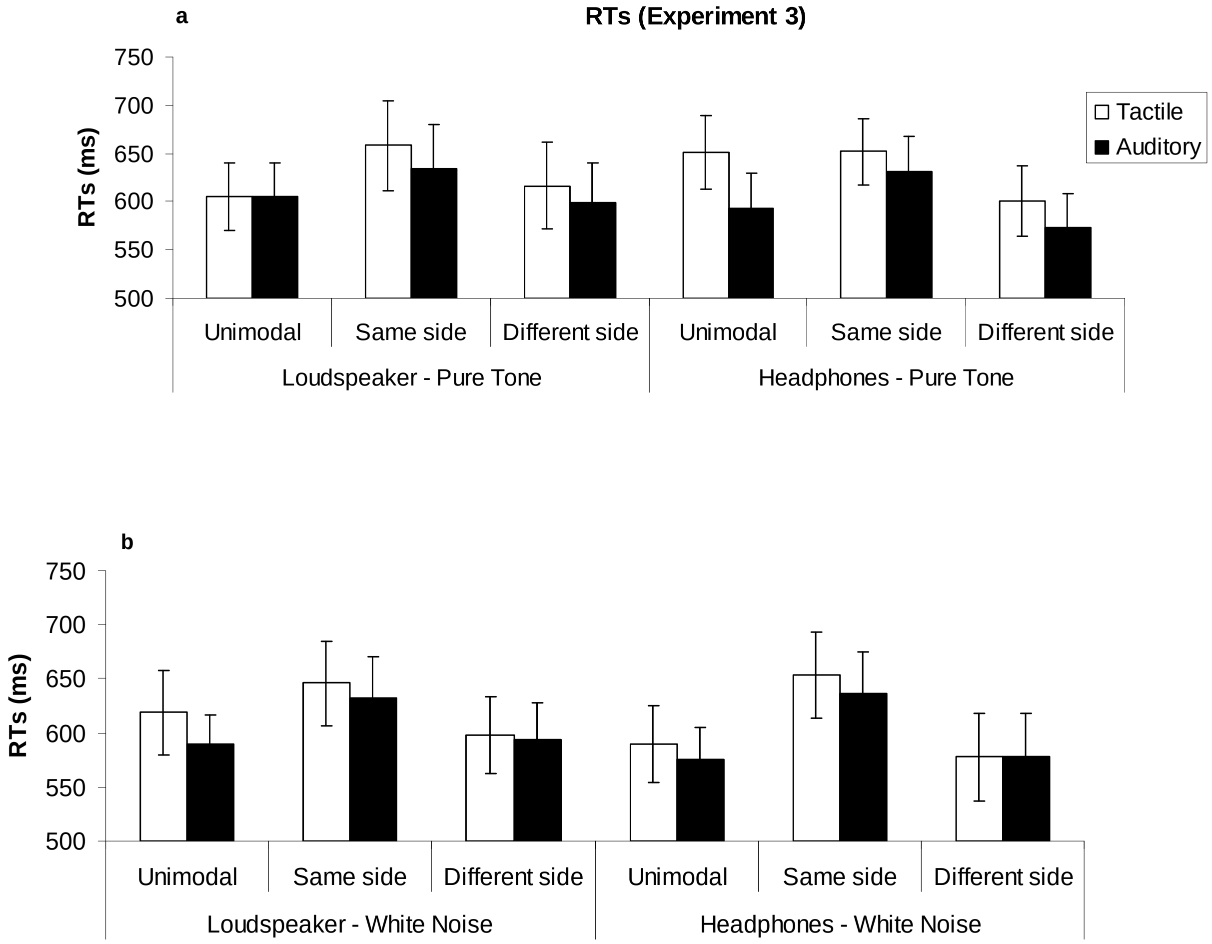

Figure 5. RTs reported in the unimodal and bimodal trials as a function of the complexity of the auditory stimulus (i.e., pure tones (a) vs. white noise (b)) in Experiment 3.

In order to determine whether there was any evidence of response coupling in the bimodal RT data, we ran an additional data analysis designed to look for a correlation between participants' correct responses to the two elements of the bimodal targets. The results (see Table 4 and Figure 3) once again highlighted the existence of strong correlations between the RTs to the two components of the bimodal targets. These data therefore support the hypothesis that on the majority of the bimodal trials to which the participants responded correctly, the responses to the tactile and the auditory components of the bimodal targets were coupled.

RT correlation values	Same Position		Different Positions	
	White Noise	Pure Tone	White Noise	Pure Tone
Headphones	r(234) = .916*	r(247) = .902*	r(278) = .971*	r(264) = .960*
Loudspeaker	r(258) = .845*	r(256) = .953*	r(277) = .983*	r(272) = .938*

* indicates p < .01.

Table 4. Values of the correlations between the response latencies reported in Experiment 3.

7.5. General discussion of Experiments 1, 2 and 3

In the present study, we investigated the effect of varying the physical properties (i.e., intensity and complexity) of the auditory stimuli and the relative and absolute position of auditory and tactile stimuli on the audiotactile Colavita dominance effect. In Experiment 1, the stimuli were presented from a spatially coincident location in frontal space (cf. Hecht & Reiner, 2009). In Experiment 2, two different spatial locations were used to present the stimuli (in different blocks of trials), both in touch (i.e., face vs. hand) and in audition (i.e., loudspeaker vs. headphones). In Experiment 3, the stimuli were presented from the space behind the participant’s head. The tactile stimuli were presented to the side (right or left) of the back of the participant’s neck while the auditory stimuli (consisting of either white noise bursts or pure tones) were presented over headphones or from the loudspeakers located behind the participant’s head.

Experiment 1 showed that the simultaneous presentation of auditory and tactile stimuli presented from a single location from the frontal space in a speeded detection/discrimination task did not result in participants extinguishing one of the two sensory components of the target (see also Hecht & Reiner, 2009). This result could be taken to support the hypothesis that, for the specific spatial arrangement tested in Experiment 1, the simultaneously-presented tactile and auditory stimuli tend to be bound together automatically (cf. Bresciani & Ernst, 2007; Caetano & Jousmäki, 2006; Foxe, Morocz, Murray, Higgins, Javitt, & Schroeder, 2000; Lütkenhöner, Lammertmann, Simões, & Hari, 2002), thus rendering the discrimination of each sensory component harder to perform.

The hypothesis that simultaneous auditory and tactile signals tend to be automatically bound together is supported by the results of a study conducted by Kayser and colleagues (Kayser et al., 2005). These researchers used fMRI-BOLD measurements in order to assess the degree of integration of auditory and tactile stimuli (presented to the hand and foot) in anaesthetized monkeys. Kayser et al. reported that the presentation of a tactile stimulus simultaneously with an auditory stimulus resulted in a supra-additive integration of the two signals in the caudomedial and the caudolateral belt areas of the auditory cortex. Two pieces of evidence support the automaticity of this process: first, it occurs in an area which is located early in the auditory pathway; second, it occurs in anesthetized monkeys, thus ruling out the possibility that the observed effect can be affected by attentional and/or cognitive top-down factors.

These findings have been recently extended by Sperdin and coworkers (Sperdin, Cappe, Foxe, & Murray, 2009), who provided evidence that early-latency auditory-somatosensory neural interactions in humans are strongly reflected in their behavioural performance. In their study, both behavioural and EEG data were recorded during a simple RT task in response to auditory, somatosensory or simultaneous auditory-somatosensory stimuli. By averaging the trials leading to fast and slow RTs for each experimental condition, the authors found that only trials producing faster RTs required interactions at the neural level, namely a facilitation of RTs in excess of probability summation. On the contrary, trials producing slower RTs did not exhibit any such violation, but only the typically observed facilitation of mean RTs observed with respect to unisensory condition (cf. Miller, 1982). Moreover, supra-additive neural response interactions were evident over the 40-84 ms post-stimulus period only when RTs were fast, whereas later effects (at 86-128 ms) were observed regardless of RT. Even though the individuation of mechanisms mediating the modulation of multisensory integration and RT speed is at the moment still speculative (and deserving of further investigation), the data reported by Sperdin and colleagues provide interesting evidence in support of a strict connection between behavioural performance and early low-level multisensory phenomena.

Considering the large number of participants tested in Experiment 1 (N = 45), and given the high number of trials completed by each participant, we can conclude that the pattern of results found here reflects solid empirical evidence in support of an absent audiotactile Colavita effect under the specific conditions tested here. The additional statistical analysis (see Footnote 1) further strengthens the assumption that in Experiment 1 the difference between the errors reported for bimodal trials (i.e., auditory-only and tactile-only responses) is so negligible to consider the two measures as statistically "equivalent" (Gallistel, 2009; Lecoudre & Derzko, 2001).

In contrast to Experiment 1 (see also Hecht & Reiner, 2009), the results of Experiments 2 and 3 showed that, under the appropriate conditions, a significant audiotactile Colavita effect, with audition dominating over touch on the bimodal target trials[2]. In a previous study, recording of the magnetic fields evoked by audiotactile stimulation showed major deflections of opposite polarities around 140 and 220 ms which seem to arise mainly from the secondary somatosensory cortex (SII) region, thus possibly suggesting that the auditory stimulus resulted in a partial inhibition in SII. (Lütkenhöner et al., 2002). However, in a subsequent study, Gobbelé and colleagues (Gobbelé, Schürmann, Forss, Juottonen, Buchner, & Hari, 2003) showed that multisensory integration activity between SII and the auditory cortices was characterized by a closer similarity to responses to the tactile stimulation than to the auditory stimulation, thus possibly suggesting a suppression of the responses to the auditory component of the audiotactile stimulus pairings.

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[2] It should be noted that in Experiment 1 (see also Hecht & Reiner, 2009), the auditory and tactile stimuli were only ever presented from a single location (i.e., sounds coming from a central position in front of the participant and the tactile stimuli to one of the participant's hands lying on a table, respectively). Thus, the only condition in Experiment 2 that is in any way comparable to the Experiment 1 was the one condition in which the auditory stimuli were presented from the loudspeaker cones and the tactile stimuli to the participants' fingertips. Interestingly, statistical comparison of the errors made in the bimodal trials in this condition provided no evidence of a Colavita effect (either in the same side trials, $t(9)=-.58$; n.s., or in the different sides trials, $t(9)<1$; n.s.; cf. Hecht & Reiner, 2009). Hence, it can be inferred that the Colavita effect highlighted in Experiment 2 can be attributed to the omissions made in the conditions that were different from those tested in previous research (i.e., auditory stimuli presented from the loudspeaker and the tactile stimuli presented on the hand; Experiment 1). This result suggests that the critical factor for the emergence of the audiotactile Colavita effect highlighted in Experiment 2 lies in other aspects of the experimental design, possibly on the presentation of the auditory stimuli in close spatial proximity to the participant's head (i.e., from the headphones in our study; see main text; though see also Colavita, 1982).

As pointed out by the authors themselves, this discrepancy could reflect the specific nature of the stimulation used rather than a genuine perceptual phenomenon. Namely, when sounds were more salient than the tactile stimuli, as in Lütkenhöner et al.’s (2002) study (using 60 dB pure tones and a balloon diaphragm), responses indicated partial inhibition in the SII region. Instead, pairs with more salient tactile than auditory stimuli (like the ones induced by electric stimulation; Gobbelè et al., 2003) indicated suppression of the auditory responses. Note that in our study, the auditory stimuli were presented at 70 dB (and were thus louder than the stimuli used by Lütkenhöner et al. and comparable to those used by Gobbelè et al.), whereas the tactile stimuli consisted of vibrations (and were thus likely less salient than the tactile stimulation used by Gobbelé et al.). In contrast to Gobbelé et al.’s participants, who reported that tactile inputs dominated during audiotactile stimulation, no such self-reports were detected during the present study.

Even though the difference in the latencies of the responses to auditory versus tactile targets only reached significance in Experiment 3, participants tended to react more rapidly to the auditory stimuli than to the tactile stimuli overall. These results are consistent with a previous study investigating the modulatory effect of spatial alignment on participants’ responses to auditory, somatosensory, and simultaneous auditory-somatosensory stimuli (Tajadura-Jiménez et al., 2009; Experiment 2; see also Diederich & Colonius, 2004). It can be hypothesized that the audiotactile Colavita effect found here may result from the more rapid processing of the auditory stimuli as compared to the tactile stimuli. In fact, in Experiment 1 in which we failed to find an audiotactile Colavita effect, no difference between the response latencies to auditory and tactile stimuli was reported (though see Hecht & Reiner, 2009). However, since the discrepancy in the response latencies to the two sensory components was not always accompanied by a significant Colavita effect (cf. the failure to demonstrate a Colavita effect in the “different side” condition; Experiment 3), this interpretation of the Colavita effect could not be completely justified. Indeed,

Moreover, it should also be remembered that in each experiment, on the bimodal trials, the participants were allowed to provide a second response after having made a first response. This means that if the participants had detected one sensory component (i.e., the auditory stimulus) before the other (i.e., the tactile stimulus), they still had the opportunity to report the second stimulus provided they did so within 1,450 ms of target onset. This pattern of results, along with the generalized tendency of participants to select the responses to both inputs at the same time (as shown by the response coupling effects reported in both experiments, see Tables 3 and 4 and Figure 3) makes a simple RT-based explanation of the audiotactile Colavita effect implausible (cf. Koppen & Spence, 2007b; see below for an alternative explanation).

Another result to emerge from Experiments 2 and 3 is that participants' performance was affected by the position from which the stimuli were presented. More specifically, across the different conditions tested here, participants tended to make errors (i.e., omissions) significantly more frequently when the stimuli were both presented from the same side than when they were presented from different sides. This result mirrors evidence obtained previously in studies that have explored the effect of the spatial manipulation of the audiovisual (Koppen & Spence, 2007b) and visuotactile (Hartcher O'Brien et al., 2008; Experiment 3) versions of the Colavita effect. In both of these studies, the proportion of errors was higher when the stimuli were presented from the same spatial position than when they were presented from different positions (though see Colavita, 1982, for contradictory findings). The fact that in the present study the number of errors was significantly higher when the stimuli were presented from the same side rather than from different sides (resulting in a selective Colavita effect for the former condition in Experiment 2), might suggest an alternative explanation for the existence of the audiotactile Colavita effect. Indeed, the spatial and temporal co-occurrence of the auditory and tactile signals could have induced the binding of these signals into a single perceptual object (cf. Senkowski, Schneider, Foxe, & Engel, 2008; Spence, 2007; Vatakis & Spence, 2007). As a consequence, the participants would have found it harder to disambiguate each component and for whatever reason resolved the conflict in favour of auditory responses. By contrast, the redundancy of spatial information, which is exclusively available in the different sides condition, could have facilitated the discrimination and thus the detection of the two discrete sensory components of the audiotactile stimulus pairing (cf. Hartcher O'Brien et al., 2008; Zampini, Shore, & Spence, 2003a; although see also Zampini, Torresan, Spence, & Murray, 2007).

In Experiment 2, the effect of spatial congruency between the auditory and tactile stimuli was more pronounced when the tactile stimuli were presented on a participant's face than when they were presented to their hands. This finding is consistent with the results of a previous magnetoencephalography (MEG) study conducted by Menning and collaborators (2005) that investigated audiotactile spatial interactions occurring between tactile primes and auditory targets. The tactile stimuli in Menning et al.'s study could be presented on the right or left side of the participant's face or to the right or left hand, whereas the auditory stimuli were presented in the space surrounding the face and the hands, respectively. The results showed that when the tactile prime was presented to the participant's face, the N100 component evoked by the auditory stimuli was increased when the stimuli were presented from the same side (Menning et al., 2005). Similarly, the P50 component was more pronounced when the source of stimulation was proximal (i.e., presented from close to the participant's face). According to Menning et al., this evidence is consistent with the hypothesis that stimuli presented within close peripersonal space are more prominent in attracting attentional resources than are stimuli that happen to be presented in more distant regions (see also Ho & Spence, 2009).

Surprisingly, our study failed to highlight an overall difference between the two parts of the body stimulated (i.e., face and hands). It has been shown that each part of the surface of the face is represented differently in terms of the extent of the cortical representation and the prominence of the response triggered by the stimulation. For instance, the area around the mouth is more extensively represented and more sensitive to stimulation than are other regions on the face, such as the cheeks or forehead (Nevalainen, Ramstad, Isotalo, Haapanen, & Lauronen, 2006; Nguyen et al., 2004). A null main effect of the body-part stimulated can possibly be explained by taking into account the fact that the facial regions stimulated in our study (i.e., the cheeks) aren't considered to be the most sensitive ones (cf. James, Essick, Kelly, Tappouni, & McGlone, 2000; Weinstein, 1968).

The pattern of results reported in Experiment 3 confirms the results of previous studies showing that the absence of visual information typically results in an improvement in the processing of spatial cues in the other sensory modalities (i.e., audition and touch; e.g., Chen et al., 2006; Collignon et al., 2006; Kitagawa et al., 2005; Röder et al., 2004, 2007; Röder & Rösler, 2004). This result is normally accompanied by shorter response latencies in those conditions in which the stimuli were presented from different hemispaces (rather than from the same hemispace). Interestingly, the spatial modulation of response latencies was selectively observed in those conditions in which the stimuli were presented from close to the participant's head. This result mirrors Tajadura-Jiménez et al.'s (2009; Experiment 1) findings. In their study, electrocutaneous stimuli were presented to the participant's earlobes, while auditory stimuli were presented from the same vs. opposite sides, either close or far from the participant's head (i.e., 20 vs. 70 cm away). A spatial modulation of the Colavita effect was selectively observed under those conditions in which the auditory stimuli were presented from close to the participant's head. This result suggests that when stimulation involves auditory stimulation originating from close to the head it is somehow distinctive and gives rise to effects that cannot necessarily be detected when the stimulation is delivered far from the head (e.g., in the peri-hand space; see also Menning et al., 2005)[3].

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[3] In order to clarify whether the proximity of the sound does indeed represent a key factor modulating the results of Experiment 2, we conducted an additional ANOVA with the factors of Sound Proximity (Close vs. Far), Side (Same vs. Different), and Target Modality (Tactile vs. Auditory). The analysis revealed a significant main effect of Sound Proximity, F(1,9)=11.58; p=.008, with participants making slightly more errors in those trials in which the auditory stimuli were presented from headphones rather than from external loudspeakers (3.2% vs. 2.5%, respectively). The main effect of Side was also significant, F(1,9)=247.77; p<.001, with participants making more errors in those conditions in which the tactile and auditory stimuli were presented from the same (vs. different) side (3.9% vs. 1.8%, respectively). As expected, there was a significant main effect of Target Modality, F(1,9)=15.06; p=.004, indicating that participants made more auditory-only than tactile-only responses (3.4% vs. 2.3%, respectively). The Sound Proximity x Side interaction was also significant, F(1,9)=6.14; p=.035, indicating that the effect of spatial alignment (i.e., whether the stimuli presented on the same vs. different side) was more pronounced in those conditions in which the auditory stimuli were presented from loudspeakers than when the stimuli were presented over headphones instead (2.3% vs. 1.8%, respectively). Interestingly, there was a significant interaction between Sound Proximity and Modality, F(1,9)=54.5; p<.001, showing that the difference between auditory-only and tactile-only responses was only significant when the auditory stimuli were presented over headphones, t(9)=-5.72; p<.001, and not when they were presented from external loudspeakers, t(9)=-1.38; p=.20. This result shows that the Colavita effect is attributable to the condition in which the auditory stimuli were presented within close peripersonal space, and not to the condition where they were

In Experiment 3, the potential effect of sound complexity was also explored. Sound complexity modulated the audiotactile Colavita effect, which was selectively observed when the auditory stimuli consisted of white noise bursts. If it is true that complex auditory stimuli are more likely to interact – and possibly to be integrated – with the auditory stimuli in rear space (cf. Graziano et al., 1999), the auditory pure tone stimuli might have been more discriminable as compared to the white noise bursts (see Moore, 1997). This, in turn, could have facilitated the detection of both discrete sensory components of the bimodal trials in the present study (cf. Kitagawa et al., 2005; Experiment 2). This evidence is also accompanied by a more pronounced discrepancy in the latencies of participants' responses (i.e., longer RTs for tactile vs. auditory stimuli) for stimuli consisting of pure tones than for white noise bursts. The evidence according to which the RTs are faster in response to white noise bursts than to pure tones replicates previous neurophysiological findings (Lakatos, Pincze, Fu, Javitt, Karmos, & Schroeder, 2005). In their study, Lakatos and collaborators found that, whereas the response latencies did not differ between pure tones and broadband noise in the primary auditory cortex, latencies were significantly longer in response to pure tones (vs. noise) in belt regions. According to the authors, these data suggest the existence of discrete transmission systems for each type of sound, with complex sound inputs being mediated by direct – and faster – afferents from the thalamus (i.e., dorsal and magnocellular divisions of the medial geniculate complex; see also Hackett, Stepniewska, & Kaas, 1998; Rauschecker, 1997). Interestingly, a high percentage of the neurons in the caudal parabelt area

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presented further from the participant. Since the three-way interaction between Sound Proximity, Side, and Modality was also significant, F(1,9)=12.29; p=.007, separate analyses were performed for each level of the Sound Proximity (i.e., close vs. far) factor. In the close condition, the effect of Side was significant, F(1,9)=304.89; p<.001, with more errors being reported in the same (vs. different) side condition (4.2% vs. 2.4%, respectively). The effect of Modality was also significant, F(1,9)=32.79; p<.001, with more auditory-only than tactile-only errors (4.6% vs. 2.1%, respectively) being reported. The interaction between Side and Target Modality was significant, F(1,9)=87.87; p<.001, with a larger spatial modulation of the Colavita effect being observed when the stimuli were presented from the same (vs. different) side (3.6% vs. 1.4%, respectively). In those conditions in which the auditory stimuli were presented from external loudspeakers, only the main effect of Side was significant, F(1,9)=119.82; p<.001, with participants making more errors when the stimuli were presented from the same side, rather than from different sides (3.7% vs. 1.3%, respectively). In summary, it seems as though the presentation of auditory stimuli via headphones is crucial for the emergence of the audiotactile Colavita effect, probably because it might involve a stronger integration of the signals, making the detection of the two discrete sensory components harder to perform (though see also Colavita, 1982; Koppen et al., 2008).

responsive to complex auditory stimuli have also been shown to be responsive to somesthetic stimulation applied to the ear, neck, and shoulder. This would suggest the potential involvement of this area in the integration mechanisms between tactile and complex auditory stimuli (Leinonen, Hyvarinen, & Sovijarvi, 1980). For both types of sound, however, our participants tended to respond more slowly when the stimuli were presented from the same side of space as compared to when they were presented in isolation (i.e., in the unimodal trials) or from different sides (in the bimodal trials).

In summary, the present study investigated the effect of manipulating the spatial relations between tactile and auditory stimuli on the audiotactile Colavita effect. The results of Experiments 2 and 3 showed a significant audiotactile Colavita effect for the first time, with participants preferentially reporting the auditory (vs. tactile) component of the bimodal trials. The spatial manipulation turned out to be effective in modulating participants' performance, with participants making more errors when the stimuli were presented from the same hemispace as compared to when they were presented from different sides of space. In contrast to what was shown in Experiment 1, the results of Experiment 3 showed that the Colavita effect was selective for auditory stimuli consisting of white noise (vs. pure tones), suggesting that this kind of auditory stimuli are more likely to be bound together with the somatosensory stimuli when presented from the rear space (cf. Farnè & Làdavas, 2002; Kitagawa et al., 2005; Suzuki et al., 2008).The final point to note here concerns the fact that across all of the experimental conditions tested here, participants' performance showed a high degree of variability in both Experiment 1 (i.e., 7.8% for tactile and 4.4% for auditory responses) and Experiment 2 (i.e., 17.7% for tactile and 8.1% for auditory responses) (see Hecht & Reiner, 2009 for similar results). As some participants preferentially neglected the tactile component and others neglected the auditory component of the bimodal trials, the consequence was that the overall performance resulted in a null Colavita dominance effect. Since this pattern of performance showed up several times across the study, it may be that, comparably to what has been found in audiovisual research, there is a high inter-individual variability in the sensory modality that people preferentially rely on (attend to) when identifying stimuli (cf. Giard & Peronnet, 1999; Mollon & Perkins, 1996; Stone, Hunkin, Porrill, Wood, Keeler, Beanland, Port, & Porter, 2001). In their study, Giard and Peronnet presented two objects, each defined by visual attributes alone, auditory attributes alone, or combined congruent attributes. The results showed that some participants were faster at identifying the objects on the basis of vision while others were better at identifying them on the basis of their auditory properties instead, thus leading the authors to categorize the participants as being either "visually dominant" or "auditory dominant". This discrepancy in the preferential modality was observed both in the behavioural (i.e., shorter and more accurate responses) and electrophysiological data (i.e., an enhanced neural activity in the early stage of sensory analysis elicited in the cortex of the non-dominant sensory modality). The assumption that audiovisual multisensory integration operates in a flexible manner, and that it is to a certain extent tuned to the subjective perceptual individualities (cf. Giard & Peronnet, 1999), could thus be extended to the case of audiotactile interactions, as also tentatively suggested by Lütkenhöner, Lammertmann, Simões, and Hari (2002). Further investigations are needed to fully understand the role of individual processing preferences.

Chapter 8.

Temporal interactions between hearing and touch

8.1. Introduction

Perceptual interactions between hearing and touch are distinguishing amongst the associations occurring between other sensory modality pairings (Gescheider, 1970; Soto-Faraco & Deco, 2009; von Békésy; 1959). Indeed, auditory and vibrotactile stimuli are generated by the same physical mechanism, consisting of the mechanical stimulation of, respectively, the basilar membrane and the skin. Hence, both auditory and vibrotactile stimuli can be described according to their specific periodic patterns of stimulation (i.e., their frequency), defined as the number of repetitions of the sound waveforms (cf. Plack, 2004; Siebert, 1970) or of the tactile pulses (cf. Luna, Hernández, Brody, & Romo, 2005), respectively, per unit time.

In mammals, the ability to discriminate auditory frequency has been considered as reflecting the frequency resolution characterizing the auditory pathway at both the peripheral (i.e., the basilar membrane of the cochlea; Robles & Ruggero, 2001) and central (i.e., the primary auditory cortex; Langers, Backes, & van Dijk, 2007; Tramo, Cariani, Koh, Makris, & Braida, 2005) stages of auditory information processing. The systematic spatial mapping of frequency coding in the brain (known as tonotopy) and the filtering properties of auditory neurons and sensory receptors have been considered responsible for decoding the frequency of auditory stimulation (see Schreiner, Read, & Sutter, 2000, for a review; see also Elhilali, Ma, Micheyl, Oxenham, & Shamma, 2009; Romani, Williamson, & Kaufman, 1982; Schnupp & King, 2008). However, the tonotopic structure of the auditory system is not the only candidate for the representation of the temporal characteristics of the auditory stimuli. Indeed, the activity of neurons at different stages of the auditory pathway has been shown to change as a function of the repetition rates of the auditory events being processed (see Bendor & Wang, 2007, for a review). More specifically, acoustic signals within the flutter range are coded by neurons that synchronize their activity to the temporal profile of repetitive signals. These neurons have been observed both along the auditory-nerve fibres and in the inferior colliculus, the medial geniculate body, and in a specific neuronal population along the anterolateral border of the primary auditory cortex (AI; Dicke, Ewert, Dau, & Kollmeier, 2007; Oshurkova, Scheich, & Brosch, 2008; Wang, Lu, Bendor, & Bartlett, 2008). Other mechanisms regulate the activity of the neural population coding for auditory signals presented at higher repetition rates (i.e., above the perceptual flutter range). These neurons modify their discharge rates – not their spike timing – as a function of the frequency of the auditory events that are being processed (Oshurkova et al., 2008; Wang et al., 2008). Thus, the temporal profile of the auditory stimuli can be represented in AI by a dual process (i.e., stimulus-synchronized firing pattern and discharge rate), each involving specific sub-populations of neurons. The distinct neural encoding of auditory stimuli differing in frequency may also be responsible for the discrepancy in the perceptual impression conveyed by auditory stimuli. Indeed, when auditory events are presented at rates within the range 10-45 Hz (i.e., flutter) range, the resulting percepts tend to consist of sequential and discrete sounds (i.e., acoustic flutter; Bendor & Wang, 2007; see also Besser, 1967). According to Bendor and Wang, the discrete impression of the flutter percept could be considered as the direct outcome of the synchronized responses representing the event at different neural stages of the auditory pathway. On the other hand, the neurons encoding of stimuli with repetition rates beyond this range do not synchronize with the stimuli, thus failing to induce the impression of discrete sound events and instead giving rise to continuous-sounding percepts having a specific pitch (Bendor & Wang, 2007; Cariani, 1999; Hall, Edmondson-Jones, & Fridriksson, 2006; Tramo et al.,, 2005; Wang et al., 2008; Will & Berg, 2007; see also Deutscher, Kurt, Scheich, & Schulze, 2006).

In the somatosensory domain, the discrimination of vibrotactile stimuli differing in frequency has been investigated in monkeys (de Lafuente & Romo, 2005; Hernández, Salinas, García, & Romo, 1997; Mountcastle, LaMotte, & Carli, 1972; Mountcastle, Steinmetz, & Romo, 1990; Romo & Salinas, 2003; Werner & Mountcastle, 1965) as well as in humans (Bensmaïa, Hollins, & Yau, 2005; Horch, 1991; Iggo & Muir, 1969; LaMotte & Mountcastle, 1975; Mountcastle et al., 1972; Talbot, Darian-Smith, Kornhuber, & Mountcastle; 1968; Verrillo, 1985;

Werner & Mountcastle, 1965. See also Harrington & Downs, 2001). In their seminal studies, Mountcastle and his coworkers investigated the capabilities of both humans and monkeys to discriminate between pairs of vibrotactile stimuli presented at different frequencies (e.g., LaMotte & Mountcastle, 1975; Mountcastle et al., 1972; Mountcastle, Talbot, Darian-Smith, & Kornhuber, 1967; Mountcastle, Talbot, Sakata, & Hyvärinen, 1969). The psychophysical investigations provided evidence that both monkeys and humans have nearly identical abilities in the discrimination of the vibrations in the sense of flutter (i.e., the difference limen for frequency discrimination overlapped nearly perfectly; see LaMotte & Mountcastle, 1975; Mountcastle et al., 1990; although see Imai, Kamping, Breitenstein, Pantev, Lütkenhöner, & Knecht, 2003).

Other studies have clarified the neural substrates subserving the encoding of vibrotactile frequency, in both humans (Bolanowski, Gescheider, Verrillo, & Checkosky, 1988; Burton, Sinclair, Wingert, & Dierker, 2008; Francis, Kelly, Bowtell, Dunseath, Folger, & McGlone, 2000; Gescheider, Bolanowski, & Hardick, 2001; Gescheider, Bolanowski, & Verrillo, 2004; Harris, Miniussi, Harris, & Diamond, 2002; Iguchi, Hoshi, Nemoto, Taira, & Hashimoto, 2007; Mahns, Perkins, Sahai, Robinson, & Rowe, 2006; Morley, Vickery, Stuart, & Turman, 2007; Romo, Hernández, Zainos, Brody, & Salinas, 2002) and monkeys (Ahissar & Vaadia, 1990; Coleman, Bahramali, Zhang, & Rowe, 2001; de Lafuente & Romo, 2005; Luna et al., 2005; Mountcastle et al., 1972; Mountcastle et al., 1967; Mountcastle et al., 1969; Romo & Salinas, 2003; Salinas, Hernandez, Zainos, & Romo, 2000). It has been demonstrated that the identification and the discrimination of stimuli differing in frequency rely on the differential sensitivity of sense organs and afferent nerve fibres supplying different portions of the skin (Johansson & Vallbo, 1979a, b; Morioka, Whitehouse, & Griffin, 2008). Animal studies suggest that one possible candidate for signalling information about the frequency of vibrotactile stimuli is an impulse pattern code, according to which the responses of rapidly adapting afferents are phase-locked to the periodicity of the vibrotactile stimulus. The strict correspondence between the temporal features of the vibrotactile stimuli and the impulse patterns have not only been observed in the periphery (i.e., along the sensory fibres), but also in neurons at higher levels along the ascending somatosensory pathway (Hérnandez et al., 2000; Mountcastle et al., 1990; Salinas et al., 2000). A recent fMRI study showed that the decrease of hemodynamic activity observed when pairs of stimuli sharing the same frequency are compared to pairs of stimuli with different frequencies involves an extended region. Beyond the areas typically involved in this kind of task (i.e., SI and . See also Kahru & Tesche, 1999), other areas, such as the superior temporal gyrus, the precentral gyrus, ipsilateral insula, and supplementary motor area were also found to contribute (Li Hegner, Saur, Veit, Butts, Leiberg, Grodd, & Braun, 2007). Interestingly, the superior temporal gyrus is an area known for mediating the interaction between auditory and somatosensory stimuli, in both humans (Foxe, Wylie, Martinez, Schroeder, Javitt, Guilfoyle, Ritter, & Murray, 2002; Schroeder, Lindsley, Specht, Marcovici, Smiley, & Javitt, 2001) and monkeys (Fu, Johnston, Shah, Arnold, Smiley, Hackett, Garraghty, & Schroeder, 2003; Kayser, Petkov, Augath, & Logothetis, 2005). Neurons in the auditory belt areas not only respond to pulsed tactile stimulation, but also to vibratory stimuli, thus suggesting that the auditory association cortex acts as a cortical convergence location between auditory and tactile inputs during the discrimination of tactile frequency (Iguchi et al., 2007; Li Hegner et al., 2007; Schürmann, Caetano, Hlushchuk, Jousmäki, & Hari, 2006; see also Caetano & Jousmäki, 2006; Golaszewski, Siedentopf, Koppelstaetter, Fend, Ischebeck, Gonzalez-Felipe, Haala, Struhal, Mottaghy, Gallasch, Felber, & Gerstenbrand, 2006). The evidence suggesting that the auditory areas involved in the processing of tactile stimuli are endowed by specific frequency temporal profiles and contribute to the vibrotactile frequency discrimination process, raises the intriguing possibility of anatomo-functional similarities between cortical regions devoted to the processing of the periodicity in both vibrotactile and auditory stimulation (see also Bendor & Wang, 2007; Wang et al., 2008).

On the basis of the above-mentioned evidence, it seems somehow surprising that the investigations of audiotactile interactions on the basis of their frequencies similarities has rarely been investigated thus far (although see Harris, Fucci, & Petrosino, 1986, 1991; Petrosino, 1989;

Ro, Hsu, Yasar, Caitlin Elmore, & Beauchamp, 2009). Preliminary evidence from Nagarajan and colleagues (1998), however, has suggested that temporal information processing is governed by common mechanisms across the auditory and the tactile sensory systems. In their study, participants were presented with pairs of vibratory pulses and trained to discriminate the temporal interval separating them. The results not only suggested a decrease of threshold as a function of training, but also the generalization of the improved interval discrimination to the auditory modality. Even though the generalization was constrained to an auditory base interval similar to the one which had been trained in touch, these results are intriguing in suggesting that the coding of time intervals could be centrally represented (i.e., shared among modalities). Additionally, recent neurophysiological evidence in humans has shown that the discrimination of tactile stimuli with frequency properties (i.e. vibrotactile stimuli) was significantly improved in many of the participants undergoing the task by simply adding auditory feedback - with the same frequency - after the presentation of the tactile stimulation (Iguchi et al., 2007; though see Yau et al., 2009 for opposite results; and see Ro et al., 2009, for evidence from a tactile detection task). The investigation of the neural substrates of this effect led to the conclusion that the increase of the perceptual accuracy and the speeding-up of the discrimination of the tactile frequencies were subserved by the co-activation of the SII and the supratemporal auditory cortices along with upper bank of the superior temporal sulcus. This study adds evidence to previous investigations showing considerable crossmodal convergence in the posterior auditory cortex of not only tactile stimulation (e.g., Foxe et al., 2002; Kayser et al., 2005) but also of stimulation with frequency properties, in both normal hearing (e.g., Caetano and Jousmäki, 2006; Schürmann et al., 2006) and deaf humans (Levänen & Hamdorf, 2001).

In Experiments 4 and 5, we address the issue of whether, and to what extent, people are able to match stimuli having comparable temporal rate features. The participants were presented with pairs of stimuli that could either be presented within the same sensory modality (i.e., audition or touch) or else across modalities (i.e., one in touch and the other in audition). On each trial, a standard stimulus, presented at a fixed frequency, and a test stimulus, presented at one of a range of different frequencies was presented. Since the perceptual encoding boundary for repetition rates producing low- and high-frequencies stimuli is the same for both audition and touch (i.e., ~ 40-50 Hz), two different perceptual ranges can legitimately be investigated (i.e., the flutter range in Experiment 4; the vibration range in Experiment 5). The sensation of flutter (tactile or auditory) is induced by periodic trains of impulses at frequencies between ~5 and ~40 Hz, whereas higher repetition rates (~40-400 Hz; Mountcastle et al., 1972; Mountcastle, 1993) induce, respectively, in touch a sensation of “vibration/buzzing” (Blakemore, Tavassoli, Calò, Thomas, Catmur, Frith, & Haggard, 2006; LaMotte & Mountcastle, 1975; Luna et al., 2005; Romo et al., 2002; Talbot et al., 1968) and in hearing the sensation of pitch (Bendor & Wang, 2007; Tramo et al., 2005). If the human ability to match stimuli having the same temporal profile within, respectively, touch (LaMotte & Mountcastle, 1975; Mountcastle et al., 1972; Talbot et al., 1968) and audition (Dicke et al., 2007; Oshurkova et al., 2008; Wang et al., 2008) should extend to the condition when pairs of stimuli are presented across modalities, then one might expect a pattern of performance (expressed in terms of d' values) that paralleled that observed during unimodal conditions.

8.2. Experiment 4. Audiotactile frequency matching in the flutter range

In Experiment 4, frequencies within the flutter range (i.e., below 50 Hz; cf. Bendor & Wang, 2007; Mountcastle, 1993) were tested. The standard stimulus was presented at a fixed frequency of 24 Hz, while the test stimuli were presented at frequencies of 12, 16, 20, 24, 28, 32 or 36 Hz.

8.2.1. Method

Participants. Fourteen participants (10 females; mean age of 26 years; range from 19 to 35 years; all right-handed) took part in this experiment. The experiment took approximately 60 minutes to complete and was conducted in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki, as well as the ethical guidelines of the Department of Experimental Psychology, Oxford University. All of the participants gave their informed consent prior to their inclusion in the study. The participants were given a £10 (UK Sterling) gift voucher in return for taking part in the study.

Apparatus and stimuli. Participants sat at a table in a completely dark testing booth. A computer monitor was placed at a distance of about 60 cm in front of them. This was used to display instructions during the experiment. A centrally located tactile stimulator was placed in front of the monitor (see below). The participants placed their right hand palm-down on the tabletop, with the index finger resting on the upper surface of the tactile stimulator. Their other hand was placed on a keyboard that was situated on the table in a comfortable position for the participant. The keyboard was used by the participant to initiate the training and experimental blocks. White noise was presented at 63 dB(A) via closed headphones (Cordless Stereo Headphone SBC HC075, Philips) worn by the participant throughout the experiment, and from a loudspeaker positioned directly behind the vibrotactile stimulator, in order to mask any noise elicited by its operation. The vibrotactile stimuli consisted of the activation (for 500 ms; cf. Hérnandez et al., 1997; Luna et al., 2005) of a 12-volt solenoid driving a metal rod with a blunt conical tip against the fingertip whenever a current was passed through it. The vibrotactile stimuli were presented at the fingertip of the right index finger (Harris, Arabzadeh, Fairhall, Benito, & Diamond, 2006). Each vibratory tactile stimulus consisted of a sequence of brief pulses repeated as many times as according to the frequency of the stimulus (i.e. 6, 8, 10, 12, 14, 16, 18 cycles). The increased intensity of the vibrotactile stimuli as a function of their frequency (Goff, 1967; Harris et al., 2006; LaMotte, & Mountcastle, 1975) was controlled for by manipulating the contact time between rod and skin, which was varied between 3 and 5 ms, just as in previous research (e.g., Forster, Eardley, & Eimer, 2007). The time interval between the onset of successive pulses of the vibratory tactile stimulus was 78, 58, 45, 38, 33, 28, and 25 ms, corresponding to a stimulation frequency of approximately 12, 16, 20, 24, 28, 32 and 36 Hz, respectively. The interval between the onset of the first pulse and the offset of the last pulse was of 500 ± 2 ms.

The auditory stimuli consisted of the sound files of the recordings of the sound produced by the activation of the solenoid[4] presented for 500 ms (cf. Sinnott & Brown, 1993). The resulting sound files were played via loudspeakers (Creative, Cambridge Soundwork, MA) situated on each side of the computer monitor. Each of the seven auditory stimuli used had the same frequency and duration as the tactile stimulus. The amplitude of the auditory stimuli was adjusted by mean of the function "Volume control" embedded in the E-prime software (Psychology Software Tools Inc.; www.pstnet.com/eprime) in order to avoid the possibility that any increase in frequency would be perceived as an increase in the pitch of the stimulus, which could be a confound in the task at hand (Morley & Rowe, 1990). The auditory stimuli were presented at 76dB(A) as measured from the participant's head position.

For both auditory and the tactile presentations, seven stimulus frequencies were chosen: 12, 16, 20, 24, 28, 32 and 36 Hz. The standard stimulus was presented at a fixed frequency (i.e., 24 Hz), while the other (the test) was presented at different frequencies (i.e., 12, 16, 20, 24, 28, 32 or 36 Hz), separated by steps of 4 Hz (cf. Hérnandez et al., 1997). Two footpedals were placed under the table in order to collect participants' responses.

Procedure. At the beginning of the experimental session, participants were given a brief demonstration of either auditory or tactile stimuli and asked to follow the instructions presented on the computer monitor throughout the experiment. Next, a practice block of 40 trials, which was composed like an experimental block, except for the number of the trials, was presented to familiarize participants with the stimuli and the experimental procedure. After confirming that the participants understood the task, the experimental blocks were presented. Participants were instructed to provide a response on each and every trial. The task was unspeeded, and participants

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[4] We chose this kind of auditory stimuli since the auditory stimuli with repetition rates higher than the flutter range can give rise to the perception of a specific pitch (see Bendor & Wang, 2007). The auditory stimuli used in the present study are not endowed with a specific pitch which could serve as a cue to frequency discrimination but are rather perceived as discrete acoustic events.

were informed that they should respond only when confident of their response (although within the 2,500 ms allowed before the termination of the trial).

The first trial was presented 500 ms after the participant pressed the “space bar” with the hand resting on the response key. The first and second intervals of each trial were marked by the digits “1” and “2” displayed on the monitor and had a duration of 500 ms each. The interstimulus interval randomly assumed the values of 100, 150 or 200 ms (cf. Burton et al., 2008; Harris et al., 2002; Hérnandez et al., 1997) in order to minimize the impairing effect of the limits of working memory storage (Harris et al., 2002; Preuschhof, Heekeren, Taskin, Schubert, & Villringer, 2006; Sinclair & Burton, 1996; Sörös, Marmurek, Tam, Baker, Staines, & Graham, 2007). The order of presentation of the standard and test stimuli was counterbalanced, with half of all trials beginning with the presentation of the standard stimulus and the other half with the test stimulus (see Romo & Salinas, 2003). In half of the trials the standard stimulus was presented in touch and in the other half in audition. Once both of the stimuli had been presented, the instruction “Enter response” was displayed on the screen, signalling the participants to report whether the two stimuli presented had the same or a different stimulus frequency. One of the footpedals was assigned to the response “same frequency”, whilst the other was assigned the response “different frequency”, with the location (i.e., right vs. left) of the footpedals counterbalanced across participants. Half of participants completed the experiment using the left pedal to make a "same" response, while the other half completed the experiment using the right pedal for the same purpose. Responses were made by lifting either the left or right foot off the respective pedal. No feedback concerning the accuracy of a participant’s performance was provided. The interstimulus interval between successive trials was 2500 ms.

Design. A 3 x 7 factorial design was used, with stimulus modality pairing and frequency as factors. The stimulus modality pairing condition had three levels (i.e., tactile, auditory, and crossmodal), whilst the frequency condition had seven levels (see above). In total, each participant performed 672 experimental trials (32 trials per condition) divided into four blocks of 168 trials each and presented in random order. The practice trials were not included in the data analysis.

8.2.2. Results.

In the analysis, the same-different paradigm (Macmillan & Creelman, 2005) was applied. The proportions of trials on which each pair of stimuli was judged as different were used to derive each participant's sensitivity to differences in the frequency of the stimuli presented, just as in other studies (cf. Bensmaïa & Hollins, 2000; Bensmaïa, Hollins, & Yau, 2005). The hit rate for each different pair was calculated as the proportion of trials that each pair differing in frequency was correctly judged as different. The false alarm rate indicated the proportion of times that the each pair of stimuli with the same frequency was judged as different. For each frequency range and each modality pairing (i.e., auditory-auditory, tactile-tactile, tactile-auditory or auditory-tactile) d´s were determined using the "differencing rule" tables in the Appendix of Macmillan and Creelman (2005).

Next, an analysis of variance (ANOVA) was performed with the within-participants factors of Modality Pairing (i.e., auditory-auditory, tactile-tactile, tactile-auditory or auditory-tactile) and Frequency (i.e., 12-24Hz, 16-24Hz, 20-24Hz, 28-24Hz, 32-24Hz, and 36-24Hz). The analysis revealed a significant main effect of Modality Pairing, F(2,24)=11.23; p<.001. The results indicated that the participants' ability to match a difference in frequency between the standard and the test was higher when both of the stimuli were auditory (i.e., d´=3.03) than when both were tactile (d´=1.98, p=.047) or when the stimuli were presented in different modalities (d´=1.39; p=.002), but the difference between tactile and crossmodal stimulus pairings was not significant (p=.18; see Figure 6).

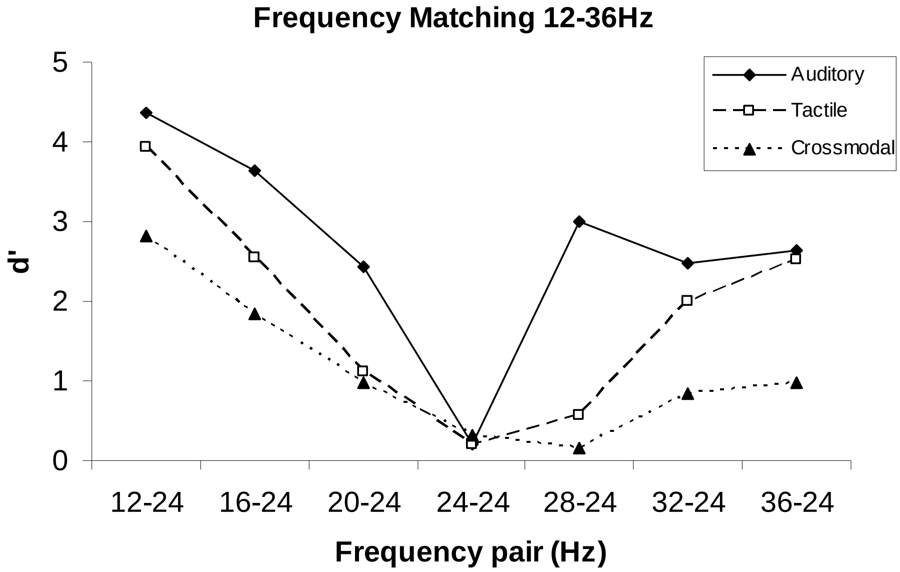

Figure 6. d' values observed for each stimulus pairing in the Experiment 4. Each line represents one of the three conditions tested (i.e., auditory, tactile, and crossmodal).

The analysis also revealed a significant main effect of Frequency, F(5,60)=34.46; p<.001, showing an increase in the difficulty of discriminating the difference in frequency as a function of the step in the frequency range, with comparison stimuli having a higher frequency difference (as compared to the standard) being more easily discriminated as compared to comparison stimuli having a smaller frequency difference as compared to the standard. This speculation was confirmed by post-hoc comparisons. The summary of the significant terms is reported in the Table 5.

	12-24Hz	**16-24Hz**	**20-24Hz**	**28-24Hz**	**32-24Hz**	**36-24Hz**
12-24 Hz	---	p<.001	p<.001	P<.001	p<.001	p<.001
16-24 Hz	p<.001	---	p=.001	P<.001	n.s.	n.s.
20-24 Hz	p<.001	p=.001	---	n.s.	n.s.	p=.009
28-24 Hz	p<.001	p<.001	n.s.	---	p=.009	p=.009
32-24 Hz	p<.001	n.s.	n.s.	P=.009	---	n.s.
36-24 Hz	p<.001	n.s.	p=.009	P=.009	n.s.	---

Table 5. d’ values across the levels of the Frequency factor (Experiment 4).

Effects of order and modality of the standard stimulus

In order to test for the effect of the order of the standard and comparison stimulus within the stimuli pair, an additional analysis was performed with the factors of Order (i.e., first or second) of the standard stimulus and of Frequency (i.e., 12-24Hz, 16-24Hz, 20-24Hz, 28-24Hz, 32-24Hz and 36-24Hz). The analysis revealed a significant main effect of the Order, F(1,13)=14.60; p=.002, with higher sensitivity being reported when the standard stimulus was presented as first within the stimulus pairing (i.e., d´=2.26 vs. 1.89). The effect of Frequency was also significant, F(5,65)=32.62; p<.001 (see above). The interaction between Order and Frequency was not significant, F(5,65)<1; n.s.

An additional analysis was performed to test the effect of the modality (i.e., tactile or auditory) of the standard stimulus at each frequency (i.e., 12-24Hz, 16-24Hz, 20-24Hz, 28-24Hz, 32-24Hz, and 36-24Hz). The analysis revealed a significant effect of the Modality, F(1,13)=16.75; p=.001, with greater sensitivity shown when the standard stimulus was presented auditorily (d´=2.71) than when it was presented in touch (d´=1.54). As expected (see above), the effect of Frequency was also significant, F(5,65)=9.54; p<.001. The interaction between Modality and Frequency was not significant, F(5,65)<1, n.s.

8.3. Experiment 5. Audiotactile frequency matching in the vibration range

In Experiment 5, frequencies within the vibration range (i.e., frequency higher than 40 Hz; Bendor & Wang, 2007; LaMotte & Mountcastle, 1975) were tested. The standard stimulus was presented at a fixed frequency of 60 Hz, whereas the test stimulus was presented at frequencies of 48, 52, 56, 60, 64, 68 or 72 Hz.

8.3.1. Method

Participants. The same participants as Experiment 4 took part in this experiment.

Apparatus, materials, design, and procedure. These were the same as for Experiment 4, with the following exception: We tested frequencies in the range 48-72 Hz. The standard stimulus was presented at a frequency of 60 Hz, whilst the test stimuli were presented at frequencies of 48, 52, 56, 60, 64, 68 or 72 Hz. Hence, each vibratory tactile stimulus consisted of a sequence of brief pulses repeated as many times as according to the frequency of the stimulus (i.e., 24, 26, 28, 30, 32, 34, 36 Hz). The time interval between the onsets of successive pulses of a vibratory tactile stimulus was 18, 16, 14, 12, 11, 10, 9 ms, respectively. The interval between the onset of the first pulse and the offset of the last pulse was of 500 ± 2 ms.

8.3.2. Results.

As in Experiment 4, the same-different paradigm was applied (Macmillan & Creelman, 2005) to derive participants' sensitivity to differences in the frequency of the stimuli presented. An ANOVA was conducted with the within participants factors of Modality Pairing (i.e., auditory-auditory, tactile-tactile, tactile-auditory, or auditory-tactile) and Frequency (48-60Hz, 52-60Hz, 56-60Hz, 64-60Hz, 68-60Hz, 72-60Hz). The analysis revealed a significant main effect of Modality Pairing, F(2,26)=44.40; p<.001, with participants responding more accurately when discriminating the stimulus pairing presented in the auditory modality (d´= 3.59) than when discriminating stimuli presented in the tactile modality (d´= 0.77; p<.001), or across modalities (d´= 0.79; p<.001). There was no difference between tactile and crossmodal stimulus pairings (p=1.00; see Figure 7).

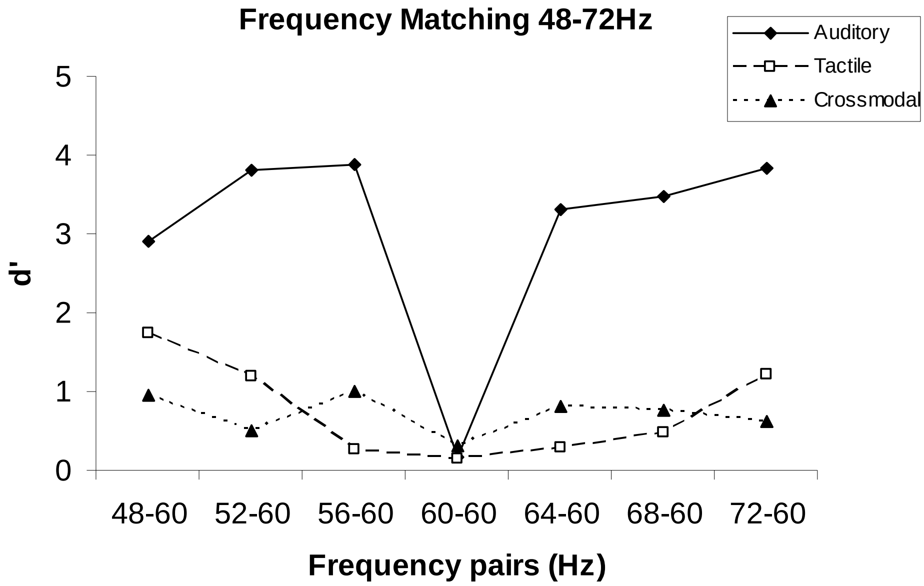

Figure 7. d' values observed for each stimulus pairing in the Experiment 5. Each line represents one of the three conditions tested (i.e., auditory, tactile, and crossmodal).

There was no main effect of Frequency, F(5,65)=1.64; p=.19. The interaction between Modality Pairing and Frequency Range was, however, significant, F(10,130)=3.64; p=.008. This interaction shows that performance was modulated by the frequency similarity of the stimuli presented in the tactile modality, F(5,65)=7.27; p<.001, but not in the auditory modality, F(5,65)=2.12; p=.11, or in the crossmodal condition, F(5,65)<1; n.s. The tactile stimulus pairings with higher frequency differences were more easily discriminable than pairs with a smaller frequency difference. Post-hoc comparisons were calculated to further evaluate significance levels. The summary of the significant terms is reported in Table 6.

Unimodal Tactile						
	48-60 Hz	**52-60 Hz**	**56-60 Hz**	**64-60 Hz**	**68-60 Hz**	**72-60 Hz**
48-60 Hz	---	p=.043	p=.002	p=.001	p=.007	n.s.
52-60 Hz	p=.043	---	p=.011	p=.005	n.s.	n.s.
56-60 Hz	p=.002	p=.011	---	n.s.	n.s.	n.s.
64-60 Hz	p=.001	p=.005	n.s.	---	n.s.	P=.005
68-60 Hz	p=.007	n.s.	n.s.	n.s.	---	P=.026
72-60 Hz	n.s.	n.s.	n.s.	p=.005	p=.026	---

Table 6. d' values across the levels of the Frequency factor within touch (Experiment 5).

An additional analysis performed with the factors of Order (i.e., first or second) of the standard stimulus and Frequency (48-60Hz, 52-60Hz, 56-60Hz, 64-60Hz, 68-60Hz, 72-60Hz) revealed a significant effect of Order, F(1,13)=7.20; p=.02, with higher sensitivity being observed when the standard stimulus was presented first in the stimulus pairing (i.e., d´= 1.88 vs. 1.00). The effect of Frequency was also significant, F(5,65)=4.66; p=.001, with sensitivity differing between the pairs 48-60Hz and 64-60Hz (d´= 2.00 vs. 1.35). The interaction between Order and Frequency was not significant, F(5,65)=1.44; p=.22.

An additional analysis testing the effect of the modality (i.e., tactile or auditory) of the standard stimulus for each frequency (48-60Hz, 52-60Hz, 56-60Hz, 64-60Hz, 68-60Hz, and 72-60Hz) revealed a significant effect of Modality, F(1,13)=27.83; p<.001, with higher sensitivity being reported when the standard stimulus was presented in audition (d´=2.53) than in touch (d´=0.81). The effect of Frequency was significant, F(5,65)=4.55; p=.006 (see above). The interaction between Modality and Frequency was not significant, F(5,65)<1; n.s.

8.4. General discussion of Experiments 4 and 5

In Experiments 4 and 5, we investigated the ability of people to discriminate pairs of auditory and vibrotactile stimuli having either the same or different frequency. The pairs of stimuli could either be presented within the same sensory modality (i.e., audition or touch) or else in different modalities (i.e., one in touch and the other in audition), and were presented in either the flutter or vibration range (Experiments 4 and 5, respectively). Irrespective of the range tested, the results of both experiments showed that the ability to discriminate (and thus match) the stimuli when both are presented in audition was significantly higher than when the stimuli were both presented in touch or across modalities (i.e., one in touch and the other in audition). The finding showing that frequency discrimination in audition is highly accurate is consistent with evidence showing that below 4000 Hz humans can detect a frequency difference of 0.2% (Moore, 1973; see also Pollack, 1968; Sams, Paavilainen, Alho, & Näätänen, 1985). Visual inspection of the data (see Figures 6 and 7) would also appear to suggest a trend toward more accurate auditory frequency discrimination in the vibration (vs. flutter) range[5]. These data are consistent with previous evidence

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[5] In order to investigate whether any difference could emerge from the performance across the experiments, we performed an additional ANOVA with the factors of Range (i.e., Flutter vs. Vibration), Modality Pairing (i.e., auditory-auditory, tactile-tactile, tactile-auditory or auditory-tactile) and Frequency Interval (i.e., 12-24Hz or 48-60Hz, 16-24Hz or 52-60Hz, 20-24Hz or 56-60Hz, 28-24Hz or 64-60Hz, 32-24Hz or 68-60Hz, and 36-24Hz or 72-60Hz). The analysis failed to highlight a significant overall difference between the two frequency ranges, F(1, 12)=3.81; p=.08. There was, however, a significant main effect of Modality Pairing, F(2,24)=33.8; p<.001, with participants performing better when matching the auditory stimuli than when matching the tactile stimuli, t(13)=5.67; p<.001, and stimuli across modalities, t(13)=7.16; p<.001, and no difference emerging from the comparison between the tactile stimuli and crossmodal stimuli, t(13)<1; n.s. Of interest in terms of the present study is the finding that better performance was observed in the flutter (vs. vibration) range in matching the tactile stimuli, t(13)=3.4; p=.01 and no significant difference for the stimuli

showing better discriminative performance for higher vs. lower frequency ranges (Pollack, 1968, 1990), and add to studies suggesting that there may be a segregation in the perceptual analysis of different auditory percepts (e.g., Deutscher et al., 2006). Whereas the frequency discrimination of auditory stimuli within the flutter range is modulated as a function of the frequency difference between the standard and the comparison stimuli, giving rise to a U-shaped pattern of results (see Figure 6), frequency discriminating performance for high-frequency auditory stimuli does not exhibit this profile. Indeed, in this frequency range, the discrimination performance does not significantly differ across different pairings of stimuli (see Results section of Experiment 5 and Figure 7). However, as can be inferred from Figure 7, the high level of accuracy reported within this frequency range in the auditory modality could have reduced the effect of the frequency discrepancy between the standard and comparison stimuli.

Within the flutter range, participants' ability to discriminate the frequency differences was very accurate not only in the auditory but also in the tactile modality. A large body of research has investigated the performance of both monkeys (de Lafuente & Romo, 2005; Hernández et al., 1997; Mountcastle et al., 1972; Mountcastle et al., 1990; Romo & Salinas, 2003) and humans (Bensmaïa, Hollins, & Yau, 2005; LaMotte & Mountcastle, 1975; Mountcastle et al., 1972; Talbot et al., 1968; Verrillo, 1985) in decoding the frequencies of vibrotactile stimuli. In particular, LaMotte and Mountcastle compared the capability of both monkeys and humans to discriminate pairs of frequencies presented within the flutter range (i.e., standard stimulus of 30 Hz and comparison stimuli presented at higher or lower frequencies, from 24 to 36 Hz) matched for subjective intensity. The results not only show that the capacity for frequency discrimination is comparable between the two species (see also Mountcastle et al., 1972), but also that the human ability to detect changes in the frequency of the stimuli is surprisingly good (e.g., LaMotte & Mountcastle, 1975; Mountcastle et al., 1972; Talbot et al., 1968). The results of Experiment 5, in which discrimination of higher frequencies was investigated, suggest that human discrimination ability within the higher frequency

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across the modalities, t(13)=.05. A trend towards higher sensitivity in discriminating vibration (vs. flutter) auditory frequencies also emerged for the auditory stimuli, t(13)=.06.

range is somewhat lower, even though not significantly, than the flutter range tested in the Experiment 4 (see Footnote 5). Previous studies provided controversial evidence on the differential discrimination ability of vibrotactile stimuli within higher frequency ranges (e.g., Tommerdahl, Delmos, Whitsel, Favorov, & Metz, 1999). Goff (1967) showed that the differential threshold curve of vibratory frequency discrimination (varying between 25 and 800 Hz) starts to sharply rise for frequencies close to 50 Hz. On the contrary, Mountcastle and his coworkers (1990) failed to observe any decrease in discriminatory performance when testing shifted from the flutter (i.e. 5-40 Hz) to the vibration range (i.e., 100 and 200 Hz) and difference limens which yielded Weber fractions below 10%. In the present study, an overall decrease in the accuracy in discriminating tactile frequency in the vibration (vs. flutter) range can be seen. In both experiments reported in this study, however, a modulation of the accuracy performance as a function of the frequency difference between the standard and the comparison tactile stimuli can be observed.

The novelty of the present study consists primarily in the introduction of the crossmodal condition, by presenting in each pair of stimuli, one tactile and one auditory stimulus. To the best of our knowledge, no previous investigations have been carried out in order to study the proficiency of humans in crossmodally matching stimuli having different frequencies. This is surprising, given that there is evidence to suggest a potential neural basis for the discrimination of frequencies delivered across modalities (cf. Bendor et al., 2007). Indeed, neurons whose spike rate can be positively or negatively related to the stimulus repetition rate have been observed not only in the auditory cortex, but also in the somatosensory cortex in SII (Bendor & Wang, 2007; Salinas et al., 2000). The fact that neurons showing positive and negative monotonic tuning to stimulus repetition rate could be observed in both auditory and somatosensory cortices (Luna et al., 2005; Salinas et al., 2000) points to a commonality in how these two sensory systems might encode variations in the temporal profile of, respectively, auditory and vibrotactile stimuli (Bendor & Wang, 2007; Wang et al., 2008; see also Soto-Faraco & Deco, 2009).

The results of both experiments in the present study show that the d′ rates for the crossmodal condition were lower than the ones reported for both the auditory-only and the tactile-only conditions. Even though the difference between the tactile-only and the crossmodal conditions did not reach significance, the matching of the frequencies presented across modalities turned out to be the hardest condition to perform. (see Results section). It is well known that tasks requiring the comparison and matching of sensory dimensions arising from different sensory channels are subject to methodological constraints, such as decisional as well as perceptual biases (Pepermans & Corlett, 1983; Poulton, 1989). Thus, it is plausible that these factors, that of necessity affect crossmodal judgments, could have contributed to the lower proficiency shown by participants in matching frequencies presented across modalities as compared to the conditions where the frequencies were presented within a single sensory modality in the present study. It must be noted, however, the representation of d′ rates reported for audiotactile stimuli presented in the flutter range yielded a U-shaped response function with its minimum at the lowest frequency difference between the standard and comparison stimulus. Hence, it seems that in this frequency range, performance is modulated by the frequency disparity existing between the standard and comparison stimulus, with better performance for pairs of stimuli differing more in their temporal profile.

The results reported here are nevertheless consistent with the data reported in previous studies investigating the ability of people to match visual and auditory periodic pulse trains differing in frequency (e.g., Benjamins, van der Smagt, & Verstraten, 2008; Fujisaki & Nishida, 2005). For instance, Fujisaki and Nishida showed that the temporal limits in frequency matching significantly differ across the conditions of stimulation, being lower in the crossmodal than within-modality conditions. Fujisaki and Nishida’ data could be due to the fact that the coding of the temporal patterns of visual and auditory stimuli is based on the comparison of the temporal features preliminarily coded within each sensory stream. Moreover, similar to what has been found in the present study, the performance of audio-visual frequency matching is also modulated by the frequency range tested, with accuracy decreasing as a function of frequency increase of the stimuli presented. The authors attribute these results to the stronger tendency for higher-frequency stimuli to be bound together within each modality, thus limiting the participants' ability to perform the task in which a crossmodal comparison is required. Even though a direct comparison between the results observed in those studies with the ones obtained in the present study cannot be made, because of the discrepancies in both the experimental design (i.e., simultaneous presentation vs. two-interval forced choice) and the task requirements, both studies indicate that participants find the crossmodal condition harder to perform than the unimodal conditions.

In summary, the results of Experiments 4 and 5 show that people are able to match the frequencies of stimuli presented within audition (cf. Plack, 2004; Pollack, 1968). In touch, performance is modulated as a function of the frequency range tested, with higher level of accuracy shown within the flutter than in the vibration range (see Footnote 5; cf. LaMotte & Mountcastle, 1975; Mountcastle et al., 1990). The novel condition introduced here (i.e., audiotactile crossmodal frequency matching) turned out to be the most difficult condition for our participants to perform in both frequency ranges tested. However, it should be noted that, despite the difficulty in matching the temporal rates of auditory and tactile frequency stimuli, in the flutter range the pattern of participants' performance was modulated by the magnitude of the discrepancy between the standard and comparison stimuli. Thus, despite the fact that the participants showed worse (i.e., less sensitive) performance in this condition as compared to the within-modality conditions, a certain degree of proficiency in matching the frequency feature across modalities can be observed, selectively for stimuli presented in the low- (vs. high-) frequency range (cf. Footnote 5).

Chapter 9.

Interactions between touch and hearing in the spatial domain

9.1. Introduction

As documented previously (see Chapters 1 and 2), hearing and skin sensations share many functional similarities, as both might be induced by the mechanical stimulation (i.e., changes in pressure and/or vibratory rates) of, respectively, the basilar membrane and the skin (see Gescheider, 1970; Sherrick, 1970; von Békésy, 1959). If it is true that auditory and tactile stimuli are in some sense physically linked, it might be argued that the pattern of results reported by Soto-Faraco and his collaborators (2004b) could be strictly related to the particular nature of the stimuli used in that study. If this were to be the case, the asymmetric crossmodal capture effect they reported could be reduced, or even reversed, by manipulating the specific properties of the stimuli presented in one of the two stimulus modalities.

In the next two experiments, we explicitly tested whether, and to what extent, the change of the complexity of auditory stimuli (i.e., noise vs. pure tone; Experiment 6) and the sound intensity (i.e., 75 vs. 82 dB; Experiment 7) would affect the crossmodal capture effect between audition and touch in a crossmodal dynamic capture task. We examined the effect of varying on the audiotactile crossmodal dynamic capture effect. Participants discriminated the direction of a target stream (tactile or auditory) while simultaneously trying to ignore the direction of a distracting auditory or tactile apparent motion stream presented in a different sensory modality (i.e., auditory or tactile). The distractor stream could either be spatiotemporally congruent or incongruent with respect to the target stream on each trial (see Section 4.7 for further details).

It is well-known that auditory stimuli of different complexities are processed by segregated cortical areas, in both monkey (e.g., Kajikawa, de La Mothe, Blumell, & Hackett, 2005) and man (Hall, Edmondson-Jones, & Fridriksson, 2006; Schönwiesner, Rübsamen, & von Cramon, 2005; Schroeder et al., 2001. See also Section 5.6).

To date, the majority of studies that have investigated the effect of sound complexity on audiotactile interactions have examined the space surrounding the face, with far less research investigating audiotactile links in those regions of space that surround the other parts of the body (e.g.., the hands). Fu and colleagues (2003) explored the somatosensory afferences to the caudomedial region of macaque auditory cortex, a region known to respond preferentially to complex white noise stimuli. Fu et al. highlighted the existence of sites within this area that were also responsive to cutaneous stimulation of the hand, suggesting the potential existence of a neural system subserving the integration of tactile and complex auditory signals delivered to portions of the body other than the head (i.e., in peri-hand space).

It should be noted that the manipulation of the spectral complexity of auditory stimuli is also likely to affect their localizability. Indeed, it has been documented that spectrally-dense auditory stimuli (i.e., stimuli that contain a wide range of frequencies) are advantageous for the encoding of interaural time differences (see Middlebrooks & Green, 1991, for a review), thus rendering complex sounds more easily localizable than stimuli composed of just a single frequency (e.g., Catchpole, McKeown, & Withington, 2004).

In an influential paper, Alais and Burr (2004) showed that the manipulation of the localizability of the auditory stimuli significantly affects the outcome of the process by which the information from different sensory modalities (vision and audition, in their case) is integrated. Since spatial resolution is usually superior in vision than in audition, auditory stimuli are typically mislocalized toward the position of temporally synchronized visual stimuli in audiovisual ventriloquism studies (e.g., Slutsky & Recanzone, 2001). However, Alais and Burr showed that if a visual stimulus is blurred spatially (such that the localization of that visual stimulus is impaired), sounds may bias participants' judgments regarding the localization of simultaneously-presented visual stimuli. These findings show that the ventriloquism effect results not from one modality 'capturing' the other but rather from a near-optimal estimation of the spatial cues, where the information is weighted according to the relative uncertainty of the information conveyed by each modality. Therefore, the stimulus from the modality that is more precisely localizable (i.e., the variance related to the localization judgments is lower; see Ernst & Bülthoff, 2004), also provides the most reliable spatial information thus increasing its weight.

On the basis of this evidence, the manipulation of the complexity (and thus localizability) of the auditory stimuli in the Experiment 6 should influence the estimation of the inputs from each sensory modality and the relative weight each modality acquires in the task under investigation. More specifically, it should be expected that for auditory targets, the use of noise stimuli should increase the reliability of localization information compared with pure tone stimuli. Hence, tactile task-irrelevant motion should result in a more distracting influence on the auditory pure tone stream than on the noise stream. Conversely, for tactile targets, the auditory distractors are likely to be more reliable when they consist of noise than when they consist of pure tone stimuli, thus resulting in a stronger crossmodal capture of tactile target in the former condition.

In Experiment 7, the auditory stimuli could be presented at one of two sound intensities (75 or 82 dB(A)). Given that stimulus intensity is a dimension that is inherent to the stimuli presented in all sensory modalities, previous studies have investigated how this dimension can be differentially coded and compared across the senses (see also Section 2.3). For instance, Marks has repeatedly tried to quantify the perceptual similarity of stimulus intensity across differing sensory modalities and to what extent these crossmodal equivalences can be considered absolute (e.g., see Marks, 1988; Marks, Szczesiul, & Ohlott, 1986). Meanwhile, other researchers have investigated how the concurrent presentation of vibrotactile stimuli affects the perceived intensity of auditory stimuli. For example, Schürmann, Caetano, Jousmäki, and Hari (2004) have shown facilitatory interactions between simultaneously-presented auditory and tactile stimuli (i.e., enhanced audiotactile multisensory interactions have been reported at low intensities of auditory and tactile stimuli). Similarly, Gillmeister and Eimer (2007) have recently shown that the tactile enhancement of auditory loudness is more pronounced when sounds are presented at a lower stimulus intensity, and that this effect declines with increasing auditory intensity. The most important difference between these previous studies and the present one lies in the methodology adopted: in previous studies, the participants were explicitly required to judge the intensity of the perceived stimuli. By contrast, in the present study, the effect of stimulus intensity on performance was tested indirectly by comparing the magnitude of the observed crossmodal dynamic capture effect, by varying from block to block both the intensity of the sound (i.e., 75 vs. 82 dB(A)) and the target modality (i.e., tactile or auditory).

If the manipulation of this dimension is crucial for the stimuli presented in one sensory modality to influence those presented in another, one might expect that when the target modality is presented auditorily, the tactile distractor motion should induce a stronger influence on the less intense auditory stream than on the more intense stream. Conversely, the crossmodal capture effect of tactile target motion should be stronger when the task-irrelevant motion is constituted by more intense rather than by less intense auditory stimuli. Therefore, the magnitude of the congruency effect between audition and touch and between touch and audition should vary as a function of the intensity of the auditory stimuli.

9.2. Experiment 6. Assessing the effect of sound complexity on audiotactile crossmodal dynamic capture

9.2.1. Method

Participants. Twenty-two blindfolded participants took part in this study (14 female; mean age of 27 years; range: 21-49 years). All of the participants reported normal hearing and tactile sensitivity. The experiment took approximately 45 minutes to complete and was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki (most recently amended in 2004, Tokyo). All of the participants gave their informed consent prior to their inclusion in the study.

Apparatus, materials, design, and procedure. Two loudspeaker cones (Dell, A215; Round Rock, TX) positioned on the table-top in front of the participant were used to present the auditory stimuli. The loudspeaker cones were placed approximately 50 cm from the participant’s body, 15 cm to either side of their midline. Two vibrotactile stimulators (bone conduction vibrators, Oticon-A, 100 Ohm; Hamilton, Scotland) were placed in front of each loudspeaker cone, to ensure that the sounds and vibrations came from the same location. Each stimulator was activated by the same sound file that was used to generate the auditory stimuli. Participants responded by means of footpedals located under the table (one beneath the toes of their right foot and the other beneath the toes of their left foot). The loudspeaker cones, vibrotactile stimulators, and footpedals were all controlled via a computer parallel port using the E-Prime programming language (http://www.pstnet.com), and a custom-built relay box. The experiment was conducted in a dimly-illuminated room. The auditory stimuli consisted of two 50-ms sounds (82 dB(A) sound pressure level as measured from the participant’s head position; bandwidth of the noise stimuli: 20-10,000 Hz), one presented from each loudspeaker cone, separated by a 100 ms inter-stimulus-interval (ISI; this ISI remained constant across all conditions). The tactile displays consisted of two 50-ms suprathreshold vibrations, one presented from each vibrator separated by an ISI of 100 ms[6].

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[6] From the company producing the vibrotactile stimulators (bone conduction vibrators, Oticon-A, 100 Ohm; Hamilton, Scotland) we know that the band of frequency activating the stimulators is included within the range 200-4000 Hz, with the frequencies most suitable for its operation include those frequencies within the range 550-750 Hz (as from the data sheet provided by the company).

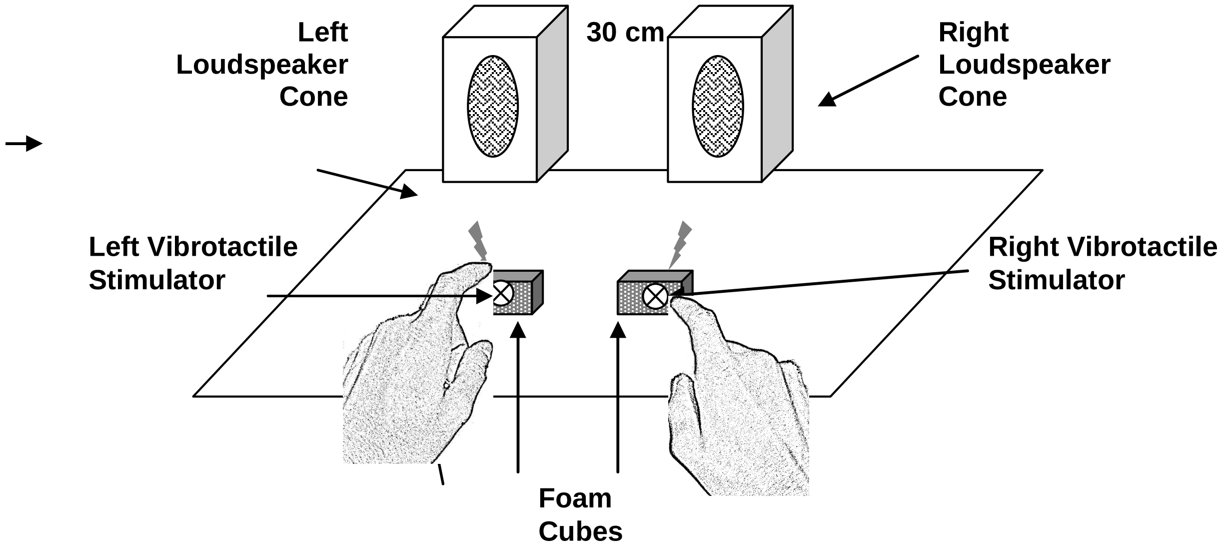

Figure 8. Schematic diagram illustrating the experimental set-up.

Procedure. The participants sat in front of the loudspeaker cones. The two vibrotactile stimulators placed directly in front of the loudspeaker cones lay on two foam rectangles (3 cm thick) in order to attenuate any noise resulting from their operation. The participants had to rest their left index fingertip on the left vibrotactile stimulator and their right index fingertip on the right vibrotactile stimulator. The participants were instructed to rest their feet on the footpedals and to keep their head still while looking straight ahead throughout each block of experimental trials. 75 dB noise (bandwidth: 20-10,000 Hz) was presented throughout the experimental session from two loudspeaker cones positioned behind the loudspeaker cones used to present the target stimuli (60 cm from the participant) in order to mask any subtle auditory cues elicited by the activation of the vibrotactile stimulators. In each condition (auditory or tactile targets), the participants were presented with two blocks of 96 trials. In one block, the auditory stimuli consisted of noise, while in the other block the auditory stimuli consisted of pure tones. Block order was counterbalanced across participants (i.e., half participants started the experimental session performing the tactile target blocks and the other half performing the auditory target blocks). To discourage participants from focusing on any potential subtle acoustic differences between the loudspeaker cones that might have helped them to perform the task, the frequency of the pair of pure tones comprising the auditory sequence in each trial was varied between three possible values (450, 500, and 550 Hz; note that these values were based on those used in previous studies: Sanabria et al., 2005; Soto-Faraco et al., 2004b). In a typical trial, the participants were presented with the target stream to which they had to make an unspeeded footpedal discrimination response, and a distractor stream, which they were instructed to try and ignore. The distractor stream could either be presented at the same time as the target auditory stream (synchronous) or 500 ms later (asynchronous) and in either the same (congruent) or opposite (incongruent) direction (from right-to-left or left-to-right). The participants were instructed to respond to the direction of the target stream (tactile in the first condition, auditory in the second) by releasing the corresponding footpedal (left for leftward moving targets, and right for rightward moving targets) and to ignore the distractors (auditory in the first condition, tactile in the second) as much as possible. The participants were asked to prioritize response accuracy over response speed. Responses were only collected 750 ms after the beginning of the trial, in order to ensure that any lack of an effect of the distractors on the perception of the target stream in the asynchronous condition was not caused simply by the participants responding to the target before the distractors had been presented (see Soto-Faraco et al., 2004b, on this point). After a response had been recorded, there was a random interval (of 1900, 1950, 2000, 2050, or 2100 ms) before the start of the next trial. At the end of each block of trials, the participants were instructed to use two 7-point Likert scales in order to judge the strength of the perception of apparent movement elicited by the target stream (1 = no sensation of movement; 7 = high sensation of movement) and their confidence in their response (1 = no confidence in their response; 7 = high confidence in responses). The participants completed one block of 12 practice trials at the start of each experimental session in which the target streams were presented in the absence of any distractors, to familiarize them with the task at hand.

9.2.2. Results

The accuracy data were normalized using the arcsine transformation of the square root of the proportion obtained in each condition for each participant. This procedure converts binomially distributed data, such as proportions, into normally distributed data, thus enabling parametric analysis of one’s data (Bartlett, 1947). First, performance in the practice (i.e., unimodal) trials did not differ significantly amongst the various conditions, F(3,63)<1; n.s.: tactile stimuli (M= 99%, standard error of the mean, SEM=.70), pure tone auditory stimuli (M=97%, SEM=1.53) and noise burst stimuli (M=98%, SEM=.97). Next, for each experimental condition (i.e., tactile or auditory apparent motion target), the transformed accuracy data were submitted to repeated measures analysis of variance (ANOVA) with Synchrony (Synchronous vs. Asynchronous), Sound Type (Pure Tone vs. Noise), and Congruency (Congruent vs. Incongruent) as the within-participants factors. Post-hoc Bonferroni adjustments were calculated to further evaluate significance levels.

In the first experimental condition (i.e., tactile apparent motion target presented with auditory distractors) the overall analysis revealed main effects of Synchrony, F(1,21)=75.59; p<.001, with participants responding more accurately in the asynchronous condition than in the synchronous condition overall (M = 95%, SEM=2.12 vs. 76%, SEM=2.98, respectively). The main effect of Congruency was also significant, F(1,21)=87.09; p<.001, with participants responding more accurately in congruent than in incongruent trials overall (M = 95%, SEM=1.33 vs. 71%, SEM=3.34 respectively). Participants also responded more accurately in the Pure Tone auditory distractor condition than in the Noise distractor condition (M = 86%, SEM=2.45 vs. 81%, SEM=2.06, respectively), giving rise to a main effect of Sound Type, F(1,21)=21.12; p<.001. There was a significant interaction between Congruency and Synchrony, F(1,21)=49.69; p<.001, attributable to a significant effect of Congruency being present in the synchronous condition, t(21)=10.06; p<.001, but not in the asynchronous condition, t(21)=1.41; p=.17. Crucially, the interaction between Sound Type and Congruency was also significant, F(1,21)=4.45; p=.047, reflecting the fact that the congruency effect (measured as the difference in accuracy between the congruent and incongruent conditions) was bigger with noise than with pure tone auditory distractors (30% vs. 18%, respectively). Neither the interaction between Synchrony and Sound Type, F(1,21)=1.47; p=.24, nor the three-way interaction between Congruency, Synchrony, and Sound Type, F(1,21)=.45; p=.51, reached significance.

In the second experimental condition (i.e., auditory apparent motion target presented with tactile distractors), the transformed accuracy data were submitted to a repeated measures ANOVA with Synchrony (Synchronous vs. Asynchronous), Sound Type (Pure Tone vs. Noise), and Congruency (Congruent vs. Incongruent) as the within-participant factors. The analysis revealed a significant main effect of Sound Type, F(1,21)=5.80; p=.025, with participants responding more accurately to noise (M=98%, SEM=.50) than to pure tone target (M=95%, SEM=1.53) streams. Neither the main effect of Congruency, F(1,21)=3.15; p=.90, nor the main effect of Synchrony, F(1,21)=.34; p=.57, reached significance. None of the other terms reached significance.

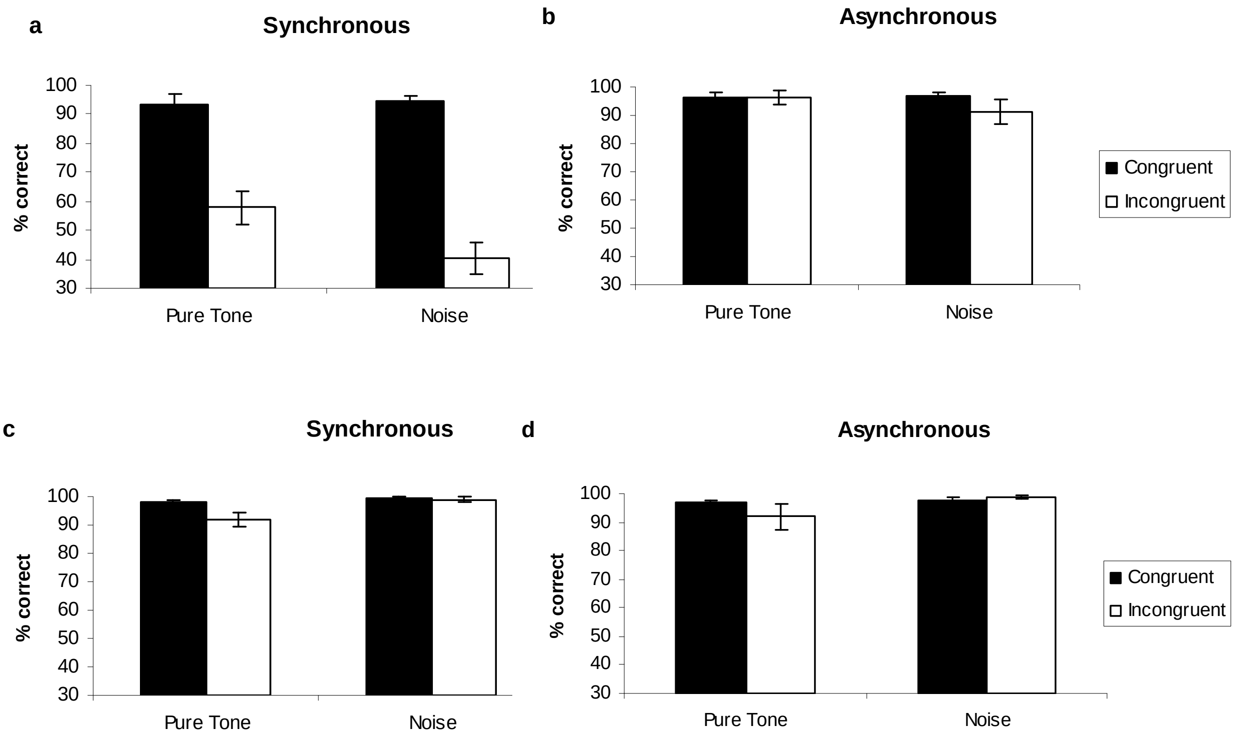

Figure 9. Mean percentage of correct responses in the tactile (a and b) and the auditory (c and d) direction discrimination tasks as a function of Sound Type and Congruency in the synchronous (a and c) and asynchronous (b and d) conditions. The error bars represent the standard errors of the means.

Perceived apparent motion ratings. The Likert scale ratings of the impression of apparent motion were submitted to a repeated measures ANOVA with the factors of Target Modality (i.e., Touch vs. Hearing) and of Sound Type (i.e., Pure Tone vs. Noise).

The analysis showed a significant difference in the ratings of apparent motion between auditory and tactile streams, F(1,21)=12.22; p=.002, with higher impressions of motion conveyed by the auditory (vs. tactile) stimuli (M=5.52 vs. M=4.57). Neither the effect of Sound Type, F(1,21)=2.71; p=.12, nor the interaction between Target Modality and Sound Type, F(1,21)<1; n.s., reached significance.

Response confidence ratings. The Likert scale ratings of the impression of apparent motion were submitted to a repeated measures ANOVA with the factors of Target Modality (i.e., Touch vs. Hearing) and of Sound Type (i.e., Pure Tone vs. Noise). This analysis showed a significant main effect of Target Modality, F(1,21)=6.54; p=.02, suggesting that the confidence of participants' responses was higher in the auditory target blocks than in tactile target blocks (M=5.41 vs. M=4.68, respectively). The interaction between Target Modality and Sound Type was also significant, F(1,21)=6.41; p=.02, with participants being more confident when reporting the direction of the noise rather than the pure tone motion (M=5.77 vs. M=5.04, respectively), and when reporting the direction of tactile motion presented with pure tone (vs. noise) distractors (M=4.86 vs. M=4.50, respectively). This result is consistent with participants finding it easier to localize (and thus discriminate the direction of) the noise (vs. pure tone) auditory stimuli and being more captured by noise vs. pure tone distractors while discriminating the direction of tactile motion (see the Section 9.4 on these points). The analysis failed to reveal a significant main effect of Sound Type, F(1,21)=1.65; p=.21.

Condition	Target modality	Sound type	Perceived apparent motion ratings	Response confidence ratings
1	Tactile	Pure tone	4.50 (1.14)	4.86 (1.36)
		Noise	4.64 (1.14)	4.50 (1.10)
2	Auditory	Pure tone	5.27 (1.45)	5.05 (1.09)
		Noise	5.77 (1.41)	5.77 (1.11)

The standard deviations of the mean are reported in parentheses.

Table 7. Summary of the Likert scale ratings

9.3. Experiment 7. The effect of sound intensity on the audiotactile crossmodal dynamic capture effect

9.3.1. Method

Participants. Twenty blindfolded participants took part in this study (6 male and 14 female; mean age of 24 years; range from 19 to 44 years). All of the participants reported normal hearing and normal tactile sensitivity. The experiment took approximately 45 min to complete and was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki (most recently amended in 2004, Tokyo; see Blackmer & Haddad, 2005). All of the participants gave their informed consent prior to their inclusion in the study.

Apparatus, material, design and procedure. The experimental conditions and procedure as well as the spatiotemporal relations between the target and distractor modalities were the same as in the Experiment 6, except for the following differences. In the tactile target condition[7], the auditory distractor stimuli were presented at 75 dB(A) in one block, while in the other block, the auditory distractors were presented at 82 dB(A)[8]. The intensity of white noise used to mask any

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[7] To test whether the impression of apparent motion could be conveyed by the kind of stimulation utilized in the present study, we asked ten blindfolded control participants (5 male and 5 female; mean age of 25 years; range from 21 to 31 years) to rate the strength of apparent motion following unimodal stimulation (i.e., 12 streams presented in isolation). The mean apparent motion rates were 4.1 for the tactile motion, 4.0 for the quiet auditory motion, and 4.7 for the loud auditory motion, showing that an impression of motion was present (cf. Sanabria et al., 2005, for similar results).

[8] Ten blindfolded control participants (5 male and 5 female; mean age of 25 years; range from 21 to 31 years) were asked to evaluate whether the auditory stimuli (12 trials presented in the absence of any distractors) presented at the two intensities differed from each other. Six of the participants could not perceive any difference, two perceived a

subtle auditory cues elicited by the activation of the vibrotactile stimulators was also varied from block to block. The intensity of the white noise was set at 75 dB(A) for the blocks in which the auditory stimuli were presented at 82dB(A) and 70 dB(A) for those blocks in which the auditory stimuli were presented at 75 dB(A). The participants completed one block of 12 practice trials at the start of their experimental session in which the tactile streams were presented in the absence of any distractors, to familiarize them with the task at hand. In the auditory target condition, the participants now had to report the direction in which the auditory stimuli appeared to move whilst trying to ignore the tactile distractors (i.e., the roles of stimuli in the two modalities, as target and distractor, were reversed). Before starting the experiment the participants completed one block of 12 practice trials with less intense (75 dB(A)) or more intense (82 dB(A)) auditory stimuli presented in isolation (i.e., without the distracting tactile stimuli). Finally, the participants completed a second block of trials in which they had to respond to the direction of the unimodal auditory streams presented at the intensity not presented in the first unimodal block. The order of presentation of these unimodal blocks was counterbalanced across participants. The order of presentation of the blocks was counterbalanced across participants.

9.3.2. Results

For each experimental condition (i.e., tactile or auditory apparent motion target), the transformed accuracy data (see Section 9.2.2) were submitted to repeated measures analysis of variance (ANOVA) with Synchrony (synchronous vs. asynchronous), Sound Intensity (less vs. more intense), and Congruency (congruent vs. incongruent) as the within-participant factors. Post-hoc Bonferroni adjustments were calculated to further evaluate significance levels.

In the first experimental condition (i.e., tactile apparent motion target presented with auditory distractors), the overall analysis revealed a significant main effect of Synchrony, F(1,19)=78.77; p<.001, with the participants responding more accurately in the asynchronous

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difference, in a dimension other than the one manipulated (i.e., the louder stimuli were perceived as being “quicker” or “more similar” than the quieter stimuli), one perceived a difference but was unable to verbalize in which way they differed. Only one participant reported having perceived that the stimuli differed in intensity.

condition than in the synchronous condition overall (M = 94% vs. 69%, respectively). The main effect of Congruency (measured as the difference in accuracy between the congruent and incongruent conditions) was also significant, F(1,19)=133.83; p<.001, with participants responding more accurately in the congruent trials than in incongruent trials overall (M = 97% vs. 65%, respectively). There was a significant effect of Congruency in the synchronous condition (p<.001), but not in the asynchronous condition, (p = 1.00) (mean congruency effect of 58% and 5%, respectively), giving rise to the significant interaction between Congruency and Synchrony, F(1,19)=104.60; p<.001. The three-way interaction between Synchrony, Sound Intensity, and Congruency was also significant, F(1,19)=9.35; p=.006. In order to determine the cause of this interaction, we performed separate ANOVAs for each level of the Synchrony factor. The analysis of the data from the synchronous trials provided significant main effects of Sound Intensity, F(1,19)=4.63; p=.044, and of Congruency, F(1,19)=181.64; p<.001. The participants responded more accurately when presented with the less intense auditory distractors than with the more intense auditory distractors (M = 72% vs. 66% correct, respectively) and in congruent trials as compared to incongruent trials (M = 98% vs. 40% correct, respectively). The interaction between Intensity and Congruency was not significant, F(1,19)=2.98; p=.10. No significant terms emerged from the analysis of the data from the asynchronous trials. In fact, although the difference between the congruent and incongruent (less intense) trials had a magnitude of approximately 10% (see Table 8), the t-test comparison between these two conditions failed to reach significance, t(19) = 1.84, p=.08.

In the second experimental condition (i.e., auditory apparent motion target presented with tactile distractors), reported with unimodal trials involving the presentation of more vs. less intense sounds were submitted to a t-test comparison. Sound Intensity was found to effect participants' performance, t(19)= -2.13; p=.046, resulting in more accurate responses for the more intense sounds than for the less intense sounds (100% vs. 98%, respectively). Next, the transformed data from the experimental blocks were submitted to a repeated measures ANOVA with Synchrony (synchronous vs. asynchronous), Sound Intensity (less vs. more intense), and Congruency (congruent vs. incongruent) as the within-participant factors. Post-hoc Bonferroni adjustments were used to determine significance levels. The analysis revealed a significant main effect of Synchrony, F(1,19)=7.65; p=.012, with the participants responding more accurately in the asynchronous condition than in the synchronous condition (M = 98% vs. 96%, respectively). There was also a significant main effect of Congruency, F(1,19)=34.93; p<.001, with participants responding more accurately in the congruent trials than in the incongruent trials overall (M = 99% vs. 95%, respectively). There was also a significant main effect of Sound Intensity, F(1,19)=10.95; p=.004, with participants responding more accurately to the more intense auditory targets than to the less intense target stimuli (M = 99% vs. 96%, respectively). The Congruency effect (i.e., mean difference between incongruent vs. congruent condition) was significant in the synchronous trials (p<.001), but not in the asynchronous trials (M = 6% vs. 1%; p=1.00), giving rise to a significant interaction between Congruency and Synchrony, F(1,19)=10.31; p=.005. The Congruency effect was larger in the less intense auditory target trials (p<.001), than in the more intense auditory trials (p<.001; M = 5% vs. 1%, respectively), giving rise to a significant interaction between Congruency and Sound Intensity, F(1,19)=7.38; p=.014. The three-way interaction between Synchrony, Sound Intensity, and Congruency was also significant, F(1,19)=7.93; p=.011.

Separate ANOVAs were performed at each level of the Synchrony factor. In the synchronous trials, the main effect of Sound Intensity was significant, F(1,19)=10.45; p=.004, with participants responding more accurately in response to the more intense auditory targets than to the less intense targets (M = 99% vs. 93%, respectively). The main effect of Congruency was also significant, F(1,19)=27.37; p<.001 (M = 93% in incongruent vs. 99% in congruent trials). When the two apparent motion streams were concurrently presented moving in opposite directions, the probability that the participants would report having perceived the auditory motion as moving in the wrong direction (i.e., in the direction in which the distractor motion happened to move) was significantly higher if the target auditory motion consisted of the less intense (p<.001), rather than the more intense sounds (p<.001; congruency effect of 11% and 1%, respectively), giving rise to a significant interaction between Sound Intensity and Congruency, F(1,19)=12.25; p=.002.

No significant terms emerged from the analysis of the data from the asynchronous trials.

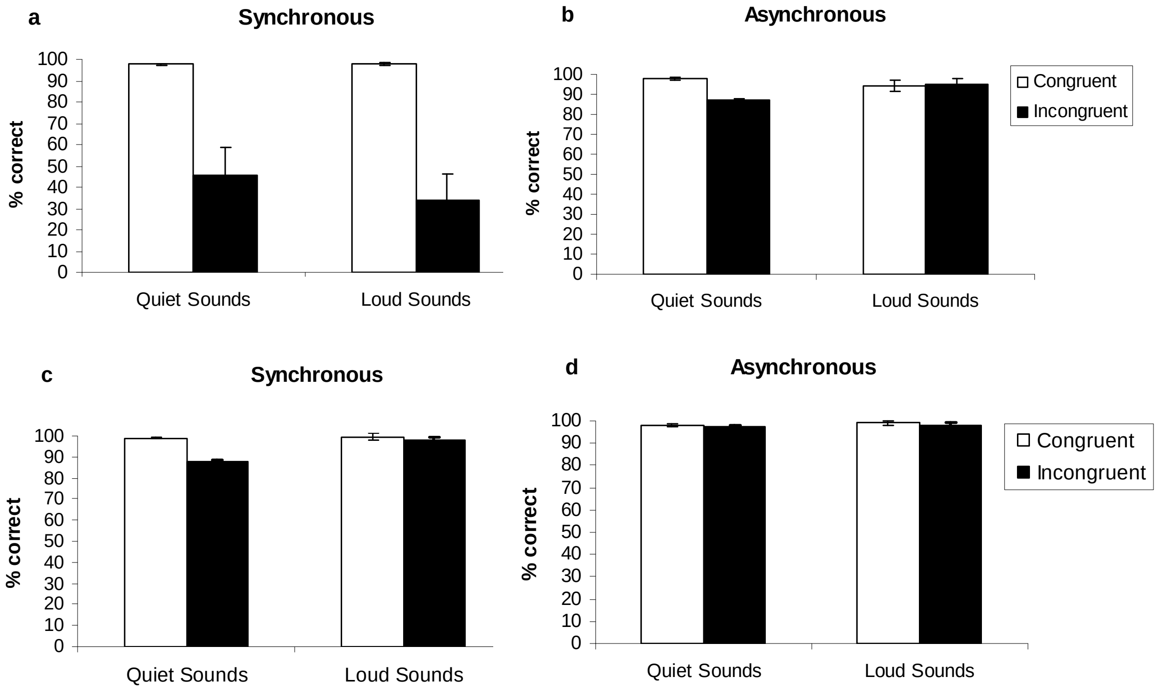

Figure 10. Mean percentage of correct responses in the tactile (a and b) and the auditory (c and d) direction discrimination tasks as a function of Sound Type and Congruency in the synchronous (a and c) and asynchronous (b and d) conditions. The error bars represent the standard errors of the means.

Perceived apparent motion ratings[9]. The ratings of apparent motion given by the participants (see Table 8) were subjected to a repeated measures ANOVA with Modality (touch vs. hearing) and

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[9] It is worth noting that the average rating for the impression of apparent motion experienced by the participants was not very high (fluctuating around a rating of 5). One may speculate whether the effect explored here somehow requires stimulus conditions that render the perception of the target motion “fragile” and if it would thus disappear with a more robust impression of motion. In order to address this point more specifically, we have reevaluated our data, calculating the median value of the ratings for the “goodness of motion” reported by all participants for each target modality (i.e., auditory or tactile), which was equal to 5. We then performed separate analysis for those participants whose mean ratings were higher than 5 and for participants whose ratings were lower than 5. This analysis revealed that the magnitude of the capture effect did not differ between the two groups (i.e., the interaction between the Group and Congruency factors was not significant, in either the auditory target blocks, F(1,18)=.25; p=.62, or in the tactile target blocks, F(1,18)=3.05; p=.10). These data suggest, therefore, that the strength of participants’ impression of apparent motion did not affect how the modalities interacted (at least within the range of stimulus values tested in the present study).

Those studies that have investigated how intramodal visual perceptual grouping modulates both audiovisual (Sanabria, Soto-Faraco, Chan, & Spence, 2005) and visuotactile (Lyons, Sanabria, Vatakis, & Spence, 2006) motion information have provided somewhat discordant results. In both studies, the task-irrelevant visual motion consisted of either six or two lights. The results consistently showed that the six-lights condition resulted in a significantly weaker crossmodal

Sound Intensity (less vs. more intense) as the within-participants factors. Neither the main effect of Modality, F(1,19)=.39; p=.54, nor of Sound Intensity, F(1,19)=.03; p=.86, or their interaction, F(1,19)=2.06; p=.17, reached the significance.

<u>Response confidence ratings</u>. Participants' confidence rating responses (see Table 8) were subjected to a repeated measures ANOVA with Modality (touch vs. hearing) and Sound Intensity (less vs. more intense) as the within-participants factors. The analysis revealed a significant main effect of Modality, F(1,19)=5.22; p=.034, with participants giving lower confidence ratings in the tactile target blocks that in the auditory target blocks (M = 4.6 vs. 5.2, respectively). The analysis also revealed a significant main effect of Sound Intensity, F(1,19)=9.75; p=.006, with participants giving lower confidence ratings in response to trials performed with less intense than with more intense auditory targets (M = 4.6 vs. 5.1, respectively). There was a significant interaction between Modality and Sound Intensity, F(1,19)=12.69; p<.001, with significantly lower confidence ratings being given in the less intense than in the more intense auditory target blocks (M = 4.6 vs. 5.8; p<.001), while no significant difference was reported when the target modality was tactile, (M = 4.7 vs. 4.5; n.s.).

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capture of the perceived direction of auditory and tactile motion than did the two-lights condition. This result stands in apparent contrast with the evidence that the six-lights condition conveyed a stronger impression of visual apparent motion compared to the two-lights condition. These outcomes have been interpreted in terms of the six-lights condition being more likely to be segregated into two moving streams than the two-lights condition, thus resulting in a weaker crossmodal dynamic capture effect. Hence, the magnitude of crossmodal integration seems to be a more salient factor in determining the crossmodal dynamic capture effect than the strength of apparent motion per se. As yet, no attempt has been made to investigate this topic in the audiotactile domain.

Although, if it is true that the more the two streams are segregated, the weaker the dynamic capture effect, one would speculate that presenting the task-irrelevant tactile stimuli to more than one fingertip of one hand (or presenting the stimuli to more than one fingertip of each hand) would result in a decrease (or perhaps even the disappearance) of the already weak capture of the auditory targets. Conversely, presenting the auditory stimuli from more than two loudspeakers would cause a reduction of the crossmodal capture of the tactile stimuli by the auditory stimuli.

It is worth noting, however, that in these the two above-mentioned studies investigating the effect of the intramodal perceptual grouping on crossmodal dynamic capture effect (Sanabria, Soto-Faraco, Chan, & Spence, 2005; Lyons, Sanabria, Vatakis, & Spence, 2006), the impression of apparent motion was only manipulated in the task-irrelevant modality (i.e., the target streams always consisted of two stimuli). To the best of our knowledge, no previous study has investigated the magnitude of the crossmodal dynamic capture occurring between task-relevant and -irrelevant streams of stimuli, each consisting of more than two stimuli. Such a manipulation would allow one to directly investigate the extent, if any, to which the increasing of the impression of apparent motion in spatiotemporally matched target and task-irrelevant moving streams would affect the magnitude of the dynamic capture effect.

Condition	Target Modality	Sound Intensity	Perceived apparent motion ratings	Response confidence ratings
1	Tactile	Quiet	4.90 (1.52)	4.65 (1.27)
		Loud	5.10 (1.48)	4.45 (1.32)
2	Auditory	Quiet	5.25 (1.25)	4.55 (1.39)
		Loud	5.10 (1.48)	5.80 (1.20)

The standard deviations of the mean are reported in parentheses.

Table 8. Summary of the Likert scale ratings

9.4. General discussion of Experiments 6 and 7

Experiments 6 and 7 were designed to investigate whether different kinds of auditory stimulus would differentially affect the audiotactile crossmodal dynamic capture effect. To this end, we manipulated either the complexity or the intensity (i.e., 75 vs. 82 dB) of the sounds (i.e., pure tones vs. noise bursts), alternatively used as target or distractor stimuli (and the properties of the vibrotactile stimuli kept constant throughout the experiment).

The results of Experiment 6 showed that sound complexity modulated performance, decreasing the accuracy of tactile direction judgments when presented simultaneously with noise distractors, while facilitating judgments of the direction of the noise bursts (as compared to pure tones). Although auditory direction judgments were overall more accurate for noise (than for pure tone) targets, the complexity of the sound failed to modulate the tactile capture of auditory targets. These results provide the first demonstration of enhanced audiotactile interactions involving complex (vs. pure tone) auditory stimuli in the peripersonal space around the hands (previously these effects have only been reported in the space around the head). Thus, the results of the Experiment 6 suggest that in an audiotactile crossmodal dynamic capture task spectral complexity affects the perceptual representation of dynamic events and, although in a less straightforward manner, the magnitude of the crossmodal dynamic capture effect.

Participants' performance was also significantly affected by the intensity of the sounds (Experiment 7). Namely, the crossmodal capture of tactile motion by audition was stronger with the more intense (vs. less intense) auditory distractors, whereas the capture effect exerted by the tactile distractors was stronger for less intense (than for more intense) auditory targets. The crossmodal dynamic capture was larger in the first condition, with a stronger congruency effect when the target streams were presented in the tactile (vs. auditory) modality.

Taken together, the results of the present study suggest that the change of the physical properties of the auditory stimuli, such as their intensity and complexity, can affect people's performance in an audiotactile crossmodal dynamic capture (see Section 4.7 for a more extensive discussion).

The Experiment 6 was designed to investigate whether different kinds of auditory stimulus would differentially affect the audiotactile crossmodal dynamic capture effect. To this end, we manipulated the complexity of the sounds (i.e., pure tones vs. noise bursts), alternatively used as target or distractor stimuli (and the properties of the vibrotactile stimuli kept constant throughout the experiment). The complexity of the sounds not only affected the general discriminability of the direction of the tactile apparent motion streams, but more interestingly, it also modulated the magnitude of the crossmodal capture effect of the auditory distractors on the perception of the direction of the tactile target stimuli. In fact, a more pronounced crossmodal capture effect was reported when the auditory streams consisted of noise stimuli than when they consisted of pure tones.

While the results of those trials in which the participants discriminated the direction of the tactile targets highlighted the modulation of crossmodal dynamic capture as a function of the complexity of the auditory stimuli, the results of the auditory target session are somewhat more challenging to interpret. The pattern of results in this condition was generally consistent with an enhanced discrimination of the direction of the streams consisting of noise bursts (rather than pure tones), but this was independent of the spatiotemporal conditions of audiotactile stimulation (i.e., the complexity of the sounds did not modulate the capture effect exerted by the tactile distractors). It is, however, possible that in this condition, the high level of accuracy of the participants' performance could have overruled any possible effect induced by the manipulation of sound complexity.

The fact that the presentation of the tactile stimuli failed to affect the performance in the auditory task is however consistent with another study, that investigated how the presentation of a vibrotactile stimulus would affect the auditory perception of tones of the same frequency (Yarrow, Haggard, & Rothwell, 2008; Experiments 2 and 3). In this study, Yarrow and colleagues found that the addition of vibrotactile stimuli had no significant effect on participants' performance. The results of this study are therefore consistent with those observed here, in showing that under certain conditions the participants performing an auditory task can ignore the tactile stimuli, which thus fail to exert any observable influence on performance.

On the other hand, when the participants had to discriminate the direction of the tactile motion, their performance was strongly affected by the presence of auditory distractors, giving rise to a significant crossmodal dynamic capture. This means that distractors, although they should be ignored by the participants, nevertheless influenced participants' performance. Additionally, the magnitude of this interference effect changed as a function of the auditory stimulus. Thus, in this condition, the weight allocated to each sensory modality is likely to have been changed according to nature of the distractor stimuli. More precisely, when the distractors consisted of pure tones, whose localizability is less certain, then the modality coded as more reliable was indeed the target modality. On the contrary, if the distractors were noise bursts (i.e., localizable with a higher degree of certainty), then more weight was assigned to them. This could have resulted on the one hand in a more pronounced capture effect of the tactile target motion exerted by auditory distractors consisting of noise (vs. pure tone) stimuli and, as already mentioned, in more accurate auditory directional judgments. This suggestion is also mirrored by participants' self-reports: They reported responding more confidently in the block were the auditory target motion consisted in noise bursts (vs. pure tones) and when the tactile targets were presented with pure tone (vs. noise) distractors (see Results Section).

If, as shown in the present study, the manipulation of the localizability of the stimuli is effective in inducing a change in the weights assigned to the inputs provided by the different sensory modalities, then it can be speculated that a parallel process could also be observed when the localizability of the tactile stimuli – and not of the auditory stimuli – is degraded. This has been shown by a previous audiotactile study of crossmodal dynamic capture, in which the participants had to perform the task while keeping their arms in either uncrossed and crossed postures (Sanabria et al., 2005). The results demonstrated that the crossing of the hands decreased the reliability of tactile information, giving rise to different patterns of results according to the modality that from block to block served as a target. When the target modality was auditory, crossing the hands resulted in a decreased interfering effect of the tactile distractors on the discrimination of auditory motion. Conversely, this posture determined the increase of interference exerted by auditory stimuli on tactile target apparent motion. Overall, these results suggest that when the tactile stimulus can be more precisely localized (as in the uncrossed posture), the relative reliability of the tactile information is increased, thereby making the directional judgments concerning tactile motion more accurate and of auditory motion more susceptible to the effects of tactile distractors. The opposite holds when the tactile stimuli are less easily localizable (i.e., hands located in the crossed posture), thus confirming the inadequacy of considering the crossmodal interactions as an expression of a complete capture of one sensory modality by another (cf. Alais & Burr, 2004).

The fact that the auditory capture of tactile stimuli is stronger for noise (than for pure tone) distractors is consistent with previous evidence, collected using a variety of different techniques, that has shown more pronounced audiotactile interactions for complex (vs. pure tone) auditory stimuli (e.g., Suzuki, Gyoba, & Sakamoto, 2008). For instance, in right brain-damaged patients suffering from left tactile extinction, the presentation of a right auditory stimulus close to the head interfered with the detection of a concurrently presented tactile stimulus on the left side of the neck

(Farnè & Làdavas, 2002). Crucially, crossmodal audiotactile extinction was significantly more pronounced when the auditory stimuli consisted of noise bursts than when they consisted of pure tones. Research on healthy humans has also revealed that in a speeded right vs. left discrimination task for tactile stimuli presented at the earlobes, performance was worse with the contralateral presentation of a concurrent noise burst (Kitagawa, Zampini, & Spence, 2005). The crossmodal interference effect was stronger for complex (vs. pure tone) auditory stimuli and varied according to the distance from which the (complex) auditory stimuli were presented (occurring for stimuli presented close to the participant's head). One might hypothesize that the stronger interactions between somatosensory and complex auditory stimuli reflect evolutionary processes. It can be noted that in the natural environment the sounds are complex and thus more similar to white noise than to pure tones (Nelken, Rotman, & Yosef, 1999; Rauschecker, 1997). Therefore, neural substrates favouring the interplay between complex auditory stimuli and vibrotactile stimuli could result from the necessity of having to deal with the complexity of naturalistic auditory surroundings (cf. Farné & Làdavas, 2002).

Another interesting result to have emerged from the present study is that, contrary to what has been reported in previous research on the audiotactile crossmodal dynamic capture effect (Sanabria et al., 2005; Soto-Faraco et al., 2004b), we observed stronger capture by the auditory motion on tactile motion than vice versa. It is worth noting that a meaningful comparison with the results obtained in previous studies is, however, made more difficult by the fact that the intensity of the auditory stimuli used in the present study (i.e., 82 dB(A)) was overall higher than that used before (i.e., 60 dB(A) in Sanabria et al., 2005; 65 dB(A) in Soto-Faraco et al., 2004b). It is likely, however, that each of the above described variables (i.e., localizability and salience) can affect the magnitude of the reciprocal crossmodal dynamic capture between touch and audition. However, since in our study the stimuli were presented at clearly suprathreshold levels, the link between these two factors is hard to disentangle, differently to what has been shown for stimuli close to the threshold, whose localizability is significantly impaired (Altshuler & Comalli, 1975; Comalli & Altshuler, 1976).

The results of Experiment 7 revealed that the capture effect of tactile target motion was modulated significantly as a function of the relative intensity of the auditory distractor motion, with louder auditory distractors exerting a stronger crossmodal capture effect than quieter auditory distractors. This result would seem to contradict the well-known law of inverse effectiveness, according to which maximal crossmodal interactions take place when the two stimulus components are themselves minimally effective (e.g., Stein & Meredith, 1993; Stein & Stanford, 2008). One may speculate as to whether in the present study the intensity of the sound might somehow have modulated participants' perception of auditory apparent motion and, consequently, the crossmodal capture that the auditory streams were capable of exerting over the tactile streams. However, according to participants' self-reports, which did not show any change of the impression of the tactile apparent motion according to the change of the sound intensity (see Experiment 7, Results section, and Table 8), this explanation does not seem to provide an adequate explanation for our results. It seems reasonable therefore to assume that the process underlying our results involves a different mechanism, such as, for example, a shift of the focus of attention resulting from the change of sound intensity. If this were to have been the case, attention would have been shifted toward the higher intensity sounds, thus determining a stronger capability to capture the motion tactile stream. This explanation would be consistent with previous electrophysiological studies that have documented a larger amplitude P300 signal with higher intensity stimuli, which may reflect an increase in attention determined by more intense stimulus (see Lindín, Zurrón, & Díaz, 2005).

The role of attention in the crossmodal dynamic capture task has been investigated recently by Oruc, Sinnett, Bischof, Soto-Faraco, Lock, and Kingstone (2008). In their study, three different attentional conditions were introduced: the modality pairings were held constant across the block of trials, but the target modality could be either known in advance (Blocked Group) or identified by a pre-cue at the start of each trial (Pre-cued Group) or identified by a post-cue after each stimulus presentation (Post-cue Group). Hence, differently from the other groups, the Post-cued group had to attend both modality streams on each trial. The results showed that the attentional manipulations did not significantly affect the discrimination of the visual motion paired with both tactile and auditory irrelevant motion, suggesting a robust advantage of the visual modality in conveying dynamic information. In the case of the audiotactile pairings, the dynamic capture effect was found to be not only reciprocal, but also influenced by participants' attentional focus. Namely, the crossmodal dynamic capture effect increased when the participants were requested to attend to both dynamic streams as compared to when attention was only focused on the target modality. These results suggest that attention selectively affects the modalities which convey motion information of comparable magnitude, as audition and touch.

In Experiment 7, the ability of participants to correctly report the direction of auditory apparent motion was significantly better overall if the stimuli were presented at 82 dB(A) than at 75 dB(A). Even more interestingly, the accuracy of participants in determining the direction of an auditory apparent motion presented concurrently with task-irrelevant tactile motion moving in the opposite direction (i.e., the magnitude of crossmodal dynamic capture effect) varied significantly as a function of the intensity of the auditory stimuli. This result means that the congruency effect exerted by the tactile motion on the perceived direction of the auditory motion was significantly stronger for quieter than for louder auditory stimuli. This was also mirrored by participants' self-reports, as they claimed to be less confident in determining the direction of the quieter (vs. louder) auditory stimuli (see Table 8).

The pattern of results reported in the present study are consistent with those reported recently by Bresciani and Ernst (2007), and can be interpreted by taking into account the relative reliability of the two involved modalities. In that study, the authors presented series of beeps and taps and requested participants to report the number of stimuli that had been presented in the target modality while ignoring the distractors presented in the other modality. According to the maximum likelihood estimation model, the reliability of a sensory channel is related to the relative uncertainty of the information it conveys. The higher the relative variance of a sensory modality the weaker is its relative reliability (Ernst & Bülthoff, 2004). Indeed, Bresciani and Ernst found that reducing the intensity of the auditory stimuli decreased the relative reliability of the auditory modality, with participants being more accurate (i.e., their estimates were less variable) in counting the number of the louder (vs. quieter) beeps presented with irrelevant taps and, conversely, in counting the number of the taps presented with irrelevant quieter (vs. louder) beeps (see also Wozny, Beierholm, & Shams, 2008).

Another result to have emerged from the present study is that the overall accuracy of participants' performance was lower when they had to discriminate the tactile stream direction than when they had to discriminate the auditory stream direction. Thus, it seems likely that the discrimination of the direction of the target motion stream was harder when it was presented in the tactile (vs. auditory) modality and the distractors were presented in the auditory (vs. tactile) modality. Note, however, that according to participants' self-report ratings, the apparent motion presented in the two modalities was comparable in terms of its strength (see Results Section). One might attribute this result to the fact that the intensity might have not been equally measured in both modalities. Although there is evidence which shows that the crossmodal matching of intensities is a quite problematic issue, susceptible to biases and to a great individual variability and thus difficult to assess (cf. Mark, Szczesiul, & Ohlott, 1986; Spence, Shore, & Klein, 2001), it is not possible to exclude that the lacking of any preliminary crossmodal matching could have contributed to this result.

It must also be noted that the crossmodal capture effect of the tactile apparent motion on the auditory apparent motion was negligible, regardless of the intensity at which the auditory stimuli were presented.

This evidence contrasts with the results of previous audiotactile crossmodal dynamic capture studies, which have shown that the tactile apparent motion exerted a stronger capture effect on auditory motion than vice versa (Sanabria et al., 2005; Soto-Faraco et al., 2004b). It is worth noting that a meaningful comparison with the results obtained in previous studies is hard to make because the intensity of the auditory stimuli used in the present study (i.e., 75 dB(A) and 82 dB(A)) are overall higher than that used before (i.e., 60 dB(A) in Sanabria et al., 2005; 65 dB(A) in Soto-Faraco et al., 2004). Also, the typology of the sounds was different (i.e., white noise bursts in the present study vs. pure tones in previous studies), and this can constitute an additional reason of inconsistency.

In summary, the results of the present studies suggest that the change of the physical properties of the auditory stimuli, such as their complexity (Experiment 6) or intensity (Experiment 7), can affect people's performance in an audiotactile crossmodal dynamic capture.

In Experiment 6, the spectral complexity affects the perceptual representation of dynamic events and, although in a less straightforward manner, the magnitude of the crossmodal dynamic capture effect. The fact that complex auditory stimuli interact more with tactile stimuli than do pure tones suggests the possible existence in humans of a neural system subserving the integration of tactile and complex auditory stimuli delivered in the peripersonal space lying close to the hand, analogous to what has been documented previously in monkeys (Fu et al., 2003). This would suggest that the processing of complex auditory stimuli delivered in the space surrounding specific parts of our body (i.e., the hands and head; cf. Farné & Làdavas, 2002; Kitagawa et al., 2005) is privileged as compared to the processing of pure tone stimuli.

In Experiment 7, the pattern of results showed that performance was significantly affected by the intensity of the sounds. Namely, the crossmodal capture of tactile motion by audition was stronger with the more intense (vs. less intense) auditory distractors, whereas the capture effect exerted by the tactile distractors was stronger for less intense (than for more intense) auditory targets.

Further investigations are needed in order to clarify the evolutionary reasons and the neural processes underlying this behaviourally observed evidence in humans. Moreover, it will be interesting in future research to investigate whether the synaesthetic congruency between the auditory and tactile stimuli might also modulate the size of the crossmodal dynamic capture effect (cf. Parise & Spence, 2008).

Chapter 10.

Pseudosynaesthetic correspondences between touch and hearing

10.1. Introduction

In synaesthetic individuals, the presentation of a specific stimulus systematically evokes an additional sensory experience in either the same or a different sensory modality. However, it has been shown that multisensory interactions putatively reflecting the existence of associations between the attributes of stimuli presented in different sensory modalities also occur in the non-synaesthetic population (see Marks, 1983, for a review). Although the synaesthetic congruency effects demonstrated by non-synaesthetes differ from synaesthesia proper in terms of certain features (e.g., intra- and inter-individual consistency, mode of access to the associations and their nature, which is contextual in the former case and absolute in the latter, (Martino & Marks, 2001; Ward, Moore, Thompson-Lake, Salih, & Beck, 2008), there is evidence showing some similarities between the cross-modal associations reported by synaesthetic and non-synaesthetic individuals. For instance, similarity correspondences have been reported between the frequencies (i.e., high vs. low) of auditory stimuli and the visual features of size (Gallace & Spence, 2006), colour (Melara, 1989a, b) brightness, form (Melara, 1987), and elevation (Ben-Artzi & Marks, 1995; Melara & O’Brien, 1987). Across different experimental conditions, it has been shown that people consistently judge higher-pitched tones as matching (i.e., perceived as systematically corresponding with the attributes of a stimulus in another sensory modality) with small (Gallace & Spence, 2006), white (Melara, 1989a, b), bright, and/or sharp (Marks, 1987) visual stimuli, or which occupy an “upper” position (Melara & O’Brien, 1987). These crossmodal correspondences have been shown to influence participants’ performance when they discriminate the stimuli formed by synaesthetically matched (vs. unmatched) attributes more rapidly and/or accurately. Although investigated less frequently, the occurrence of synaesthetic interactions between vision and touch have also been documented, with participants preferentially matching black and white squares with low- and high-frequencies vibrotactile stimuli, respectively (Martino & Marks, 2000; see also Cinel, Humphrey, & Poli, 2002). However, to the best of our knowledge, no attempts have as yet been made to address the possible existence of synaesthetic correspondences between the pitch of sounds and tactile stimuli in non-synaesthetic individuals.

In Experiment 8, we explored whether a multisensory correspondence also exists between the pitch of a tone and the elevation of tactually-stimulated locations. Previous studies have suggested that the cognitive representation of auditory pitch in the human brain is spatial in nature, with higher-pitched frequencies being located in upper positions and lower-pitched frequencies being located in lower positions (Melara & Marks, 1990; see also Mudd, 1963; Rusconi, Kwan, Giordano, Umiltà, & Butterworth, 2006). For instance, a significant congruency effect has been observed when people perform a speeded discrimination task regarding the visually-presented syllables “HI” and “LO” and of high- and low-pitched tones, with congruent stimulus attributes being classified more rapidly than incongruent stimulus attributes (Melara & Marks, 1990).

To address this topic, we used a modified version of the Implicit Association Test (IAT; Greenwald, McGhee, & Schwartz, 1998), a paradigm initially designed in the research field of social psychology, which has been used more recently to assess multisensory perceptual interactions (e.g., Demattè, Sanabria, & Spence, 2007). In an IAT study, participants perform a speeded discrimination of two pairs of concepts/attributes using two different response keys. Critically, the assignment of each pair of stimuli and the relative response key is alternated on a block-by-block basis in order to test each possible stimulus-response mapping. It is assumed that the participants will perform better (i.e., that they will respond more rapidly and/or accurately) when the two concepts mapped onto the same response key are more strongly associated (i.e., when they share some dimensional similarity) than when they are more weakly associated.

In Experiment 8, the participants were presented with randomly-ordered unimodal tactile targets (i.e., vibrations presented to one of two vertically aligned locations on the hand) and unimodal auditory targets (i.e., 300-Hz or 4000-Hz tones). The stimulus-response mapping was manipulated on a block-by-block basis in order to evaluate the extent to which the strength of the connection between the two crossmodal dimensions under investigation (i.e., tactually stimulated elevation and auditory pitch) would affect participants’ performance. More specifically, we predicted that participants would respond more rapidly and accurately when the pairings of stimuli mapped onto the same response key were related by a stronger association (e.g., when the high-pitched sounds were paired with the vibrotactile stimuli presented in the upper location) than when they were weakly related (e.g., when the higher-pitched sounds and were paired with the vibrotactile stimuli presented from the lower location). If this prediction were to be shown to be correct, we would have provided an indirect measure of a crossmodal correspondence between auditory pitch and tactile elevation.

10.2. Experiment 8. Compatibility effects between sound frequency and tactile elevation

10.2.1. Method

Participants. Twelve non-synaesthetic participants took part in this study (4 male and 8 female; mean age: 25 years; range from 21 to 39 years). All of the participants reported normal hearing and normal tactile sensitivity. The experiment took approximately 30 min to complete.

Apparatus and stimuli. The experiment was conducted in a dark testing booth. The participants sat at a table and held a foam cube in their right hand positioned approximately 60 cm in front of them on the body midline. The foam cube was located in front of a centrally-located loudspeaker cone in order to ensure that the auditory and tactile stimuli were presented from the same position (see Figure 11 for a view of the experimental set-up). Two Oticon-A (100 Ohm, Oticon Inc., Somerset, NJ) bone conduction vibrators, with 1.6 cm x 2.4 cm vibrating surfaces were embedded in the foam cube, with participants placing their fingertip over the appropriate stimulator (i.e., the index fingertip was placed on the upper face of the cube while the thumb lay on the vibrator mounted in the lower face of the cube). The tactile stimuli consisted of clearly suprathreshold 250-Hz vibrotactile pulses presented for 400 ms. The auditory stimuli were presented from the central loudspeaker (Creative, Cambridge Soundwork, MA) and consisted of either relatively low- (300-Hz) or high-frequency (4000-Hz) tones. The stimuli were presented for 400 ms at 70 dB(A). White noise was presented over headphones at 60dB(A) throughout the experimental blocks in order to mask any sounds made by the participants and by the operation of the vibrators. Two footpedals were located under the table to collect the participant's responses.

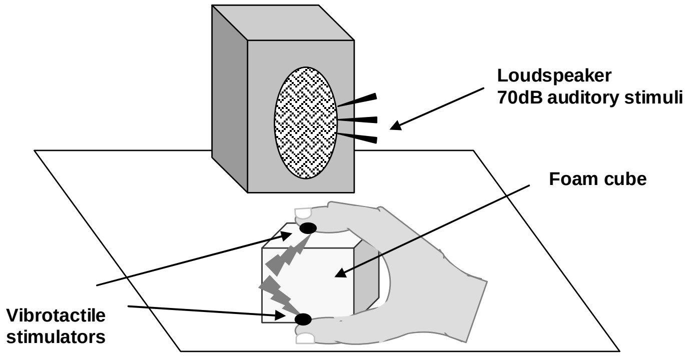


Figure 11. Schematic representation of the experimental set-up.

Design. A repeated measures within-participants experimental design was used with the factors of target stimulus (high-pitched tone, low-pitched tone, vibrotactile stimulus present to the upper location, and vibrotactile stimulus presented to the lower location) and response mapping (compatible vs. incompatible). The experimental session consisted of 12 blocks of 20 randomized trials (each stimulus was presented five times per block). The assignment of stimuli to the response keys and the order of presentation of the various blocks of stimuli were counterbalanced across participants (i.e., compatible and incompatible response mappings alternated over successive blocks of trials; see Figure 12). Prior the beginning of the main experimental session, all of the participants completed 4 blocks of 8 practice trials to familiarize themselves with the task.

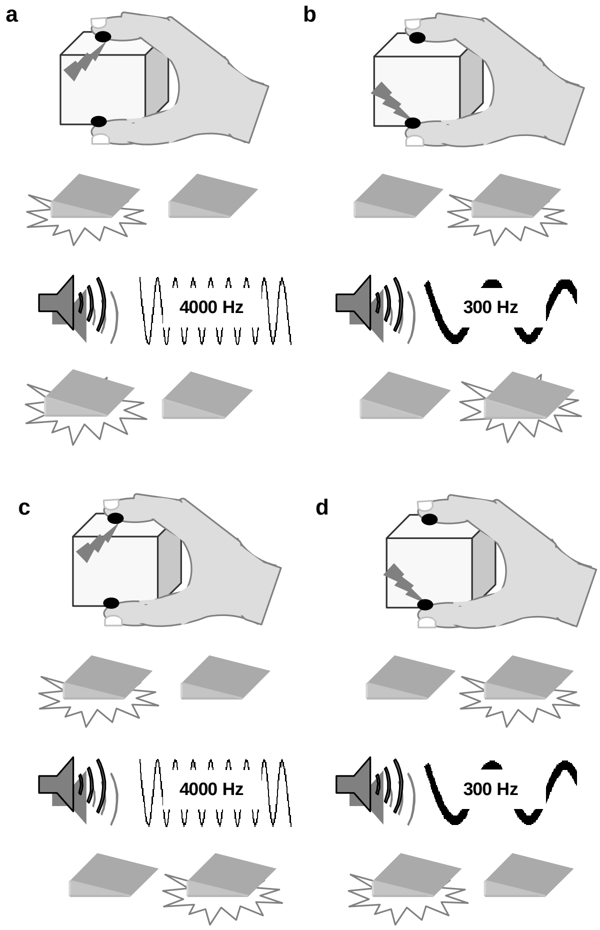


Figure 12. Examples of compatible response mapping conditions (a, b) and incompatible response mapping conditions (c, d).

Procedure. The participant sat at a table in a dark soundproof booth. They held a foam cube (7 x 7 x 6 cm) between the forefinger and thumb of the right hand. They had to keep the position of their hand fixed throughout the experimental session in order to ensure the vertical arrangement of their fingers (i.e., index finger in the upper location and thumb in the lower location). The participants were instructed to identify the target stimulus (regardless of its modality; i.e., tactile and auditory) as rapidly as possible by releasing one of the two footpedals (i.e., right or left footpedal), according to the instructions presented at the beginning of each block of trials. Both speed and accuracy in responding were stressed to the participants. Prior to the experimental blocks, participants performed four brief practice blocks (32 trials in total), one for each response mapping condition. Note that in the instructions, any expression that might subtly have subtly induced a linguistic labelling of the stimuli (i.e., high- and low-pitched tones, lower and upper location on hand) was avoided (i.e., the stimulus-response mapping was indicated by simultaneously presenting the to-be-discriminated stimulus and an arrow pointing to the left or right relative to the response key on which the stimulus had to be mapped in that particular block of trials). If no response was made within 2,400 ms of target onset, the trial was terminated; otherwise the participant's response ended the trial. Feedback concerning the speed and accuracy (i.e., the words 'correct!' or 'incorrect' and the reaction times, RTs, in ms printed in bold Courier New size 18) of the participant's response was presented for 400 ms at the end of each trial. This feedback was followed by a 300 ms delay before the onset of the next trial. Stimulus delivery and the recording of responses were controlled by E-prime (Psychology Software Tools Inc.; www.pstnet.com/eprime).

10.2.2. Results

Error rates and median RTs (for trials in which the participants responded correctly, amounting to 79% of the trials in total) were calculated for each participant for each of the four conditions resulting from combining the factors of Target modality (touch vs. audition) and Response mapping (compatible vs. incompatible). In order to take both response speed and accuracy into account, and so eliminate any potential speed-accuracy trade-offs in the data, we calculated the Inverse Efficiency (IE) scores (i.e., mean of the reaction times divided by the proportion of correct responses) for each condition (Townsend & Ashby, 1983).

The IE scores were then submitted to a repeated-measures analysis of variance (ANOVA) with the factors of Target modality (touch vs. audition) and Response mapping (compatible vs. incompatible). The analysis highlighted a significant main effect of Response mapping, F(1,11)=8.23; p=.02; power=0.74; with participants exhibiting better performance in the compatible (vs. incompatible) response mapping blocks (IE = 777 vs. 874 ms). There was also a significant main effect of Target modality, F(1,11)=13.24; p=.004; power=0.91; indicating that participants performed more efficiently when presented with auditory (vs. tactile) stimuli (IE = 757 vs. 894 ms).

Crucially, there was no interaction between Response mapping and Target modality, F(1,11)=3.56; p=.09; power=0.41 (see Table 9 for an overview of the results for each condition).

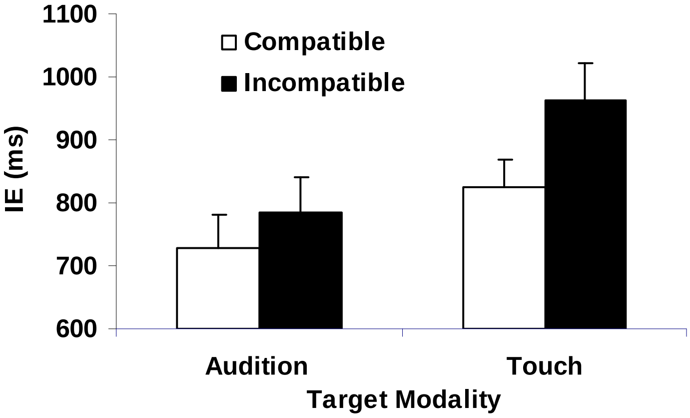


Figure 13. IE scores for auditory and tactile targets as a function of the compatibility of the stimulus–response mapping (i.e., compatible vs. incompatible). Error bars represent the standard errors of the means.

Condition	***Target modality***	***RTs (median)***	***% accuracy***	Inverse Efficiency score
Compatible	Tactile	653 (46)	79 (4)	824 (46)
	Auditory	620 (52)	85 (4)	729 (51)
Incompatible	Tactile	670 (51)	70 (4)	963 (58)
	Auditory	629 (57)	81 (5)	785 (57)

Table 9. Summary of the results. The standard errors of the mean are reported in parentheses. The discrepancies in the values reported are attributable to the rounding procedure.

10.3. Discussion of the Experiment 8

The results of the present study highlight the existence of a new crossmodal association between the pitch of sounds and the relative spatial elevation of the tactually-stimulated locations. Indeed, participants' performance (as measured by the IE scores) was significantly better when pairings of stimuli considered as more closely matched (i.e., relatively high-pitched tones and the tactile stimulation of the upper location on the hand and, conversely, relatively low-pitched tones and the tactile stimulation of the lower location on the hand) were mapped onto the same response key as compared to when they were mapped onto different response keys.

These results are consistent with previous evidence showing that people systematically map the pitch of tones into spatial coordinates, assigning the higher-pitched sound to the upper location and the lower-pitched sound to the lower location (e.g., Melara & Marks, 1990; Rusconi, Kwan, Giordano, Umiltà, & Butterworth, 2006; see also Roffler & Butler, 1968). The participants in a study by Rusconi and colleagues (2006) had to perform a spatial compatibility task involving pitch discrimination by pressing vertically-aligned response keys. Their results showed that participants benefited from the assignment of high-frequency pitches to the response key located in the upper (vs. lower) position and, conversely, of the low-frequency pitches to the response key located in the lower position).

Hence, it is plausible that the correspondence highlighted in the present study between auditory pitch and tactile elevation could have been mediated by the spontaneous mapping of these two dimensions along the vertical dimension. It is worth noting that the auditory stimuli were delivered by means of a centrally positioned loudspeaker in the present study and any indications which could prompt the participants toward an explicit coding of the stimuli in spatial coordinates or a linguistic labelling in spatial terms were carefully avoided. Moreover, in this kind of task, the response the participants had to provide did not involve an explicit estimate of the relative or absolute location (i.e., high vs. low) of the tactile stimuli, which might have induced a confound in terms of the stimulus-response mapping (cf. Melara & Marks, 1990; see also Harris, Thein, & Clifford, 2004).

As both of the explored dimensions (i.e., locations of the tactile stimulation on the hand and pitch height) can be coded in terms of “high” and “low”, it remains a question for future research to determine whether the similarities highlighted here could be in some sense linguistically-based (possibly investigating whether these crossmodal interactions occur under conditions where any linguistic interference can be excluded). If this crossmodal effect is semantically mediated, the assumption would be that each piece of perceptual information would be processed through a series of stages: the incoming sensory inputs first undergoing perceptual encoding, then subsequently being converted into an adequate linguistic code serving as the basis for a comparison of the internal representation of the percept with a reference. This, in turn, would be assumed to lead to the classification of the crossmodal dimensions and to the selection of the appropriate response. According to this hypothesis, the matching of perceptual dimensions thus turns into the comparison of semantic codes (cf. Marks, 1987). As the two dimensions tested here (i.e., auditory pitch and tactile elevation) neither share any perceptual characteristics nor convey similar information, it is plausible that the coding of the correspondence between these crossmodal attributes are rooted in higher-level cognitive processes, involving a comparison among stimulus features which is likely to be semantically – and not or not exclusively perceptually-based (see also Melara & Marks, 1990; Walker & Smith, 1984). It should, however, be noted that previous studies have documented the occurrence of multisensory associations even in new-borns, thus suggesting that similarities among sensory modalities can emerge early in the development and are unlikely to be mediated by language (e.g., Lewkowicz & Turkewitz, 1981; Spector & Maurer, 2009).

In conclusion, the results of the present study provide evidence for a new multisensory association in non-synaesthetes, showing the preferential matching of, respectively, higher-pitched sounds and tactile stimulation of upper locations and low-pitched sounds and tactile stimulation of lower locations. Further studies could investigate the role of language in mediating the multisensory correspondences occurring between touch and audition. For instance, if a semantic coding process were to be responsible for the effects reported here, then one might predict that articulatory suppression would eliminate it (cf. Stevenson & Oaten, 2008). Moreover, it would be interesting to determine whether the results found here can be attributed to the relationship established between auditory pitch and different vertically located portions of skin on the hand or, rather, between the sound pitch and different vertical portions in external space (cf. Soto-Faraco, Ronald, & Spence, 2004). If the former relation holds, then the prediction would be that placing the hand in an inverted posture (i.e., thumb on the upper stimulator and index on the lower stimulator) would give rise to a reversal of the effect (i.e., stronger association between, respectively, high-pitched sounds and tactile stimulation of the thumb and low-pitched sounds and the tactile stimulation of index finger). If the opposite correspondence holds, then a pattern of results similar to those found here could be expected. Finally, it could also be of interest in the study of multisensory correspondences occurring between touch and audition to investigate whether there is a relation can be established between tactile and auditory stimuli sharing frequency similarities, analogously to what as been shown between visual and tactile stimuli (Lovelace & Grossenbacher, 1976).

Chapter 11.

Audiotactile interactions and visual experience

11.1. Introduction

In the next sections, we will describe three experiments, conducted in order to investigate whether and how visual deprivation can affect audiotactile interactions. Three distinct domains have been investigated: temporal perception (Section 11.2), motion perception (Section 11.3) and the influence of different frames of reference coding tactile stimuli on auditory localization (Section 11.4).

11.2. Experiment 9. Audiotactile temporal order judgments in sighted and blind individuals

A great deal of research has been devoted to studying the sensitivity of sighted individuals to temporal asynchrony using multisensory temporal TOJ tasks, involving audio-visual (e.g., Keetels & Vroomen, 2005; Vatakis & Spence, 2006; Vroomen, Keetels, de Gelder, & Bertelson, 2004; Zampini, Shore, & Spence 2003a, b), visuo-tactile (e.g., Spence et al., 2001; Spence, Baddeley, Zampini, James, & Shore, 2003), and even audio-tactile (e.g., Kitagawa, Zampini, & Spence, 2005; Stone, 1926; Zampini, Brown, Shore, Maravita, Röder, & Spence, 2005) pairs of stimuli. Studies of audiovisual and visuotactile TOJs have demonstrated that performance is modulated by the relative spatial position from which the stimuli are presented. In particular, participants are significantly more sensitive (i.e., the just noticeable difference, JND, is lower) when the stimuli are presented from different spatial positions rather than from the same position (see Keetels & Vroomen, 2005; Spence et al., 2003; Zampini et al., 2003a, b).

Somewhat different findings have, however, been reported in the case of audiotactile TOJs (Kitagawa et al., 2005; Zampini et al., 2005). In particular, across several experiments, Zampini et al. were unable to demonstrate any spatial modulation of audiotactile TOJ performance when the auditory and tactile stimuli were presented from in front of the participants on either the same or opposite sides. By contrast, Kitagawa et al. observed a spatial modulation of audiotactile TOJs when the stimuli were presented from behind their participants' heads. Participants' performance was significantly better when the auditory and tactile stimuli were presented from different spatial positions rather than from the same position. Therefore, the comparison of these two audiotactile studies provides support for recent suggestions, based on both neurophysiological (Graziano, Reiss, & Gross, 1999) and neuropsychological data (Farnè & Ladavas, 2002), that audiotactile spatial interactions may be more prevalent in the region behind the head (i.e., in the part of space where vision provides no direct information) than in front of it (see Kitagawa & Spence, 2006, for a review).

In the present study, the potential effect of spatial factors on audiotactile TOJs in both the sighted and blind was examined. To this end, pairs of audiotactile stimuli were presented from either the same or different locations to the left and/or right of participants. The stimuli were separated by a variable stimulus onset asynchrony (SOA) using the method of constant stimuli. The participants were required to make unspeeded TOJ responses regarding which sensory modality had been presented first. As already mentioned, vision appears to be better suited to conveying spatial information than any other sensory modality, and represents the most reliable source of information when coding spatial position. However, it is important to note that spatial information is not only provided by visual cues. For instance, blind individuals have to base (or learn to base, in case of adventitious blindness) their experience of space on inputs from the other senses (e.g., hearing, touch, proprioception, etc). Although less adequate for coding spatial relational information, the non-visual senses nevertheless provide the opportunity to acquire a fully integrated representation of space, one that is not necessarily any less accurate than that of the sighted (Millar, 1988; Röder, Teder-Salājärvi, Sterr, Rösler, Hillyard, & Neville, 1999). If the absence of vision is associated with a strengthening of spatial audiotactile interactions (e.g., Kitagawa et al., 2005; Kóbor, Füredi, Kovács, Spence, & Vidnyánszky, 2006), then blind individuals might be expected to benefit from the redundant spatial information available when pairs of stimuli are presented from different positions (i.e., an effect of relative spatial position should be observed). In summary, it can be hypothesized that the redundant spatial information provided by non-visual information in frontal space might exert a selective influence on the performance of blind participants in a audiotactile TOJ task, while the spatial arrangement of the stimuli would not be expected to modulate the performance of the sighted controls (i.e., based on the previous null effect of relative spatial position reported by Zampini et al., 2005).

11.2.1. Method

Participants. Twenty blindfolded sighted (8 males and 12 females; mean age of 33 years; range from 20 to 55 years) and seventeen blind participants (7 males and 10 females; mean age of 35 years; range from 19 to 59 years) took part in this study. Eight of blind participants were early blind (i.e., where the onset of blindness occurred within the first three months of life); while the other nine were late blind (having been blind for between 11 and 44 years). Seven had rudimentary sensitivity to brightness; two had color and pattern vision (see Table 10 for details). The experiment took approximately 45 minutes to complete.

Nr	**Age**	**Gender**	**Visual perception**	**Age of onset**	**Duration**	**Cause of blindness**
1	25	M	Light perception	6 yrs	19	Congenital glaucoma
2*	31	M	None	19 yrs	12	Eyeball subatrophy (RE), retinal detachment (LE)
3	41	F	None	26 yrs	15	Eyeball subatrophy (RE), surgical anophthalmos (LE)
4	46	M	None	35 yrs	11	Surgical aphakia with chronic glaucoma (RE), corneal leucoma & eyeball subatrophy (LE)
5*	19	F	Light perception	Birth	19	Surgical aphakia & macular degeneration
6*	30	F	Color & pattern perception	19 yrs	11	Macular de generation
7	44	M	Light perception	Birth	44	Keratoconus with apex dystrophy, chorioretinic atrophy
8	30	F	None	3 months	30	Fibroplasia
9	30	F	None	Birth	30	Retinitis pigmentosa
10	25	F	None	10 yrs	15	Stargardt disease
11	46	M	None	34 yrs	12	Retinitis pigmentosa
12	59	M	None	37 yrs	22	Optic atrophy
13	34	F	Light perception (RE)	16 yrs	18	Central retinopathy
14	27	F	Light perception (LE)	2 months	27	Fibroplasia
15	37	M	None	Birth	37	Optic nerve damage. Unknown cause
16	33	F	Light perception	3 months	33	Fibroplasia
17	41	M	Light & pattern perception	29 yrs	12	Retinitis pigmentosa

Table 10. Description of the blind participants

Apparatus and stimuli. Two Oticon-A (100 Ohm, Oticon Inc., Somerset, NJ) bone conduction vibrators, with vibrating surfaces 1.6 cm wide x 2.4 cm long were embedded in foam cubes and placed on the table 60 cm in front of the participant, 26 cm to either side of the body midline. Two loudspeaker cones (Dell, A215; Round Rock, TX) were positioned directly behind the vibrotactile stimulators (approximately 24º to either side of the midline). The participants rested their hands on the table with their left index finger over a vibrotactile stimulator mounted on top of the left cube, and their right index finger over the vibrator mounted on top of the right cube (see Figure 14 for a schematic view of the participant and the experimental set-up). The auditory stimuli consisted of the presentation of a 9 ms white noise burst (82dB(A) as measured from the participants’ head position), and the vibrotactile stimuli consisted of the brief activation (9 ms) of one of the two bone-conduction vibrators driven by a white noise generator at 82 dB(A). Note that at the beginning of the experimental session, each tactile and auditory stimulus was presented individually from both the left and right sides of the body midline and the participant had to try and discriminate its location. This procedure was carried out in order to ensure that the source of stimulation was clear to the participants who took part in the study. All of the participants were able to perform the task, with an accuracy of 100%. White noise was presented at 75dB(A) from two loudspeakers (Dell, A215; Round Rock, TX) throughout the experiment in order to mask any noise emitted by the participant or vibrotactile stimulators. Two footpedals were located under the table to collect the participant’s responses.

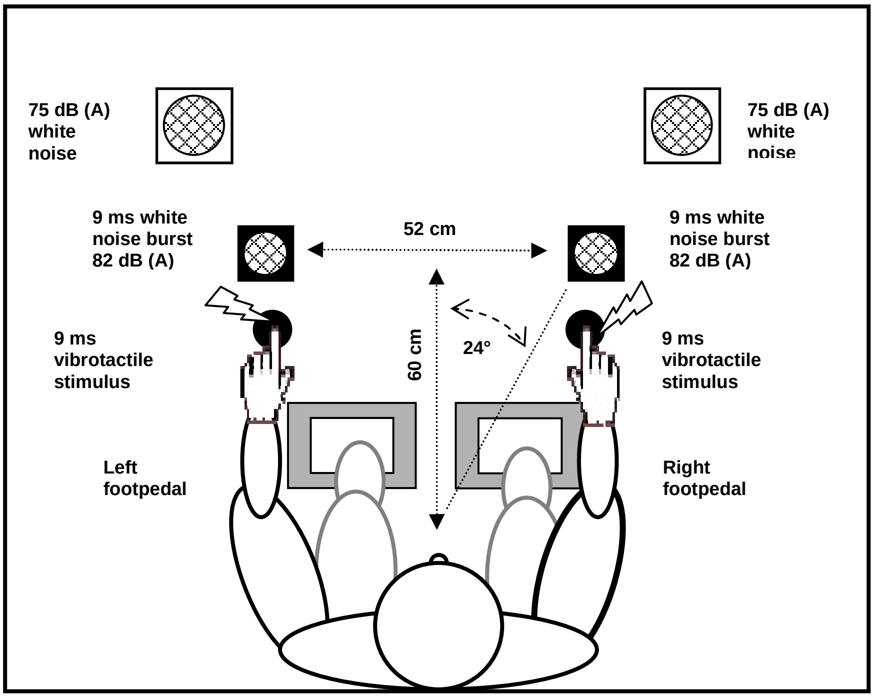


Figure 14. Schematic diagram showing the experimental set-up.

Design. There were two within-participants factors: SOA (-200 ms, -90 ms, -55 ms, -30 ms, -20 ms, +20 ms, +30 ms, +55 ms, +90 ms, and +200 ms; Negative SOAs indicate that the auditory stimulus was presented first, whereas positive values indicate that the vibrotactile stimulus was presented first) and Relative stimulus position (same vs. different). This particular range of SOAs was chosen on the basis of our previous research on audiotactile TOJs (Kitagawa et al., 2005; Zampini et al., 2005). The 40 possible conditions (10 SOAs x 4 possible stimulus configurations: sound left, touch left; sound right, touch right; sound left, touch right; and sound right, touch left) were presented twice in a pseudorandomized order within each block of experimental trials. All of the participants completed 2 blocks of 40 practice trials to familiarize themselves with the paradigm, followed by 8 blocks of 80 randomly-ordered experimental test trials.

Procedure. The participants sat in a dimly-illuminated room and were instructed to report which stimulus modality appeared to have been presented first. The sighted participants were instructed to keep their eyes closed throughout the experimental session, whereas the blind participants were requested to direct their gaze in front of them (see Discussion on this point). The experimenter monitored the direction of gaze throughout the experimental session. The first stimulus was presented from either the left or right after a delay of 750 ms; The second stimulus was presented after the SOA specified for that particular condition. Half of the participants were instructed to press the right footpedal to indicate that the auditory stimulus appeared to have been presented first and the left pedal to indicate that the tactile stimulus had been presented first (and vice versa for the other participants). The TOJ task was unspeeded, and the participants were informed that they should respond only when confident of their response (although within the 3,000 ms allowed before the termination of the trial). If a participant responded prior to the onset of the first stimulus or failed to make a response before the trial was terminated, the trial was terminated and the response discarded; otherwise, the participant's response ended the trial. Anticipatory and late responses occurred on less than 1% of the trials overall, and were not analyzed. The intervals between trials varied randomly in the range of 500-1600 ms. Stimulus delivery and the recording of responses were controlled by E-prime (Psychology Software Tools Inc.; www.pstnet.com/eprime).

11.2.2. Results

The proportion of "touch first" responses was converted to its equivalent Z-score assuming a cumulative normal distribution (see Finney, 1964). The intermediate eight SOAs were used to calculate a best-fitting straight line for each participant for each condition. The ±200 ms points were excluded from this computation because most of the participants performed nearly perfectly at this interval and so no additional variance was accounted for by these data points (cf. Spence et al., 2001). The slopes and intercepts from these best-fitting lines were used to calculate the JND (JND = 0.675/slope since ±.675 point corresponds to the 75% and 25% points on the cumulative normal distribution) and the PSS (PSS = intercept/slope) for each of the two conditions for each participant. Three of the blind participants (one early blind and two late blind) and four of the sighted participants were removed from the analysis because they performed at below 75% correct at the 200 ms SOAs, indicating their inability to perform the task.

The JND data from the remaining participants was submitted to a mixed between-within ANOVA with the factors of Relative stimulus position (same vs. different) and Group (sighted vs. blind). For the analyses reported here, post-hoc comparisons used Bonferroni-corrected t-tests (where $p<.05$ prior to correction). The analysis revealed a significant interaction between Relative stimulus position and Group [$F(1,28) = 6.25$, $p = .019$], with the blind participants responding more accurately when the two stimuli were presented from different positions (mean JND of 61 ms) than when they were presented from the same position (mean JND of 73 ms; $t(13) = 6.43$, $p = 005$). The performance of the sighted participants was not affected by the relative positions from which the two stimuli were presented (mean JND of 69 ms and 70 ms for the same position and different positions, respectively; $t(15) = -.28$, $p =.72$). Moreover, the blind participants were more accurate than the sighted participants in the different positions condition ($t(28) = 2.21$, $p = .03$). The JNDs in the same position condition did not differ between the two groups of participants ($t(28) = .46$, $p =$

.65, n.s.). There was a borderline significant main effect of Relative stimulus position [F(1,28) = 4.01, p = .055], with participants responding more sensitively in the different positions condition than in same position condition (mean JNDs of, respectively, 66 vs. 71 ms), and no main effect of Group [F<1, n.s.].

A similar analysis of the PSS data revealed that the tactile stimulus had to lead by 25 ms when the two stimuli were presented from the same position and by 29 ms when the stimuli were presented from different positions in order for the PSS to be achieved. However, the difference between these two values failed to reach statistical significance [F(1,28) = 1.26, p = .27]. Neither the main effect of Group [F(1,28) < 1, n.s.], nor the interaction between Group and Relative stimulus position [F(1,28) < 1, n.s.], was significant (see Figure 15 and Table 11).

	Sighted		Blind					
			Early-blind		Late-blind		Overall	
Relative spatial position	**JND**	**PSS**	**JND**	**PSS**	**JND**	**PSS**	**JND**	**PSS**
Same	69.28 (4.01)	26.97 (7.88)	62.13 (10.42)	17.75 (7.84)	80.55 (7.44)	27.85 (8.68)	72.66 (6.43)	23.52 (5.94)
Different	70.46 (6.03)	28.54 (8.91)	51.92 (9.97)	23.38 (8.48)	67.92 (7.65)	34.10 (9.45)	61.08 (6.26)	29.50 (6.44)

The standard errors of the mean are reported in parentheses.

Table 11. Mean and standard errors of the mean JND and PSS values (in ms) for each group of participants

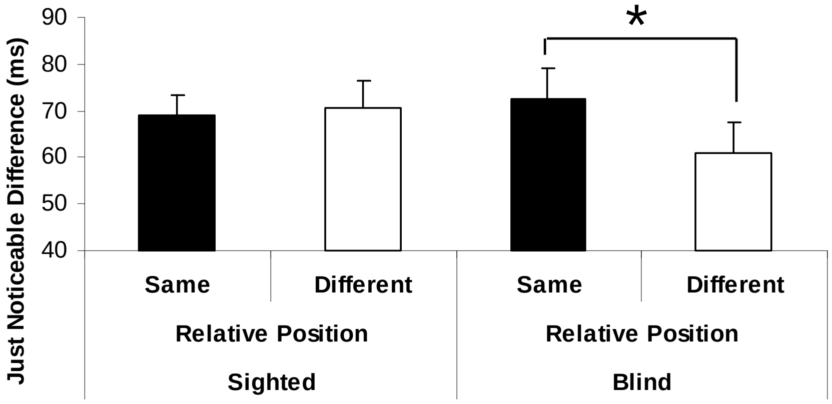


Figure 15. JNDs (in ms) for the same versus different relative spatial position for each group (blind vs. sighted), showing that the presentation of the audiotactile pairs of stimuli from different spatial positions did not facilitate the performance of the sighted participants. By contrast, when visuotactile or audiovisual stimuli were presented from different positions, the performance of the blind participants was significantly more sensitive (i.e., the JND was smaller) than when the stimuli were presented from the same position (indicated by an asterisk; p<.05). The error bars represent the standard errors of the means. Values are in milliseconds.

In order to determine whether the performance of the 6 early blind participants was any different from that of the 8 late blind participants, we conducted an additional post-hoc analysis of the data. In particular, the JND data were submitted to a mixed between-within repeated-measures ANOVA with the factors of Relative stimulus position (same vs. different) and Group (early vs. late-blind). The analysis revealed a significant between-participants effect of Relative stimulus position [F(1,12) = 37.60, p < .001], with the participants responding more accurately when the stimuli were presented from different spatial positions (JND = 61 ms) than from the same position (JND = 73 ms). When looking at overall performance on the TOJ task, the JNDs of the early blind participants (JND = 57 ms) and of the late blind participants (JND = 74 ms) were not statistically different [F(1,12) = 1.97, p = .18]. The effect of Relative stimulus position did not vary significantly according to the length of their visual deprivation, as suggested by the absence of any significant interaction between Group and Relative stimulus position [F(1,12) <1, n.s.].

11.2.3. Discussion

In Experiment 9, we compared the performance of blind and sighted participants in a crossmodal audiotactile TOJ task. Our results showed that while the performance of the sighted participants was unaffected by the relative spatial position (same vs. different) from which the two stimuli (one auditory, the other tactile) were presented, the performance of the blind participants was modulated by relative spatial position. In particular, the blind participants performed significantly more accurately when the two stimuli were presented from different spatial locations rather than from the same position. The fact that the performance of the blind – but not that of the sighted – participants was sensitive to the spatial separation between the auditory and tactile stimuli is consistent with the hypothesis that only the visually deprived group was influenced by spatial cues when performing the task. The fact that spatial incongruence (as compared to congruence) led to a selective improvement in the performance of our blind participants is consistent with previous data showing that visual deprivation results in an improved ability to process spatial cues in the spared sensory modalities (e.g., in touch: Röder et al., 2004; and in hearing: Chen, Zhang, & Zhou, 2006; Collignon, Renier, Bruyer, Tranduy, & Veraart, 2006; Röder et al., 1999). Taken together, these results establish a similarity with the pattern of performance reported recently in sighted participants in both visuotactile (e.g., Spence et al., 2001; Spence et al., 2003) and audiovisual TOJ tasks (e.g., Keetels & Vroomen, 2005; Vatakis & Spence, 2006; Vroomen, Keetels, de Gelder, Bertelson, 2004; Zampini et al., 2003a, b).

As a numbers of authors have suggested previously (e.g., Keetels & Vroomen, 2005; Spence et al., 2001; Vatakis & Spence, 2006; Vroomen, Keetels, de Gelder, & Bertelson, 2004; Zampini et al. 2003a), the spatial modulation of TOJ performance may be attributable to the availability of redundant spatial information in the different-positions trials. As the TOJ task was presumably difficult for participants at the shorter SOAs, they may have utilized information concerning which position they perceived as having been stimulated first in order to facilitate their judgments concerning the correct order of presentation of the two modalities of stimuli. As these spatial cues are only available when the stimuli are presented from different positions, a selective facilitation of performance would only be expected to be observed in the different-positions (vs. same-position) condition. The significant effect of relative spatial position shown by the blind participants provides evidence of their enhanced ability to use the spatial cues available in the intact residual senses (e.g., hearing and touch) resulting from visual deprivation. Conversely, the exclusive reliance on those sensory modalities that are typically considered adequate for conveying spatial information (cf. Welch & Warren, 1980) failed to induce any advantage in terms of the performance of the blindfolded sighted participants.

An alternative explanation for the relative spatial position effect reported in the present study assumes that the performance of the blind participants may have been influenced by multisensory binding: according to the spatio-temporal rules of multisensory integration (e.g., Stein, Meredith, & Wallace, 1993; Stein & Stanford, 2008), spatially and temporally co-occurring signals are more likely to be perceived as referring to the same external event (e.g., Calvert & Thesen, 2004; Driver & Spence, 2000; King & Calvert, 2005; Spence, 2007). Thus, stimuli from different sensory modalities that are be presented from the same spatial position at approximately the same time tend to be bound together by the brain, thus giving rise to representations of unitary objects with multisensory properties (or attributes; see Zampini et al., 2003a, for a similar claim). The pattern of performance demonstrated by the blind participants in the audiotactile TOJ task is compatible with this explanation. The experimental data reveal that larger SOAs are needed in order for participants to be able to correctly determine the order in which the pairs of stimuli were presented in the same- versus in the different-positions condition. Indeed, in the former condition, the spatial and temporal co-occurrence of signals makes the order of onset of temporally discrepant stimuli particularly difficult to disambiguate, thus perhaps giving rise to less sensitive TOJ performance. This data might be taken to suggest that the prolonged absence of visual information results in the strengthening of crossmodal links between audition and touch compared to those exhibited by control participants, who presumably base their spatial coding preferentially on visual cues instead. However, the overall performance of the blind and sighted participants did not differ significantly, thus making this an unlikely explanation for the results of the present study.

It should be noted that the blind participants did not perform the task while blindfolded. In order to control for the possible influence of saccades on the coding of spatial cues, they were requested to direct their gaze in front of them. Note that previous studies that have investigated the role of eye movements in mediating auditory localization in blind participants have found that auditory spatial abilities are independent of the mechanisms of attentional orienting (Després, Candas, & Dufour, 2005; cf. Röder, Spence, & Rösler, 2000). This seems to rule out the possibility that the occurrence of saccades may have played any significant role in the present study.

The performance of the sighted participants in the present study was unaffected by the relative spatial position from which the auditory and tactile stimuli were presented (see Zampini et al. 2005, for similar results). This null result might be explained by considering the crucial role of vision in the processing of spatial information in frontal space. Vision allows for the simultaneous perception of a large field of view and it is well known that visual cues are particularly important for the efficient localization and identification of objects (Thinus-Blanc & Gaunet, 1997). Thus audiotactile interactions may be somewhat less ‘spatial’ than other multisensory interactions involving vision as one of the component sensory modalities when stimuli are presented in the frontal space (e.g., audiovisual and visuotactile stimulus pairings; see Spence et al., 2003; Zampini et al., 2003a, b) or when audiotactile stimuli are presented behind a person’s head (Kitagawa et al., 2005). Kitagawa and his colleagues have suggested that the space behind the head, where no visual inputs are typically available, might be a more appropriate part of space in which to examine spatial interactions between auditory and tactile information processing. Similarly, both neurophysiological (e.g., Graziano et al., 1999) and neuropsychological data (e.g., Farné & Làdavas, 2002) suggest that audiotactile interactions may be more prevalent in the region behind the head (i.e., in the region where vision provides no direct information). This evidence may therefore account for the discrepancy between the results reported in audiotactile TOJ tasks for stimuli presented from the back and the frontal space (Kitagawa et al., 2005; Zampini et al., 2005). The absence of any spatial modulation of performance in the latter condition is likely attributable to the reduced spatial resolution of auditory and tactile sensory systems compared to vision (Eimer, 2004).

The results reported here suggest that visual deprivation can result in qualitatively different ways of processing auditory and tactile information, thus helping to shed light on the still unresolved issue concerning the existence of quantitative versus qualitative perceptual differences between the sighted and blind (cf. Eimer, 2004). In fact, in the present study, no quantitative differences in temporal resolution were found between these two groups of participants. This result is compatible with the results obtained by Weaver and Stevens (2006), who showed comparable performance of early blind participants and sighted controls on an auditory gap detection task.

However, our results contrast with those reported in other studies involving more complex perceptual skills. Indeed, previous TOJ studies have demonstrated higher sensitivity in the visually deprived when judging the temporal order in which tones (Stevens & Weaver, 2005) and tactile stimuli are presented (Röder et al., 2004). Meanwhile, Stevens and Weaver (2005) reported lower temporal thresholds in early blind participants (vs. sighted controls), suggesting a more rapid perceptual consolidation of auditory stimuli in this group of participants. Röder et al. observed better temporal resolution only in congenitally blind (but, interestingly, not in the late blind). The latter result was interpreted by Röder and her colleagues as constituting evidence that the congenitally blind localize tactile stimuli in space using only a body-centered frame of reference (instead of both body-centered and external codes like sighted and late blind individuals) before determining their temporal order (cf. Kitazawa, 2002). This might explain the advantage (i.e., better temporal resolution) in the congenitally blind as compared to the other two groups in tactile TOJ tasks. Research on compensatory processes triggered by the loss of vision is consistent with the claim that sensory deprivation results in the extensive use of the remaining sensory systems, with a consequent improvement in the efficiency of their operation (Eimer, 2004; Pascual-Leone, Amedi, Fregni, & Merabet, 2005). The claim that blindness also induces increased acuity within the spared sensory modalities is, however, rather more controversial (Gougoux, Lepore, Lassonde, Voss, Zatorre, & Belin, 2004; Grant et al., 2000; Stevens, Foulke, & Patterson, 1996).

An interesting question relating to these observations concerns whether the spatial modulation of performance that was observed in the blind participants in the present study reflects an increased sensitivity within the spared sensory modalities or whether instead it reflects a more proficient use of non-visual information. The group of sighted participants, although able to discriminate the location of the stimuli without problem, did not seem to rely on the redundancy of spatial cues in order to perform the experimental task. This might suggest the intriguing possibility that the difference observed between the performance of the two groups of participants rely on differences in the spatial coding of auditory and tactile stimuli of sighted and visually deprived participants. In particular, there might be some automatic or subconscious difference in the spatial localization of the auditory and tactile stimuli. Therefore, one might suggest that the performance of sighted participants would be made somewhat more similar to that of the blind participants by informing them of the potential benefits to be had from using spatial redundancy as a cue.

11.3. Experiment 10. Crossmodal dynamic capture in blind and sighted individuals.

An increasing amount of research has recently explored the consequences of visual deprivation in humans: the experimental evidence strongly suggests that the loss of vision determines perceptual and behavioural changes within the remaining sensory modalities (e.g., Pascual-Leone & Hamilton, 2001; Théoret, Merabet, & Pascual-Leone, 2004. See Chapter 6 for an extensive discussion on this topic) and an underlying dramatic reorganization of cortical architecture (e.g., Amedi, Merabet, Bermpohl, & Pascual-Leone, 2005; Kujala, Ahlo, & Näätänen, 2000; Pascual-Leone, Amedi, Fregni, & Merabet, 2005). For instance, it has been documented that the occipital cortex - commonly associated with the processing of visual information – is recruited in a compensatory cross-modal manner and is functionally involved both tactile (e.g., Burton, Snyder, Conturo, Akbudak, Ollinger, & Raichle, 2002; Sadato, Pascual-Leone, Grafman, Deiber, Ibanez, & Hallett, 1998; Sadato, Okada, Kubota & Yonekura, 2004) and auditory tasks (e.g., Kujala, Palva, Salonen, Alkuf, Huotilainen, Järvinen, & Näätänen, 2005; Collignon, Lassonde, Lepore, Bastien, & Veraart, 2007). One can speculate on whether the functional adjustment of spared sensory modalities to the demands of visual deprivation results in an increased perceptual sensibility within the remaining senses (e.g. hearing and touch) or to an amelioration of the capability to code non-visual cues to perform auditory and tactile tasks.

Few of these research have focused on the perception of motion in blind people presented in spared modalities (i.e., touch: Goyal, Hansen, & Blakemore, 2006; Kellogg, 1962; Ricciardi, Vanello, Sani, Gentili, Scilingo, Landini, Guazzelli, Bicchi, Haxby, & Pietrini, 2007; and audition: Poirier, Collignon, Scheiber, Renier, Vanlierde, Tranduy, Veraart, & De Volder, 2006. See also: Juurmaa & Suonio, 1975; Saenz, Lewis, Huth, Fine, & Koch, 2008). This is somewhat surprising, considering the central role of perception of motion in performing many everyday activities, such as navigating along the streets of a city (e.g., Loomis, Klatzky, Golledge, Cicinelli, Pellegrino, & Fry, 1993; Loomis, Klatzky, & Golledge, 2001; Klatzky, Loomis, Golledge, Cicinelli, Doherty, & Pellegrino, 1990; Rieser, Ashmead, Talor, & Youngquist, 1990).

In one of these few studies, Poirier and colleagues (2006) showed that in early blind individuals the auditory motion processing recruited not only auditory motion areas and V5 and V3/V3A visual motion areas, but also primary V1/V2 visual areas. These data suggest that the brain areas involved in visual motion processing can also be recruited by auditory motion processing in blind individuals. Analogously, Ricciardi and colleagues (2007) showed that the tactile flow perception activates a larger region in blind people than the one activated in sighted people, including the lateral occipital and inferior temporal cortical areas (see also Goyal et al., 2006 for similar results).

It is well known that crossing the hands over the midline induces a conflict between the frame of references commonly used to code the localization of tactile stimuli presented on the hands (i.e., externally and body-centered frame of references; e.g., Shore, Spry, & Spence, 2002; Yamamoto & Kitazawa, 2001). This is mirrored in the decrement of performance in judging the temporal order of two tactile stimuli, each presented to the left and right middle fingers of the crossed hands as compared to when the hands are kept in the uncrossed posture (e.g., Yamamoto & Kitazawa, 2001). Interestingly, the magnitude of this effect is significantly modulated by the visual status of the people performing the task (Röder et al., 2004; Röder, Föcker, Hötting, & Spence, 2008). A tactile TOJ study investigated the ability to correctly order pairs of stimuli delivered to the left and right middle fingers of uncrossed and crossed hands in visually deprived and sighted participants. Röder and colleagues found that the performance of sighted group was significantly affected by crossing the hands. The interval required for judging the temporal order between the two tactile stimuli presented to crossed hands doubled (i.e., the task was noticeably more difficult) as compared to the uncrossed posture condition. These data support the notion that the localization of touch is extensively based on both externally and body-centered defined coordinates and that, when these coordinates are in conflict (i.e. crossed posture), more time is required to localize the tactile stimuli (and, thus, to determine their correct temporal order). Interestingly, according to the hypothesis that visual input may lead to an impairment of TOJs for tactile stimuli when unusual postures are adopted, no effect of posture on early-blind performance has been documented. Röder and colleagues suggested that the exclusive reliance of congenitally blind on proprioceptive cues within a body-centered frame of reference had preserved their performances from the decrement induced by crossed-hands effect, facilitating the computing of localization of tactile stimuli and the subsequent identification of their temporal order. On the contrary, the hand-crossed posture exerts a strong effect on performance of late blind participants, determining a significant impairment of their ability to judge the temporal order of tactile stimuli. This evidence demonstrates that the visual input during development lead to the establishment of a visual frame of reference that persists even after the occurrence of blindness, resulting in a dramatic biasing of tactile localization by visual cues.

The effect of crossing hands has been investigated not only in the perception of static tactile stimuli, but also, although far less extensively, in the perception of apparent motion. Sanabria and colleagues (2005) studied the influence of the hand posture on the interactions occurring between apparent moving tactile and auditory displays by applying the crossmodal dynamic capture paradigm (see also Sections 9.2 and 9.3 In Sanabria and colleagues´ study, participants had to discriminate the direction of an auditory stream while attempting to ignore a task-irrelevant tactile stream or to discriminate the direction of a tactile stream while attempting to ignore a task-irrelevant auditory stream. In both tasks, the hand posture was manipulated, with participants adopting either the uncrossed or the crossed hand postures. The results revealed that the performance was significantly more accurate in the congruent (vs. incongruent) conditions (congruency as always defined relative to the direction in external space) across the four different experimental condition. Even more interestingly, the posture change significantly affected the performance, with different implications as a function of modality in which the target streams were presented. More specifically, when the target streams were presented in the auditory modality, a significant decrease in performance was observed when the task was performed in the uncrossed (vs. crossed) hand posture. The opposite pattern of results was reported when the target streams were presented in the tactile modality. In this condition, the performance was worse when the hands were placed in the crossed (vs. uncrossed) posture. Taken together, these results suggest that in an audiotactile crossmodal dynamic capture task, tactile information is likely to be coded according to both a somatotopic and an externally based frames of reference and it is considered as less reliable when the hands are crossed, thus modulating the reciprocal interactions between touch and audition.

The present study is thus designed to address the potential modulation of the crossing hand effect on the perception of motion within the crossmodal dynamic capture task as a function of the visual status of the participants (cf. Röder et al., 2004). To address this issue, three groups of participants (i.e., early/congenitally blind, late blind and sighted) are requested to discriminate the direction of a target stream (tactile, Condition a; auditory, Condition b) while trying to ignore the direction of a distractor stream presented in a different modality (auditory, Condition a; tactile, Condition b) while placing the hands in the uncrossed or crossed postures (cf. Sanabria et al., 2005).

When the participants perform the task by placing the hands in the uncrossed hand posture, we would expect significant audiotactile interactions, with participants responding more accurately when the target and task-irrelevant streams are spatially congruent then when they have opposite directions. If the visual experience affects the perception and/or the discrimination of the apparent motion and the audiotactile interactions as explored by the crossmodal dynamic capture paradigm, then we would predict a modulation of the accuracy of performance as a function of the onset of blindness (i.e., congenitally vs. late blind). Consistently with the data reported by Sanabria et al.’s study, when the hands are placed in the crossed (vs. uncrossed) posture we predict a decrease of the reliability attributable to the tactile modality, with, respectively, a stronger interfering effect exerted by the auditory streams on the discrimination of the direction of the tactile streams (Condition a) and a weaker capture effect of the tactile streams on the discrimination of the direction of the auditory streams (Condition b). In the crossed hand experimental condition, if the absence of any visual experience (i.e., congenitally blindness) induce the exclusive reliance on non-visual cues and the establishment of a somatotopic frame of reference for the coding of tactile stimuli, then we could expect a decrease – or even the reverse – of the congruency effect (i.e., the direction of the tactile motion defined by somatotopic or external frame of reference should be the opposite when the hands are crossed).In turn, this would not determine the decrease of the capture effect of the tactile distractor on the auditory stream direction discrimination in the crossed (vs. uncrossed) nor the increase of the interfering effect of the auditory streams on the discrimination of the direction of the tactile streams

In summary, the results are expected to provide insight into the functional links between hearing and touch and the perceptual consequences of visual deprivation in motion perception processing. In particular, the investigation of the dynamic features of auditory and tactile sensory modalities and their reciprocal interactions in blind people may contribute to the understanding of the relative weight played by each spared modality in the compensatory processes following the visual deprivation in the motion perception domain.

11.3.1. Method

Participants. Sixteen blindfolded sighted (12 females; mean age of 26 years; range from 19 to 36 years) and fifteen blind participants (10 females; mean age of 32 years; range from 21 to 41 years) took part in this study. Five of blind participants were congenitally or early blind, while the other ten were late blind (having been blind for between 5 and 26 years). Four had rudimentary sensitivity to brightness; two had colour and pattern vision (see Table 12 for details). All of the participants reported normal hearing and normal tactile sensitivity. The experiment took approximately 45 min to complete and was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. All of the participants gave their informed consent prior to their inclusion in the study.

Nr	Age	Gender	Visual perception	Age of onset	Duration	Cause of blindness
1	34	F	Color & pattern perception	19 yrs	15	Macular degeneration
2	41	F	None	25 yrs	16	Eyeball subatrophy (RE), surgical anophthalmos (LE)
3	32	M	None	18 yrs	14	Eyeball subatrophy (RE), retinal detachment (LE)
4	21	F	Light perception	Birth	21	Surgical aphakia & macular degeneration
5	26	M	Light perception	7 yrs	19	Congenital glaucoma
6	31	F	None	Birth	31	Retinitis pigmentosa
7	23	M	None	Birth	23	Unknown
8	27	F	None	10 yrs	17	Stargardt disease
9	31	M	None	18 yrs	13	Unknown
10	39	M	None	26 yrs	23	Unknown
11	35	F	None	4 yrs	31	Unknown
12	33	F	None	27 yrs	6	Car accident
13	37	M	None	31 yrs	6	Retinitis pigmentosa
14	41	F	Light perception	36 yrs	5	Unknown
15	29	F	Light & pattern perception	22 yrs	7	Unknown

Table 12. Description of the blind participants

Apparatus and stimuli. Two loudspeaker cones (Dell, A215; Round Rock, TX) positioned on the table-top in front of the participant were used to present the auditory stimuli. The loudspeaker cones were placed approximately 50 cm from the participant’s body, 15 cm to either side of their midline. Two vibrotactile stimulators (bone conduction vibrators, Oticon-A, 100 Ohm; Hamilton, Scotland) were placed in front of each loudspeaker cone, to ensure that the sounds and vibrotactile stimuli came from the same spatial locations (see Figure 16 for a schematic view of the experimental set-up). The participants responded using footpedals located under the table (one beneath the toes of the right foot and the other beneath the toes of the left foot). The loudspeaker cones, vibrotactile stimulators, and footpedals were all controlled via a computer parallel port using the E-Prime programming language (http://www.pstnet.com), and a custom-built relay box. The experiment was conducted in a dimly-illuminated room. The auditory stimuli consisted of two 50-ms white noise bursts, one presented from each loudspeaker cone, separated by a 100 ms inter-stimulus-interval (ISI) that remained constant across all conditions. The tactile displays consisted of two 50-ms suprathreshold vibrations, one presented from each vibrator, separated by an ISI of 100 ms.

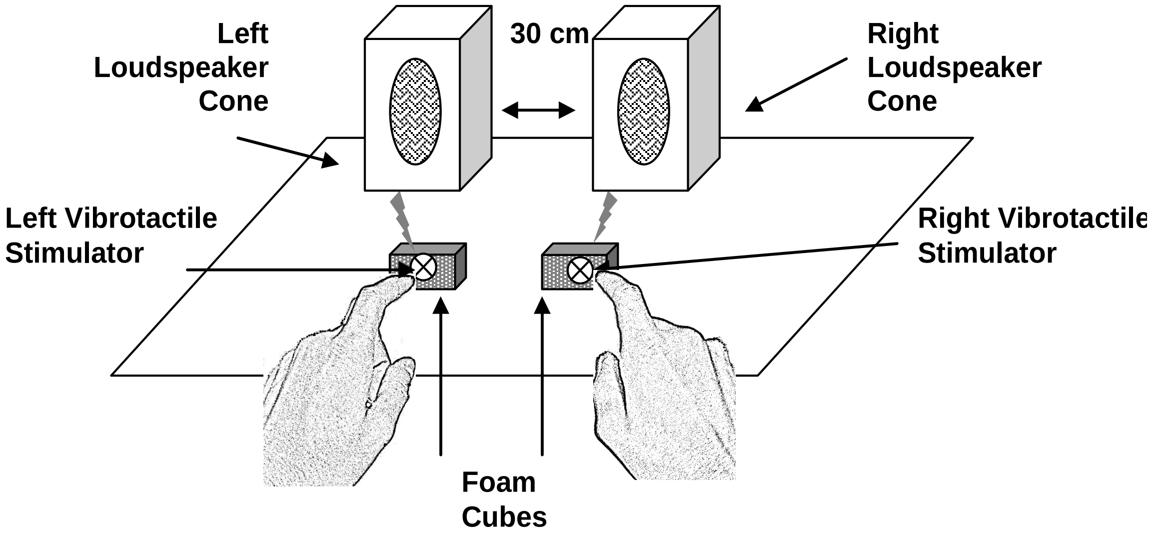


Figure 16. Schematic diagram illustrating the experimental set-up.

Procedure. The participants sat in front of the loudspeaker cones. To attenuate any noise resulting from their operation the two vibrotactile stimulators lay on two foam rectangles (3 cm thick), placed directly in front of the loudspeaker cones. The participants were requested to rest their left index fingertip on the left vibrotactile stimulator and their right index fingertip on the right vibrotactile stimulator. The participants were instructed to rest their feet on the footpedals and to keep their head still while looking straight ahead throughout each block of experimental trials.

White noise was presented from two loudspeaker cones positioned 60 cm behind the loudspeaker cones used to present the target stimuli, to mask any auditory cues elicited by the activation of the vibrotactile stimulators. In each condition (a and b), the participants were presented with two blocks of trials, each consisting of 96 trials. The participants then completed one block of 96 trials in the crossed-hands posture and one block of 96 trials in the uncrossed-hands posture. The order of presentation of the blocks was counterbalanced across participants. White noise set at 75 dB(A) was used to mask any subtle auditory cues elicited by the activation of the vibrotactile stimulators.

In a typical trial, the participants were presented with the target vibrotactile stream to which they had to make an unspeeded footpedal discrimination response, and a distractor auditory stream, which they were instructed to try and ignore. The distractor stream could either be presented at the same time as the target tactile stream (synchronous) or else 500 ms later (asynchronous) and in either the same (congruent) or opposite (incongruent) direction (from right-to-left or left-to-right). The participants were instructed to respond to the direction of the tactile (Condition a) or auditory (Condition b) stream by pressing the corresponding footpedal (left for leftward-moving targets, and right for rightward-moving targets) and to ignore the distractors as much as possible. The participants were instructed to prioritize response accuracy over response speed. Responses were only collected after 750 ms from the beginning of the trial (i.e., after the complete display of the stimuli), in order to ensure that any lack of an effect of the distractors on the perception of the target stream in the asynchronous condition was not caused simply by the participants responding to the tactile target before the auditory distractors had been presented (see Soto-Faraco et al., 2004b, on this point). After a participant’s response had been recorded, there was a random interval (of 1900, 1950, 2000, 2050, or 2100 ms) before the start of the next trial. At the end of each block of trials, the participants were instructed to use two 7-point Likert scales in order to judge the strength of their perception of apparent movement elicited by the target stream (1 = no sensation of movement; 7 = strong sensation of movement) and their confidence in their response (1 = no confidence in their responses; 7 = high confidence in their responses). In condition a, the participants completed one block of 12 practice trials at the start of each experimental session in which the target streams were presented in the absence of any distractors in the uncrossed posture, to familiarize them with the task at hand. At the end of the experimental session, the participants completed a second block of trials in which they responded to the direction of the tactile streams presented in isolation (i.e., without any distractors) with their hands in a crossed posture. In condition b, before starting the experiment the participants completed one block of 12 practice trials in the uncrossed posture with auditory stimuli presented in isolation (i.e., without the distracting tactile stimuli). Finally, the participants completed a second block of trials in which they had to respond to the direction of the unimodal auditory streams keeping the arms in the crossed posture. The order of presentation of these unimodal blocks was counterbalanced across participants.

11.3.2. Results

The accuracy data were normalized using arcsine transformation of the square root of the proportion obtained in each condition for each participant. This procedure converts binomially distributed data, such as proportions, into normally distributed data, thus enabling parametric analysis of the data (Bartlett, 1947). First, the transformed accuracy data reported with unimodal trials involving the presentation of tactile streams to uncrossed or crossed hands were submitted to a repeated measures analysis of variance (ANOVA) with Posture as within-participants factor and Visual Status as between-participants factor. The effect of Posture was significant, F(1,28)=106.00; p<.001, with lower accuracy in determining the direction of the tactile streams presented to the crossed vs. uncrossed hands (M= 37 vs. 97%, respectively). No effect of Visual Status, F(2,28)=.57; p=.07, nor the interaction between Posture and Visual Status emerged, F(2,28)= 3.03, p=.07.

Then, the transformed accuracy data of the experimental trials in which the targets consisted of tactile stimuli were submitted to a repeated measures analysis of variance (ANOVA) with Synchrony (synchronous vs. asynchronous), Posture (uncrossed vs. crossed), and Congruency (congruent vs. incongruent) as the within-participant factors and Visual Status (sighted vs. early- and late-blind) as between-participants factor. Bonferroni adjustments were calculated to further evaluate significance levels. The overall analysis revealed a significant main effect of Synchrony, F(1,28)=63.81; p<.001, with the participants responding more accurately in the asynchronous condition than in the synchronous condition overall (M = 68% vs. 56%, respectively). The main effect of Congruency (measured as the difference in accuracy between the congruent and incongruent conditions) was significant, F(1,28)=15.64; p<.001, with participants responding more accurately in the congruent trials than in incongruent trials overall (M = 81% vs. 43%, respectively). The main effect of Posture was also significant, F(1,28)=84.97; p<.001, with participants responding more accurately in the uncrossed posture than in the crossed posture overall (M = 81% vs. 44%, respectively). There was a significant effect of Congruency in the synchronous condition (p<.001), but not in the asynchronous condition, (p = 1.00) (mean congruency effect of 72% and 7%, respectively), giving rise to the significant interaction between Congruency and Synchrony, F(1,28)=220.42; p<.001. The analysis revealed a larger effect of Hand Posture (measured as the difference in accuracy between the crossed and uncrossed-hands conditions) in the synchronous condition than in the asynchronous condition (M = 48 vs. 17%, respectively), as shown by the significant interaction between Synchrony and Posture, F(1,28)=47.09; p<.001. Also the interaction between Posture and Congruency reached the significance, F(1,28)=10.29; p<.05, with a more pronounced congruency effect in the crossed vs. uncrossed posture (M = 45 vs. 35%, respectively). The interaction between Synchrony and Visual Status was significant, with a less pronounced difference between synchronous and asynchronous trials in the performance of sighted participants, p=.05, than of late-, p<.001, and early/congenitally, p=.02, blind participants (M= 6 vs. 20 and 13%, respectively). Also the change of posture differently affected the performance of the three groups of participants, giving rise to a significant interaction between Posture and Visual Status, F(2,28)=3.75; p=.04. Interestingly, both the sighted, p<.001, and the late-blind participants, p<.001, performed significantly better in the uncrossed vs. crossed posture. The performance of early/congenitally participants was not affected by the change of posture, p=.22. Finally, the difference in accuracy between congruent and incongruent conditions in synchrony (vs. asynchrony) was more pronounced in the groups of sighted and late-blind participants than in the group of early/congenitally participants, giving rise to a significant three-way interaction between Synchony, Congruency and Visual Status, F(2,28)=4.49; p=.02, as can be inferred by the above described results.

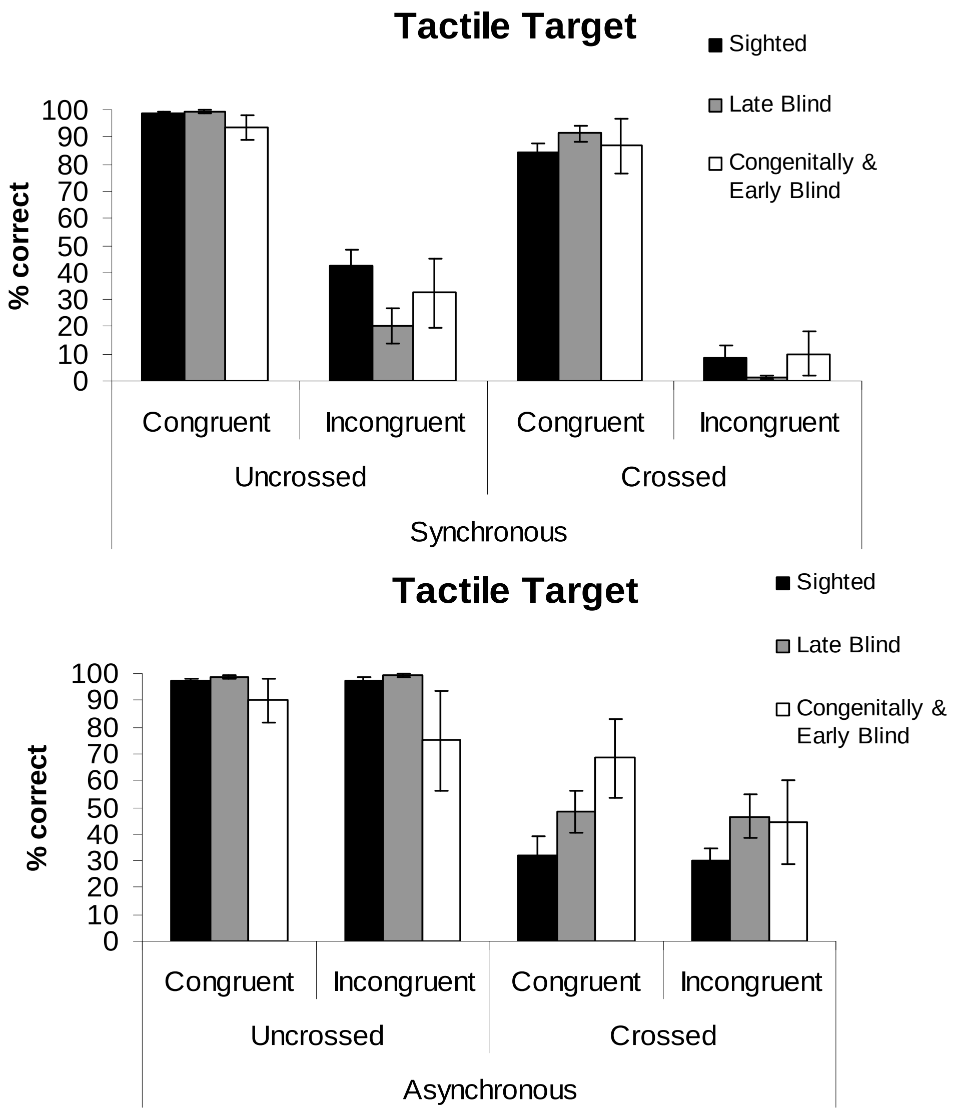


Figure 17. Summary of results (Experiment 10, condition a).

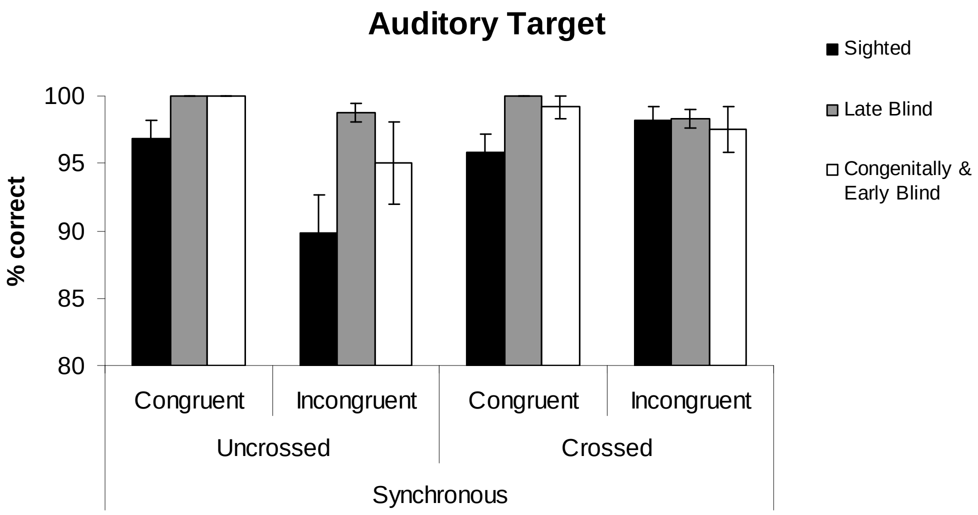
Perceived apparent motion ratings. The Likert scale ratings (see Table 13) of the perceived apparent motion for the tactile modality (presented in the either uncrossed or crossed posture conditions) were submitted to a repeated measures analysis of variance (ANOVA) with factors of Posture (uncrossed vs. crossed) and Visual Status (sighted vs. late-blindness vs. early/congenitally blindness). Neither the effect of Posture, F(1,28)=.013; p=.91, nor of the Visual Status, F(2,28)=.99; p=39, nor their interaction, F(2,28)=.73; p=.49, reached the significance.

Response confidence ratings. The Likert scale ratings (see Table 12) of the self-confidence in the uncrossed and crossed blocks were submitted to a repeated measures analysis of variance (ANOVA) with factors of Posture (uncrossed vs. crossed) and Visual Status (sighted vs. late-blindness vs. early/congenitally blindness). The effect of Posture was significant, F(1,28)=13.77; p=.001, with lower ratings given after the blocks performed with the crossed vs. uncrossed posture. The effect of Visual Status was marginally significant, F(2,28)=3.32; p=.05, with sighted participants reporting lower ratings of confidence in performing the task than both late and early/congenital blind participants. The interaction between Posture and Visual Status was not significant, F(2,28)=1.56; p=.23.

The transformed accuracy data reported with unimodal trials involving the presentation of auditory streams while keeping the hands in the uncrossed or crossed posture were submitted to a repeated measures analysis of variance (ANOVA) with Posture as within-participants factor and Visual Status as between-participants factor. The effect of Posture was significant, F(1,28)=8.46; p<.05, with lower accuracy in determining the direction of the auditory streams while keeping the hand in the uncrossed vs. crossed posture (M= 97 vs. 99%, respectively). No effect of Visual Status, F(2,28)=.48; p=.62, nor the interaction between Posture and Visual Status emerged, F(2,28)= .36, p=.70.

Next, the transformed data from the experimental blocks in which the targets consisted of auditory stimuli were submitted to a repeated measures ANOVA with Synchrony (synchronous vs. asynchronous), Posture (uncrossed vs. crossed), and Congruency (congruent vs. incongruent) as the within-participant factors and Visual Status (sighted vs. early- and late-blind) as between-participants factor.. The overall analysis revealed a significant main effect of Congruency, F(1,28)=13.07; p=.001, with the participants responding more accurately in the congruent condition than in the incongruent condition overall (M = 98% vs. 97%, respectively). Also the main effect of Visual Status, F(2,28)=3.63; p=.04, with the late-blind participants performing significantly better overall than the sighted participants, p=.04, but not than the early/congenitally blind, p=1.00. There was a significant effect of Congruency in the synchronous condition (p<.001), but not in the asynchronous condition, (p = 1.00) (mean congruency effect of 4% and .4%, respectively), giving rise to the significant interaction between Congruency and Synchrony, F(1,28)=8.69; p<.05. Also the three-way interaction between Synchrony, Posture and Congruency was significant, F(1,28)=5.34; p=.03, showing that the interaction between Posture and Congruency occurs only for stimuli presented synchronously (vs. asynchronously). More specifically, in the synchronous trials performed in the uncrossed posture the performance is significantly better in the congruent than in the incongruent condition, p<.05, and no different is present in the synchronous trials performed in the crossed posture, p=.100.

The three ways interaction between Synchrony, Posture and Visual Status was significant, F(2,28)=4.33; p=0.23, showing a larger and reversed effect of Posture (measured as the difference in accuracy between the crossed and uncrossed-hands conditions) in the synchronous condition than in the asynchronous condition for the group of sighted participants (M=4 vs 2%, respectively), and no significant interaction between Posture and Synchrony for the other two groups of participants, congenitally, F(1,9)=1.00; n.s., and late blind, F(1,4)<1; n.s. Finally, the four way interaction was significant, F(2,28)=3.44; p<.05.



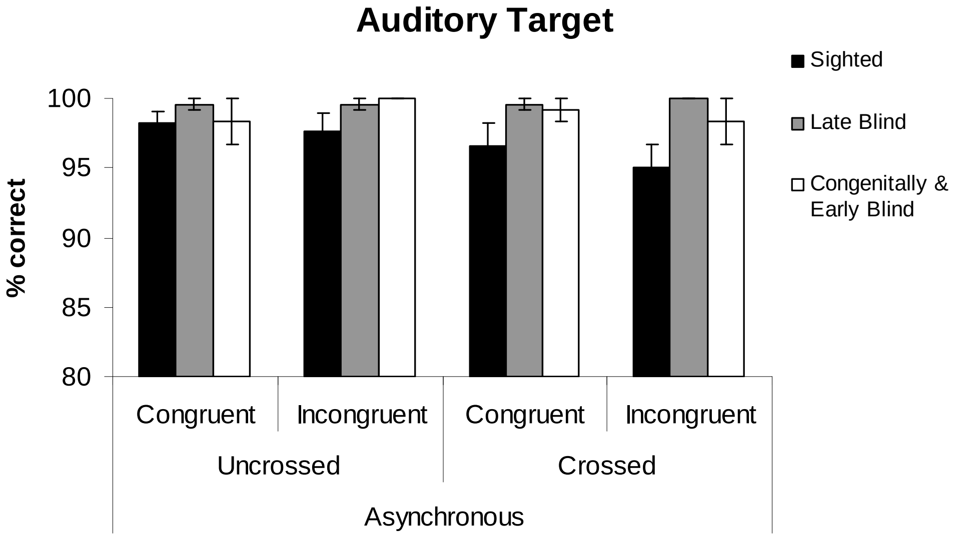


Figure 18. Summary of results (Experiment 10, condition b).

Perceived apparent motion ratings. . The Likert scale ratings (see Table 13) of the perceived apparent motion for the tactile modality (presented in the either uncrossed or crossed posture conditions) were submitted to a repeated measures analysis of variance (ANOVA) with factors of Posture (uncrossed vs. crossed) and Visual Status (sighted vs. late-blindness vs. early/congenitally blindness). Neither the effect of Posture, F(1,28)=2.03; p=.17, nor of the Visual Status, F(2,28)=1.25; p=39, nor their interaction, F(2,28)=.98; p=.39, reached the significance.

Response confidence ratings. The Likert scale ratings (see Table 13) of the perceived apparent motion for the tactile modality (presented in the either uncrossed or crossed posture conditions) were submitted to a repeated measures analysis of variance (ANOVA) with factors of

Posture (uncrossed vs. crossed) and Visual Status (sighted vs. late-blindness vs. early/congenitally blindness). The effect of Posture was not significant, F(1,28)=1.10; p=.30. The effect of Visual Status was significant, F(2,28)=5.46; p=.01, with sighted participants reporting lower confidence in performing the task than late blind participants, p <.05, but not than early/congenitally blind, p=.04. The interaction between Visual Status and Posture was not significant, F(2,28)=.84; p=.44.

Perceived apparent motion ratings (Condition a vs. b). The ratings of apparent motion given by the participants in Conditions a and b (see Table 13) were subjected to a repeated measures ANOVA with Modality (touch vs. hearing) and Posture (uncrossed vs. crossed) as the within-participants factors and Visual Status as between participants factors. The main effect of Modality was significant, F(1,28)=8.20; p<.05, with a higher impression of apparent motion conveyed by the auditory streams (M=5.18 vs. 4.57, respectively). No other terms reached the significance.

Response confidence ratings (Condition a vs. b). Participants' confidence rating responses in Conditions a and b (see Table 13) were subjected to a repeated measures ANOVA with Modality (touch vs. hearing) and Posture (uncrossed vs. crossed) as the within-participants factors as the within-participants factors and Visual Status as between participants factors. The main effect of Modality was significant, F(1,28)=65.54; p<.001, with participants reporting significantly higher ratings in the auditory vs. tactile target blocks (M=5.81 vs. 4.55, respectively). Also the main effect of Posture was significant, F(1,28)=8.30; p<.05, with participants being more confident in the uncrossed vs. crossed posture (M=5.44 vs. 4.92, respectively). The Visual Status affected the confidence in responding, F(2,28)=4.78; p=.02, with sighted participants being overall less confident in performing the task (although this difference reached the significance only in the comparison with the late-blind, p.03, and not with the early/congenitally blind, p=1.00). The participants declared to have been more confident in judging the direction of tactile streams by keeping the arms in the uncrossed vs. crossed posture, (M= 5.10 vs. 4.00; p<.001), and no difference as a function of the posture in judging the direction of auditory stream, p=1.00, giving rise to a significant interaction between Modality and Posture, F(1,28)=13.67; p=.001.

Condition	Target Modality	Visual Status	Posture	Perceived apparent motion ratings	Response confidence ratings
A	Tactile	Sighted	Uncrossed	4.38 (1.54)	4.88 (.96)
			Crossed	4.38 (1.20)	3.44 (1.15)
		Late Blind	Uncrossed	4.70 (1.38)	5.30 (1.25)
			Crossed	5.20 (1.03)	4.40 (1.17)
		Congenitally & Early Blind	Uncrossed	4.60 (1.14)	5.40 (.89)
			Crossed	4.20 (.84)	5.00 (1.00)
B	Auditory	Sighted	Uncrossed	4.75 (1.87)	5.38 (.96)
			Crossed	4.75 (1.65)	5.38 (.89)
		Late Blind	Uncrossed	5.60 (1.51)	6.40 (.70)
			Crossed	5.60 (1.51)	6.40 (.97)
		Congenitally & Early Blind	Uncrossed	5.40 (.89)	5.80 (.45)
			Crossed	5.80 (.45)	6.20 (.45)
Overall mean	Tactile		Uncrossed	4.52 (1.39)	5.10 (1.04)
			Crossed	5.13 (1.45)	4.00 (1.26)
	Auditory		Uncrossed	5.13 (1.45)	5.77 (.92)
			Crossed	5.19 (1.51)	5.84 (.97)

Table 13. Summary of the Likert scale ratings (Experiment 10). The standard deviations of the mean are reported in parentheses.

11.3.3. Discussion

In Experiment 10, we used the crossmodal dynamic capture task in order to explore the audiotactile interactions in the perception of the apparent motion and how the change of hand posture can modulate the reciprocal influence between these two sensory modalities (cf. Sanabria et al., 2005). Since the frame of reference used to code the tactile events in the space has been proved to change according the presence and the duration of previous visual experience, then three different experimental groups of participants (i.e., early/congenitally blind, late blind and sighted) have been tested.

In the condition a, the participants were requested to discriminate the direction of apparent moving tactile streams presented to the index fingers (of, respectively, uncrossed and crossed hands) while trying to ignore the distractors presented in the auditory modality. Consistently with previous evidence (Sanabria, Soto-Faraco, & Spence, 2005; Soto-Faraco et al., 2004b), the results demonstrated a significant crossmodal dynamic capture effect, with all participants showing a prominent decrease of performance when the auditory distractors were moving in the opposite direction as compared to the target streams. The effect of the directional congruency could be observed only when the stimuli were presented simultaneously - thus ruling out any possible interfering effect of decisional/post-perceptual processes (cf. Soto-Faraco, Spence, & Kingstone, 2005) – and was higher in the group of sighted and late-blind participants than in the group of early/congenitally participants. The fact that the early/congenitally blind show a lower congruency effect suggests that the absence or short lasting visual experience is related to a sharper discrimination of the direction of the stream of tactile stimuli. It must be noted, however, that the analysis of the performance in judging the direction of tactile streams presented in isolation (i.e., in absence of auditory distractors), although marginally significant, failed to highlight a difference as a function of the visual status of participants, thus making this hypothesis rather unlikely. These results can thus be explained taking into account the lower susceptibility of early/congenitally blind to be “captured” by the concurrent presentation of auditory streams. Hence, it seems plausible that the visual experience during the first years of life is critical to induce fully developed crossmodal functions, consistently whit what has been shown by studies on both animals (Wallace, Perrault, Hairston, & Stein, 2004; Wallace, Carriere, Perrault, Vaughan, & Stein, 2006) and humans (Putzar, Goerendt, Lange, Rösler, & Röder, 2007). In Putzar et al.’s study, patients who had been treated for dense congenital binocular cataracts in the first 5-24 months of life showed reduced audio-visual interactions, even though they were tested 14 years after the treatment. This study elegantly shows that adequate sensory inputs during the development are necessary to induce the cross-talk between sensory modalities in adult life. Other evidence further are consistent with the discrepancy in the performance between the congenitally/early blind sample and the late blind and sighted groups observed in the present study. For instance, Goyal and colleagues (2006) showed that in a tactile motion perception task the extrastriate areas are activated in people with adventitious blindness and not in people with congenital or early onset of blindness. The involvement of these regions not only during visual processing, but also during the tactile stimulation, only in the late blind sample suggests that the direct cross-sensory connectivity between the cerebral regions which are primarily involved in visual and tactile processing can be established only after a long-lasting visual experience. This evidence is further supported by the observation that a more extensive cerebral activation is observed in blind as compared to sighted individuals while engaged in a tactile motion task. Indeed, whereas in sighted the tactile flow perception selectively activates the anterior part of the lateral occipital and inferior temporal cortical areas, in blind it additionally activates the more posterior part of that complex. Moreover, the presence of a functional specialization of cortices (i.e., a more anterior part involved in the representation of both visual and tactile flows and a more posterior part selectively involved in the representation of visual flow) is strictly dependent on having experienced visual and tactile inputs during the development (Ricciardi et al., 2007). Unfortunately, previous studies on tactile motion discrimination in blind (Goyal et al., 2006; Ricciardi et al., 2007) do not provide behavioural data which could allow an exhaustive comparison with the present evidence of a higher accuracy of early/congenitally blind in discriminating the direction of tactile streams as compared to both late blind and sighted. Future investigations are thus needed to delve into this topic more extensively.

Another result to emerge from the Condition a is that crossing the hands across the body midline, possibly inducing a decrease of the reliability of the tactile information and a higher susceptibility to the dynamic capture exerted by the auditory stimuli, determined a significant overall decrease in the level of performance accuracy (cf. Sanabria et al., 2005). Interestingly, however, the effect of hand crossing on the performance was not observable in the whole sample, but rather varied as a function of the visual status of the participants, determining a selective impairment of the performance of sighted and late blind participants, and the change of hand posture failing to affect the performance of congenitally/early blind participants. However, the present results are not surprising, if one takes into account that visual deprivation results in an improved ability to process spatial cues and to efficiently focus attentional resources toward the spared sensory modalities (Collignon, Lassonde, Lepore, Bastien, & Veraart, 2007). The behavioural discrepancies reported in the present study could thus be attributed to the enhanced ability to process auditory and tactile inputs following visual deprivation, which can have overcome the difficulty of recode the tactile stimuli according to the adopted hand posture.

In the Condition b, the relationship between modalities was reversed, with auditory streams serving as targets and the tactile streams as distractors. The pattern of results showed that the overall accuracy of participants' performance was lower in Condition a than in Condition b, possibly indicating that the direction of the target motion stream was harder to discriminate when it was presented in the tactile (vs. auditory) modality and the distractors were presented in the auditory (vs. tactile) modality. This evidence is mirrored by the participants' self-reports, who declared to have responded with a higher level of confidence to the trials in which the target streams consisted in auditory (vs. tactile) stimuli (see Section of Results). Additionally, consistently with what had been already shown by previous investigations, the capture effect of the tactile distractors on the perception of auditory motion was, although significant, overall less pronounced than the auditory capture of the tactile motion (cf. Condition a; see Sections 9.2-9.4).. This result stands in contrast with those reported in some previous audiotactile crossmodal dynamic capture studies, showing that tactile apparent motion exerts a stronger capture effect on auditory motion than vice versa (Sanabria et al., 2005; Soto-Faraco et al., 2004b). It must be noted, however, that the auditory stimuli used in the present study differ from the ones involved in previous studies, for both intensity (i.e., 82 dB(A) vs. 60 dB(A) in Sanabria et al., 2005; 65 dB(A) in Soto-Faraco et al., 2004b) and nature (i.e., white noise vs. pure tones). These discrepancies prevent to draw an adequate comparison between the data obtained across these investigations.

Interestingly, in the temporally critical condition (i.e., when the target and distractor streams were presented synchronously), the spatial congruency effect differed according to the visual status of the participants, with higher level of proficiency showed by the groups of blind participants than of sighted participants. The behavioural evidence parallels with the participants' self-reports, with the sighted participants being less confident than visually deprived participants in responding.

As in the Condition a, it seems unlikely that these results could be attributed to a higher level of accuracy in discriminating the direction of the auditory streams (i.e., the discrimination of the auditory streams presented in absence of tactile distractors did not differ as a function of the visual status of the participants; see Section of Results), consistently with the behavioural data obtained by Poirier and collaborators (2006). More likely, it can be claimed that sighted and late blind participants are more sensitive to the tactile capture effect than congenitally/early blind participants. It must be noted that visual deprivation results in superior performances of blind as compared to sighted controls in some auditory processing tasks, such as auditory attention (Hugdahl, Ek, Takio, Rintee, Tuomainen, Haaral, & Hämäläinen, 2004), temporal auditory resolution (Weaver & Stevens, 2006). It has also been shown that blind humans exhibit a superior capability of blind to localize sounds (Lessard, Paré, Lepore, & Lassonde, 1998), especially in the peripheral space (Fieger, Röder, Teder-Sälejärvi, Hillyard, & Neville, 2006; Röder, Teder-Sälejärvi, Sterr, Rösler, Hillyard, & Neville, 1999), which can be attributed to a more strategic use of auditory features of sounds, e.g. spectral (Doucet, Guillemot Lassonde Gagné Leclerc, & Lepore, 2005) or echo cues (Dufour, Despré, & Candas, 2005). Since the encoding of auditory motion results from the proficient processing of both temporal and spatial features of the auditory stimulation (i.e., interaural time differences; see Middlebrooks & Green, 1991, for a review), it is plausible that the outperformance of blind humans in both temporal auditory resolution (Weaver & Stevens, 2006) and spatial localization (e.g., Lessard, Paré, Lepore, & Lassonde, 1998) tasks could contribute to the present results. Nevertheless, the results obtained in this study could appear even less surprising, if one consider the salience that auditory moving stimuli assume in the everyday life (cf. Zihl, von Cramon, & Mai, 1983. See Kellogg, 1962 for "facial vision" in blind). Orientation and navigation by humans depends upon the availability of multiple kinds of sensory information, which are mainly dynamic in nature, and are applied by an individual who is in turn moving, constantly changing direction and position throughout the space. For instance, walking along a crowded pavement implies the capability to effectively code the cues generated by both the self-movement and the dynamic features of inputs delivered by different sensory systems (i.e., vestibular, somatosensory, visual, auditory and olfactory systems; e.g., Loomis & Beall, 1998; Whishaw & Brooks, 1999). Additionally, the navigation strategies require the ability to effectively form, maintain and updating representations of the environment through which travel and actions take place (cf. Whishaw & Brooks, 1999). Although the absence of vision constitutes a remarkable constrain for the complete coding of the features of the space, blind participants often show an adequate internal representation of environment and a subsequent noticeable ability in navigating (cf. de Gelder, Tamietto, van Boxtel, Goebel, Sahraie, van den Stock, Stienen, Weiskrantz, & Pegna, 2008). Possibly contributing to the development of these skills is the high proficiency shown by blind people in coding subtle auditory cues for localizing auditory targets presented in the far space, where typically sensory-motor feedbacks can not be provided (Voss et al., 2004. Although see: Kallie, Schrater, & Legge, 2007). The importance of auditory cues in navigation of blind people is more directly demonstrated by Millar (1999), who showed that auditory, along with proprioceptive inputs, are crucial in the construction of the reference frames necessary for performing spatial tasks, and the calibration of self-movements. According to these empirical evidence, the recent attempts to develop navigation systems for the visually impaired involve the massive use of auditory signals (Iwamiya, Yamauchi, Shiraishi, Takada, & Sato, 2004; Loomis, Klatzky, & Golledge, 2001; Wall, Ashmead, Bentzen, & Barlow, 2004. See also: Walker & Lindsay, 2006).

In summary, since according to the ‘inverse effectiveness of the multisensory integration’ rule (Stein and Meredith, 1993) there is an inverse relationship between the saliency of the unimodal inputs and the amount of multisensory interaction, then it could be that the enhanced perceptual skills of the blind within the audition may reflect in the here observed reduced tactile capture of auditory streams.

The last remark regards the fact that the effect of the hand posture adopted by the participants while performing the task selectively influenced the performance of sighted, but not of the blind participants, independently from the lasting of visual experience. When the two streams were presented synchronously and the task was performed by placing the hands in the uncrossed posture, then posture the performance is significantly better in the congruent than in the incongruent condition. On the contrary, when the task was performed in the crossed hand posture, no congruency effect was revealed. These outcomes are consistent with previous studies, which showed that crossing the hands determines a decrease of the reliability of the tactile modality (e.g., Sanabria et al., 2005). When requested to judge the direction of the direction of the auditory stream, the participants perceive the tactile distractor as more interfering when they are delivered to the uncrossed hands then when they are presented to the crossed hands, thus resulting in the higher dynamic capture observed in the former (vs. latter) condition. This is also mirrored by the self-reports, with participants claiming to have been more confident participants declared to have been more confident in judging the direction of tactile streams by keeping the arms in the uncrossed vs. crossed posture, and no difference as a function of the posture in judging the direction of auditory stream. The fact that the performance of sighted – but not of blind individuals – were affected by the change of hand posture could suggest that the visually deprived participants are accurate in determining the direction of the auditory streams irrespectively of the posture adopted while performing the task, thus again indicating a lower susceptibility of congenitally and early visually deprived to be “captured” by the tactile distractors as a compensatory consequence of visual deprivation (cf. Hötting & Röder, 2004).

11.4. Experiment 11. Spatial audiotactile ventriloquism in blind and sighted individuals

In the literature investigating the multisensory integration, one of the most extensively investigated topic is how the presentation of spatially-discrepant visual information biases the localization of simultaneous sounds. This effect, labelled ‘ventriloquism effect’, bears its name from the illusion induced by performing ventriloquists, in which the speech they produce is erroneously perceived as coming from the moving lips of puppets (e.g., Howard & Templeton, 1966). This effect has been robustly replicated across a wide range of experimental conditions (see Recanzone & Sutter, 2008, for a review), and it has been proved to be a genuinely perceptual phenomenon (cf. Bonath, Noesselt, Martinez, Mishra, Schwiecker, Heinze, & Hillyard, 2007).

The possibility that a similar effect could also be proved for audiotactile stimulus pairings has been recently tested (Caclin et al., 2002). By using a staircase procedure (cf. Bertelson & Aschersleben, 1998), Caclin and collaborators demonstrated that the ability to correctly judge whether the auditory stimuli had been presented on the right or left side of the body midline was dramatically impaired by the concurrent presentation of – centrally located – tactile stimuli. This effect was considered as a genuine perceptual phenomenon, since it was selectively observed when the auditory and tactile stimuli were presented simultaneously and the location of the tactile stimulation was not predictive of the location of the auditory stimuli.

A successive study confirmed and indeed extended these findings, by specifically addressing whether the audio-tactile ventriloquism effect operates in an external or body-centered coordinate system (Bruns & Röder, in press). In their Bruns & Röder’s study, the participants were asked to report the perceived location of auditory stimuli presented from left, right and central locations, either alone or with simultaneous tactile stimuli located to the right or the left side of the speaker array. The results showed that participants consistently tended to localize the auditory stimuli toward the location from where the tactile stimuli were actually presented. This effect was more pronounced when the spatial discrepancy separating the two stimuli was large (vs. small), namely when the two stimuli were presented from different hemispaces as compared to when the the auditory stimulus was presented from the central position. When the task was performed by keeping the hands in the crossed posture, the effect was reduced, but still significant, in the large spatial discrepancy condition, whereas disappeared in the small spatial discrepancy. Interestingly, the mislocalization of the auditory stimuli occurred toward the external location of the tactile stimulus, and not toward the anatomical hand that was stimulated. These data corroborate the idea that the audiotactile ventriloquism effect operates according to an external coordinate system.

In the Experiment 11 we address the issue of whether blind people performing the above described task rely on an anatomical frame of reference. In a tactile TOJ task, Röder, Rösler & Spence (2004) investigated the ability of visually deprived and sighted participants to correctly order stimuli delivered to the left and right middle fingers of uncrossed and crossed hands. These authors found that the performance of sighted group, as well as of late-blind group, was significantly affected by crossing the hands: the interval required for judging the temporal order between the two tactile stimuli presented to crossed hands doubled (i.e., the task was noticeably more difficult) as compared to the uncrossed posture condition. These data support the notion that the localization of touch is extensively based on externally defined coordinates, modulated by visual cues; when these coordinates are in conflict with body-centered frame of reference (i.e. crossed posture), more time is required to localize tactile stimuli (and, thus, to determine their correct temporal order). Interestingly, according to the hypothesis that visual input may lead to an impairment of temporal order judgments for tactile stimuli when unusual postures are adopted, no effect of posture on early-blind performance has been documented. Interestingly, however, absolutely no effect of posture on early blind performance was documented; moreover, their performance showed better temporal resolution than the two other groups. Röder and her colleagues suggested that the exclusive reliance of congenitally blind on proprioceptive cues within a body-centered frame of reference had preserved their performance from the decrement induced by crossed-hands effect, facilitating the computing of localization of tactile stimuli and the subsequent identification of their temporal order. Their results nevertheless show that visual input during development leads to the establishment of a visual frame of reference that persists even after the occurrence of blindness, resulting in a dramatic biasing of tactile localization induced by external coordinates (e.g., in the crossed hands posture). In a more recent study, Collignon and colleagues (2009. See also Section 6.2) tested the ability of sighted, late- and congenitally-blind to lateralize auditory, tactile and audiotactile stimuli while keeping their hands uncrossed or crossed over the body midline. Similarly to previous evidence, they found that the crossed-hand posture had a detrimental effect for tactile performance in sighted subjects (cf. Röder et al., 2004) but a greater deficit in auditory performance in early blind ones (Röder et al., 2007; Experiment 2). Specifically, this crossed-hand effect in the auditory condition – the only condition where early blind did not outperform the other groups of participants – could be attributed to the disruption of the spatial compatibility between the anatomical coordinates of the responding hand and the external sound coordinates. In that task, the group of late blind had an intermediate pattern of performance between the scores obtained in controls and early blind (cf. Röder et al., 2004). In the audiotactile task, whereas both controls and late blind processed audiotactile signals in an integrative way, and irrespectively of the hand posture, the early blind showed an integration impairment of audiotactile signals in the crossed-hand posture. This result has been explained by the authors by considering that early blind, differently from the other two groups, do not automatically remap touch into external spatial coordinates (Röder et al., 2004, 2008), thus having to deal with the conflict induced by a mismatch between auditory and tactile frames of reference. This, in turn, could prevent efficient multisensory integration in the crossed hand posture in this group of participants.

According to this evidence, it can be argued that the crossing hands could have differential effects on the performance of sighted and congenitally-blind participants. Specifically, if the congenitally-blind use an anatomical frame of reference to code the tactile stimulation, then it can be hypothesized that the ventriloquism effect would induce a shift of the auditory stimuli toward the anatomical side where the tactile stimulation has been presented. According to Collignon et al.’s data, it can also be hypothesized that the magnitude of the ventriloquism effect could be reduced in the group of blind as compared to the group of sighted participants. However, two caveats can be advanced. First, in our experiment, the overlap between the part of the body stimulated and the effectors used to respond was accurately avoided, possibly decreasing any spatial compatibility effect between the anatomical coordinates of the responding hand and the external sound coordinates.

Furthermore, the possibility that the magnitude of the ventriloquism effect should decrease as a consequence of the supposed superiority of blind people in localizing sounds (e.g., Després, Boudard, Candas, & Dufour, 2005) may be a matter of debate, since a better performance has been proved to be selective in nature (Lewald, 2007) and especially occur in peripheral portions of space (Röder et al.,1999). However, it could also be that a potential lower ventriloquism effect in blind (vs. sighted) participants could be attributed not to the improvement of sound localization as a consequence of blindness, but rather to a finer capability to code for the spatial cues in both spared sensory modalities, touch and hearing (e.g., Eimer, 2004; Pascual-Leone et al., 2005. See also Section 11.2). Below, we will present the preliminary data collected on a group of sighted and a group of congenitally blind in an audiotactile ventriloquism task (please note that the collection of the data regarding a group of late blind is still ongoing), conduced by applying methods and procedure similar to those used by Bruns and Röder (in press).

11.4.1. Method

Participants. Eleven sighted (4 female, mean age: 35 years, range: 25-49 years, 1 left-handed) and nine congenitally blind (2 female, mean age: 37 years, range: 25-48 years, 1 left-handed, 1 bimanual) took part in the experiment. One of the congenitally blinds had rudimentary sensitivity to brightness; another had brightness and pattern perception (for details see Table 14). The informed consent of all participants was obtained prior to the study.The experiment took approximately 60 minutes to complete and was conducted in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki, as well as the ethical guidelines laid down by the University of Hamburg. All of the participants gave their informed consent prior to their inclusion in the study.

Nr	Age	Sex	Visual perception	Age of onset	Duration(yrs)	Cause of blindness
1	48	M	None	Birth	48	High oxygen supply in the incubator
2	33	M	None	Birth	33	Optic nerve damage
3	32	M	None	6 months	32	Retinoblastoma
4	29	F	Light perception	Birth	29	Retinopathy of prematurity
5	37	M	None	Birth	37	High oxygen supply in the incubator
6	34	M	Light and pattern perception	Birth	34	Hypoxia
7	48	F	None	Prenatal	48	Retinal infection
8	25	M	None	Birth	25	Genetic
9	46	F	None	Birth	46	High oxygen supply in the incubator

Table 14. Description of the blind participants

Apparatus and stimuli. The testing was carried out in a completely dark sound-attenuated room. Participants were seated in front of a table with their head laying a custom-made chinrest. Auditory stimuli were brief (10 ms) 2000 Hz tones (with 2.5 ms linear rise/fall envelopes), presented at 72 dB(A) sound pressure level as measured from the participant's head position. The tones were delivered from one of three loudspeakers, which were located centrally (A_C) and 10° to the left (A_L) and right (A_R) side at a distance of 60 cm from the participant's head. The speaker array was covered with a black, acoustically transparent curtain to avoid any visual information regarding speaker positions. Participants placed their hands on the desk in front of the curtain, so that the hands were located to the left (T_L) and right (T_R) of the speaker array at ±22.5° from the center. Note that T_L and T_R refer to external space irrespectively of which hand was stimulated.

Brief (10 ms) tactile stimuli were delivered to the tips of the index fingers via metal rods (diameter: 1.5 mm), which were electronically lifted from their resting position by a relay (lift from resting position: 0.5 mm). Relay and rod were contained in small plastic cubes placed beneath the index fingers. Participants responded with foot pedals located under the table. The loudspeakers, tactile stimulators, and foot pedals were all controlled via computer parallel ports using the Presentation software (Presentation Version 11.0, Neurobehavioral Systems Inc., Albany, CA, USA), and a custom-built relay box.

Procedure.The participants sat in front of the loudspeaker array with their hands placed on the two tactile stimulators. In the uncrossed-hands condition the participants rested their left index fingertip on the left stimulator (T_L) and their right index fingertip on the right stimulator (T_R). In the crossed-hands condition the left index finger lays on the right stimulator (T_R) and the right index finger on the left stimulator (T_L). The participants were instructed to rest their feet on the foot pedals. The tactile stimulators were placed inside standard cooking gloves in order to attenuate clicks produced by the operation of the stimulators. Additionally, constant white noise was presented at 60 dB(A) from a loudspeaker positioned 60 cm behind the participant’s head in the median plane, to mask any residual sounds elicited by the activation of the tactile stimulators.Each participant took part in 10 blocks consisting of a total of 1760 trials (16 trials per condition/block). Alternating between blocks participants adopted either a crossed or uncrossed hand posture, with the starting condition counterbalanced across participants. Tactile stimuli and tones occurring simultaneously (AT stimuli) could be presented either from the same or from different locations (i.e., A_LT_L, A_RT_R or A_CT_L, A_CT_R, A_LT_R, A_RT_L, respectively). Unimodal tactile stimuli could be presented from the right or the left side of the body midline (i.e., T_L, T_R), whereas the unimodal auditory stimuli could be presented either from the central, the right of the left loudspeaker (i.e., A_L, A_C, $A_{R,}$). A total of eleven different stimulus conditions were presented in random order with SOAs varying between 1800 and 2200 ms (see Table 15 for a schematic representation of all bimodal conditions). Participants performed a sound localization task and were explicitly instructed to ignore the tactile stimuli. They indicated the perceived location of the tone (central, left, or right) by releasing the corresponding button on the foot pedals: left heel for left responses, right heel for right responses. Half of the participants released left toes, the other half released right toes, for center responses. Responses were only recorded if they occurred within 1000 ms after the presentation of a tone; otherwise the trial was counted as a miss. Before the experimental session, the participants performed two practice blocks. In the first block, unimodal auditory trials were presented, whereas in the second block, all stimulus conditions were presented to familiarize them with the task. Practice blocks were repeated if participants missed more than 5% of the responses.

	Stimulus Location				
Label	**T_L -22.5°**	**A_L -10°**	**A_C 0°**	**A_R 10°**	**T_R 22.5°**
A_CT_L	**T**	Small Spatial Discrepancy	**A**	–	–
A_CT_R	–	–	**A**	Small Spatial Discrepancy	**T**
A_LT_R	–	**A**	Small Spatial Discrepancy	Large Spatial Discrepancy	**T**
A_RT_L	**T**	Large Spatial Discrepancy	Small Spatial Discrepancy	**A**	–
A_IT_L	**T** Spatial Coincidence	**A**	–	–	–
A_RT_R	–	–	–	**A** Spatial Coincidence	**T**

Table 15. Spatial arrangement of the bimodal stimuli used in the Experiment 11

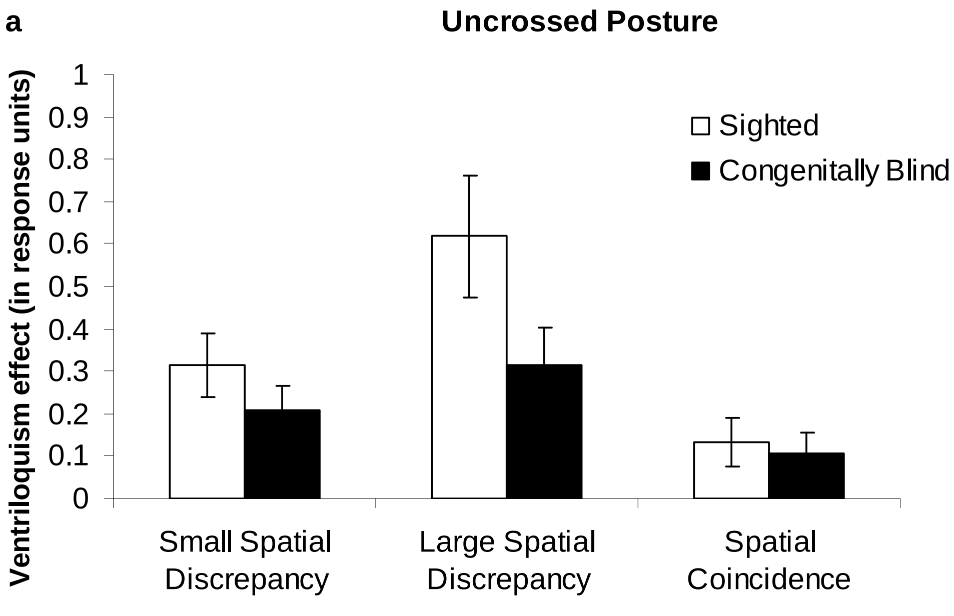
11.4.2. Results.

The percentages of correct responses reported in each of the three auditory unimodal conditions for each group were submitted to a mixed between-within ANOVA with the factors of

Hand Posture (i.e., uncrossed vs. crossed) and Group (sighted vs. congenitally blind). The analysis revealed a significant main effect of Hand Posture, F(1,18)=6.57; p=0.20, with a higher proportion of correct responses in the uncrossed than in the crossed posture (70% vs. 66% of accuracy, respectively). Importantly, the main effect of Group was not significant, F(1,18)<1; n.s., thus ruling out the possibility that potential inter-group performance differences could be attributed to baseline differences in the capability of localizing sounds as a function of the visual status of the participants (70% vs. 67% for congenitally blind and sighted, respectively). The interaction between Hand Posture and Group did not reach the significance, F(1,18)<1, n.s. Similarly, the analysis performed on the response latencies revealed a significant main effect of Hand Posture, F(1,18)=8.26; p=0.10 (598 vs. 614 for the uncrossed vs. crossed conditions), and a not significant effect of Group, F(1,18)<1; p=.43, nor of the interaction between Group and Hand Posture, F(1,18)<1; n.s.

Then, the response latencies of bimodal trials for each group were considered, separately for the condition where the sounds were correctly localized and the condition where the sounds were mislocalized toward the spatially discrepant tactile stimuli. The factors were Visual Status (blind vs. sighted), Hand Posture (i.e., uncrossed vs. crossed) and Spatial Discrepancy (i.e., Small, Large, or Coincident). The only significant value to emerge from the analysis was the main effect of Spatial Discrepancy, F(2,36)=4.66; p=.017, with the condition of Spatial Coincidence being significantly lower than both conditions of Small, t(19)=3.29; p=.004 (620 vs. 667 ms), and Large, t(19)=-2.37; p=.029 (620 vs. 662 ms), spatial discrepancies, and no difference between the latter two t(19)<1; n.s. No other main effect or interactions were significant.

For each of the three unimodal auditory and four bimodal conditions, mean localization scores were calculated by coding individual responses as -1 (left responses), 0 (center responses), or 1 (right responses; the mean percentage of responses for each category and condition are reported in Tables 16 and 17). Note that the resulting averages could thus vary from -1 (indicating 100% left responses) to 1 (indicating 100% right responses). Shifts in sound localization due to the spatially discrepant tactile stimuli in the bimodal conditions (i.e. ventriloquism effects) were then calculated by subtracting mean localization scores in the unimodal auditory conditions from those in the corresponding bimodal conditions. In order to allow collapsing data across side of tactile stimulation, these mean ventriloquism effect scores were counted as positive when shifts in sound localization were toward the external side of the tactile distractor and as negative when shifts were toward the opposite side (in the crossed-hands condition, i.e. toward the anatomical side of the hand that was stimulated). Mean values pooled over tactile stimulus locations are shown in Figure 19 separately for small (A_CT_L and A_CT_R) and large (A_RT_L and A_LT_R) audio-tactile spatial discrepancies in the uncrossed and crossed hands conditions.



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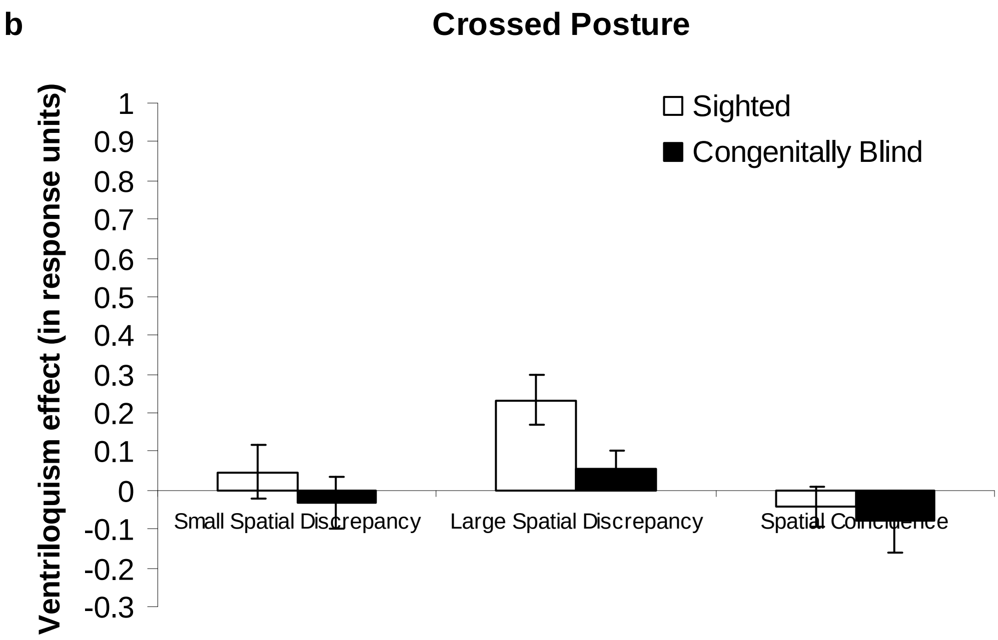

Figure 19. Mean shifts in sound localization toward the external location of the tactile stimulus (with standard errors), averaged across both tactile locations, for small (A_CT_L and A_CT_R) and large (A_LT_R and A_RT_L) audio-tactile spatial discrepancies in the uncrossed-hands (a) and crossed-hands condition (b).

The resulting values were then submitted to a repeated-measures ANOVA, with the factors of Hand Posture, Spatial Discrepancy and Group. The analysis revealed a main effect of Hand Posture, F(1,18)=14.61; p=.001, which indicated that the amount of the ventriloquism effect was significantly lower in the crossed-hand than in the uncrossed hand condition (i.e., .29 vs. .05 units). The factor of Spatial Discrepancy was also significant, F(2,36)=17.92; p<.001, with the amount of the ventriloquism effect being significantly lower in the spatial coincidence condition than in both small, t(19)=3.43; p=.003 (i.e., .05 vs. .15 units), and large, t(19)=-4.51; p<.001 (i.e., 3.0 units) spatial discrepancy conditions and in the small as compared to the large spatial discrepancy condition, t(19)=-4.24; p<.001. Interestingly, also the factor of Group reached the significance, F(1,18)=5.07; p=.04, suggesting that the group of visually-deprived participants was less prone to the ventriloquism exerted by the tactile stimuli while localizing sounds (i.e., .09 vs. .24 units, respectively). Despite a visual inspection of the data (see Figure 19) seems to suggest patterns of performance differing between the two groups as a function of spatial discrepancy and hand posture, no interactions were significant. A possible reason for that could be that the magnitude of the ventriloquism effect significantly differs from zero just in a few conditions. More specifically, separate Bonferroni-Holm corrected t-tests showed that in the uncrossed-hands condition the ventriloquism effects were significantly above zero for small, t(10)=4.72; p=.001, large spatial discrepancies, t(10)=4.61; p=.001, and spatial coincidence, t(10)=2.76; p=.02, conditions for the group of sighted participants. However, the ventriloquism effect shown by the visually deprived participants was significantly different from zero only in small, t(8)=3.55; p=.008, and large, t(8)=3.49; p=.008, spatial discrepancy conditions, but not in the spatial coincidence condition, t(8)=2.14; p=.07. In the crossed-hand condition, the ventriloquism effect was significantly above zero only in the large spatial discrepancy condition and only for the group of sighted participants, t(10)=4.13; p=.002 (cf. Bruns & Röder, in press), thus rendering any inference based on the visually observable trends only speculative.

Congenitally Blind							Sighted					
	Respond Left %		Respond Center %		Respond Right %		Respond Left %		Respond Center %		Respond Right %	
Stimulus	Mean	SEM	Mean	Stimulus	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
A_L	67.1*	4.1	34.1	3.8	0.6	0.2	63.5*	9.1	34.8	8.4	5.3	2.1
A_C	9.7	3.2	71.7*	7.9	17.5	2.9	8.0	2.2	71.9*	5.1	19.2	4.6
A_R	1.8	1.0	22.4	6.2	74.6*	7.0	2.2	0.8	20.8	4.8	77.0*	4.2
A_CT_L	17.4	5.5	64.0*	4.4	16.5	5.2	32.1	6.8	62.2*	6.9	5.8	2.1
A_CT_R	5.6	1.3	47.1*	6.9	43.8	6.7	3.0	1.3	56.4*	9.2	41.0	10.0
A_LT_R	46.9*	5.0	39.7	4.1	11.5	4.3	28.3*	7.9	44.3	8.6	26.4	9.1
A_RT_L	9.4	6.0	27.8	7.3	60.7*	10.4	22.6	8.9	40.7	5.4	36.3*	8.0
A_LT_L	74.7*	5.4	22.4	5.6	1.3	0.8	72.8*	8.1	24.0	7.9	2.7	1.0
A_RT_R	1.1	0.7	9.3	2.7	87.6*	2.9	0.6	0.4	13.2	3.3	86.0*	2.8

Table 16. Percentage of trials on which participants judged the sound location to be at the left ($_L$), center ($_C$), or right ($_R$) for each of the unimodal auditory (A) stimuli and for the bimodal auditory-tactile (AT) combinations in the uncrossed-hands condition. *Percentage of trials with correct responses.

Congenitally Blind							**Sighted**					
	Respond Left %		**Respond Center %**		**Respond Right %**		**Respond Left %**		**Respond Center %**		**Respond Right %**	
Stimulus	**Mean**	**SEM**	**Mean**	**Stimulus**	**Mean**	**SEM**	**Mean**	**SEM**	**Mean**	**SEM**	**Mean**	**SEM**
A_L	66.5*	4.8	28.8	3.9	1.5	0.5	73.4*	6.7	22.0	5.6	2.4	1.0
A_C	13.1	4.7	67.2*	5.3	17.4	4.2	13.5	3.5	65.1*	6.3	18.6	6.0
A_R	3.1	2.3	28.6	5.6	66.8*	7.1	3.3	1.4	39.1	7.8	52.4*	7.9
A_CT_L	16.4	3.5	55.4*	7.1	26.4	7.7	14.0	3.9	65.6*	5.0	16.0	4.0
A_CT_R	16.7	4.7	59.0*	5.0	22.1	4.3	13.3	5.2	63.9*	7.8	19.9	7.5
A_LT_R	59.9*	5.9	34.9	5.4	2.6	0.9	56.3*	8.1	32.6	6.6	6.1	2.5
A_RT_L	4.0	2.3	30.6	5.9	63.6*	6.2	6.1	3.1	51.3	6.2	6.1*	2.5
A_LT_L	64.4*	7.6	25.1	4.8	7.8	3.5	65.6*	7.3	25.8	6.2	4.4	1.1
A_RT_R	6.8	3.0	28.2	6.9	63.9*	8.3	5.8	3.1	37.6	8.0	52.9*	8.8

Table 17. Percentage of trials on which participants judged the sound location to be at the left ($_L$), center ($_C$), or right ($_R$) for each of the unimodal auditory (A) stimuli and for the bimodal auditory-tactile (AT) combinations in the crossed-hands condition. Note that T_L and T_R refer to the external location of the tactile stimulus, i.e. T_L indicates right hand in left space and T_R indicates left hand in right space. *Percentage of trials with correct responses.

11.4.3. Discussion

Although preliminary, the data reported in the Experiment 11 could be informative of some interesting trends in how the audiotactile ventriloquism effect differs as a function of the hand posture and the visual status of the participants. The first interesting result to emerge from the present experiment is that the pattern of results obtained for the group of sighted participants considerably replicated the results obtained in Bruns and Röder (in press) using a similar paradigm. Namely, auditory localization was biased toward the side of concurrent tactile stimuli, with larger absolute shifts in sound localization for large audio-tactile spatial discrepancies (A_LT_R and A_RT_L) as compared to small discrepancies (A_CT_L and A_CT_R) and to the new conditions added in the present study(A_LT_L and A_RT_R).

In their previous study, Bruns and Röder commented this result by taking into account the larger maximum possible shift with large discrepancies. Indeed, in those conditions, the perceived location of the sound source could be partially shifted toward the central position or completely toward the contralateral side (i.e. the side of the tactile stimulus), while with central sounds only responses toward the side of the tactile stimulus would indicate a shift in perceived sound location. Thus, according to their explanation, the audiotactile ventriloquism effects in the large discrepancy condition were expected to be at least as large as in the small discrepancy condition as their results shown.

Furthermore, the pattern of results shown by sighted participants revealed a reduced ventriloquism effect when the task was performed in the crossed (vs. uncrossed) hand-posture. As just in Bruns and Röder's study (in press), the effect was though still significant in the large spatial discrepancy condition. Even more interestingly for the present purposes, the audiotactile ventriloquism effect was shown to operate in an external coordinate system, rather than in a purely anatomically centered representation of space (see also Röder et al., 2007; Sanabria, Soto-Faraco, & Spence, 2005).

The crucial manipulation introduced in the Experiment 11 concerned the comparison of the performance of sighted and congenitally blind individuals. A preliminary evaluation of how the visual status of the participants can influence the magnitude and the direction of the audiotactile ventriloquism effect seems to support the hypothesis that the visual deprivation determines an overall benefit in the capability of correctly localize sound presented simultaneously with tactile stimuli. Indeed, the absence of any significant differences in the capability of the two groups of localizing sounds in absence of tactile distractors supports the idea that the between-group discrepancy found in the present study does not root in an aspecific finer ability of the congenitally blind in localizing sounds presented from central positions from the front (cf. Röder et al., 1999).

It is widely agreed that crossmodal interactions depend on the relative reliability of the single sensory signals constituting a multisensory event, with higher reliability attributed to the sensory modality associated to a lesser degree of variance (see Ernst & Bülthoff, 2004). If it is true that the visual deprivation determines a refining of the capabilities to independently process auditory and tactile cues (e.g., Hötting et al., 2004; Collignon et al., 2009. See also Chapter 6), then it can be argued that the group of visually deprived shows significantly higher capabilities in correctly localizing sounds presented simultaneously with tactile stimuli (i.e., a reduced audiotactile ventriloquism effect).

Even more interestingly, although more data are necessary to assess this issue with a higher degree of certainty, the pattern of results reported in the crossed-hands condition seems to suggest a discrepancy in the frame of reference on which the two groups rely on. As can be seen in the Figure 19b, the ventriloquism effect in the spatial coincidence condition has opposite directions in the two groups. Namely, whereas the group of sighted participants tended to respond toward the external location of the tactile stimulus, the group of the visually deprived participants, tended to respond as according to an anatomical frame of reference. However, the fact that the trends suggesting a discrepancy in the direction of the ventriloquism effect do not emerge in the other two conditions is questionable and hard to interpret, and thus justify the collection of further data.

General Conclusions

Across the above described experiments (see Chapters 7-11), different aspects of the crossmodal interactions occurring between audition and touch have been empirically investigated.

The first topic, concerning the - potential - existence of a sensory dominance between these two modalities, has been explored in the Experiments 1, 2, and 3 by using the Colavita paradigm. The "Colavita effect" occurs when participants performing a speeded detection/discrimination task preferentially report the visual component of pairs of audiovisual or visuotactile stimuli. To date, however, an analogous effect for audiotactile stimuli had not been demonstrated (Hecht & Reiner, 2009). Here we have investigate whether the null audiotactile Colavita effect is resistant to the manipulation of either the physical features of the auditory stimuli (Experiment 1) or the relative and absolute position of auditory and tactile stimuli in frontal (Experiment 2) and rear space (Experiment 3). The participants showed no preference for responding to one of the sensory components of the bimodal stimuli when they were presented from a single location in front of the participant (Experiment 1). However, in Experiments 2 and 3, a significant audiotactile Colavita effect was demonstrated for the first time, with participants preferentially reporting the auditory (rather than tactile) stimulus on the bimodal trials. Participants made more errors when the stimuli were presented from the same (vs. different) hemispace. In Experiment 2, the spatial modulation of the Colavita effect was significantly larger when the tactile stimuli were presented to the participant's face than when they were presented to their hand. In Experiment 3, an audiovisual Colavita effect was reported for auditory white noise bursts but not for pure tones. Taken together, these results suggest that when a tactile and an auditory stimuli are presented from a single frontal location, the participants do not encounter difficulties in reporting both sensory components (Experiment 1). In contrast, when the stimuli are presented from multiple locations, people preferentially report the auditory component, especially when they are spatially coincident (Experiments 2 and 3). Moreover, for stimuli presented from rear space, the Colavita effect was selective for auditory stimuli consisting of white noise bursts (but not for pure tones), suggesting that this kind of stimuli are more likely to be bound together with somatosensory stimuli. Albeit the present investigation does not pretend to have explored the sensory dominance between hearing and touch in an exhaustive way, these findings nevertheless contribute to shed light on this issue, suggesting that the audiotactile Colavita effect varies as a function of the spatial arrangement of the stimuli, the part of the body stimulated and, for stimuli presented behind the head, the complexity of the auditory stimuli used.

In the temporal domain, we investigated the still unexplored issue of whether people are able to match the frequency of stimuli presented within the same sensory modality (i.e., audition or touch) or across modalities (i.e., one tactile and one auditory stimulus). Participants performed a two-interval forced choice task determining whether pairs of stimuli had the same vs. different frequency. Two different frequency ranges were tested: the flutter frequency range (i.e., frequency below 40 Hz; Experiment 4); the vibration frequency range (i.e., frequency above 40 Hz; Experiment 5). The results showed that participants' ability to correctly match auditory stimuli was significantly better than their ability to match tactile stimuli or stimuli presented from the two sensory modalities. Moreover, the discrimination of auditory stimuli was modulated as a function of the frequency difference (standard vs. comparison stimuli) selectively within the flutter range (Experiment 4) but not in the vibration range (Experiment 5). In touch, the accuracy in discriminating frequency differences was higher within the flutter than in the vibration range. Interestingly, despite the difficulty in matching frequencies in the crossmodal condition, the results nevertheless showed that performance was modulated as a function of the magnitude of the discrepancy in the frequency pattern for stimuli presented in the flutter range (but not in the vibration range), possibly suggesting a finer frequency discrimination within the lower frequency range (i.e., flutter) as compared to the higher frequency range (i.e., vibration).

Moving from the temporal to the spatial domain, we argued, on the basis of a remarkable amount of neurophysiological and behavioural evidence and of the results of the Experiment 3 as well, audiotactile interactions are more pronounced for complex auditory stimuli than for pure tones. For this reason, in the Experiment 6, we specifically examined the effect of varying the complexity of auditory stimuli (i.e., noise vs. pure tone) on participants' performance in the audiotactile crossmodal dynamic capture task. Participants discriminated the direction of a target stream (tactile or auditory) while simultaneously trying to ignore the direction of a distracting auditory or tactile apparent motion stream presented in a different sensory modality (i.e., auditory or tactile). The distractor stream could either be spatiotemporally congruent or incongruent with respect to the target stream on each trial. The results showed that sound complexity modulated performance, decreasing the accuracy of tactile direction judgments when presented simultaneously with noise distractors, while facilitating judgments of the direction of the noise bursts (as compared to pure tones). Although auditory direction judgments were overall more accurate for noise (than for pure tone) targets, the complexity of the sound failed to modulate the tactile capture of auditory targets. These results provide the first demonstration of enhanced audiotactile interactions involving complex (vs. pure tone) auditory stimuli in the peripersonal space around the hands (previously these effects have only been reported in the space around the head).

By using the same experimental paradigm, we investigated the effect of varying sound intensity on the audiotactile crossmodal dynamic capture effect (Experiment 7). Participants discriminated the direction of a target stream (tactile or auditory) while trying to ignore the direction of a distractor stream presented in a different modality (auditory or tactile). The distractor streams could either be spatiotemporally congruent or incongruent with respect to the target stream. In half of the trials, the participants were presented with auditory stimuli at 75dB(A) while in the other half of the trials they were presented with auditory stimuli at 82dB(A). Participants' performance on both tasks was significantly affected by the intensity of the sounds. Namely, the crossmodal capture of tactile motion by audition was stronger with the louder (vs. quieter) auditory distractors, whereas the capture effect exerted by the tactile distractors was stronger for quieter (than for louder) auditory targets. The magnitude of the crossmodal dynamic capture was greater in the tactile target condition as compared to the auditory target condition, with a stronger congruency effect of the streams presented in the auditory (vs. tactile) modality. Two explanations are put forward to account for the modulation of audiotactile dynamic capture, an attentional biasing toward the more intense auditory stimuli, and a perceptual bias induced by the relative reliability of auditory and tactile signals, where the manipulation of sound intensity is here intended to change the relative weight assigned to each sensory modality.

In the Experiment 8, we examined the pseudosynaesthetic compatibility effects occurring between the frequency of sounds and the elevation of tactile stimuli. Participants made speeded discrimination responses to unimodal auditory (low- vs. high-frequency sounds) or vibrotactile stimuli (presented to the index finger, upper location vs. to the thumb, lower location). In the compatible blocks of trials, the implicitly-related stimuli (i.e., higher-frequency sounds and upper tactile stimuli; and the lower-frequency sounds and the lower tactile stimuli) were associated with the same response key; in the incompatible blocks, weakly-related stimuli (i.e., high-frequency sounds and lower tactile stimuli; and the low-frequency sounds and the upper tactile stimuli) were associated with the same response key. Better performance was observed in the compatible (vs. incompatible) blocks, thus providing empirical support for the existence of a crossmodal association between the relative frequency of a sound and the relative elevation of a tactile stimulus.

In the last three experiments, we investigated the consequences of long term visual deprivation on audiotactile interactions in humans. More specifically, in the Experiment 9, we examined the potential modulatory effect of relative spatial position on audiotactile temporal order judgments (TOJs) in sighted, early-, and late-blind adults. Pairs of auditory and tactile stimuli were presented from the left and/or right of participants at varying stimulus onset asynchronies (SOAs) using the method of constant stimuli. The participants had to make unspeeded TOJs regarding which sensory modality had been presented first on each trial. Systematic differences between the participants emerged: While the performance of the sighted participants was unaffected by whether the two stimuli were presented from the same or different positions (replicating the results of several recent studies), the blind participants (regardless of the age of onset of blindness) were significantly more accurate when the auditory and tactile stimuli were presented from different positions rather than from the same position. These results provide the first empirical evidence to suggest a spatial modulation of audiotactile interactions in a temporal task performed by visually impaired humans. The fact that the performance of the blind participants was modulated by the relative spatial position of the stimuli is consistent with data showing that visual deprivation results in an improved ability to process spatial cues within the residual tactile and auditory modalities. These results support the hypothesis that the absence of visual cues results in the emergence of more pronounced audiotactile spatial interactions.

Both Experiments 10 and 11 regarded in particular the modulation of the frame of reference, used to code and process auditory and tactile stimuli, as a function of visual experience. In both investigations, the topic has been explored by means of the crossing hand effect (i.e., the decrease of the ability to localize tactile stimuli presented to the hands induced by the conflict between the externally and body-centered frames of references). In the Experiment 10, the consequences of this effect have been studied in the context of the audiotactile crossmodal dynamic capture task, whereas the Experiment 11 focused on how this effect modules the mislocalization of auditory stimuli induced by tactile stimuli.

In Experiment 10, congenitally/early blind, late blind and sighted participants had to discriminate the direction of a target stream (tactile or auditory, respectively) while trying to ignore the direction of a distractor stream presented in a different modality (auditory or tactile, respectively). The distractor streams could either be spatiotemporally congruent or incongruent with respect to the target stream. In half of the trials, the participants adopted an uncrossed hands posture, while in half of the trials they crossed theirs hands across the body midline. The results showed a significant crossmodal dynamic capture effect in both experimental conditions, with a more pronounced interfering effect of the auditory distractors on the discrimination of the tactile stream directions as compared to when the task was performed with the reversed sensory modalities. More interestingly, the magnitude of the crossmodal interfering effect was significantly modulated by both the hand posture and the visual status of the participants. In the tactile target condition, crossing the hands across the midline selectively affected the performance of sighted and late-blind participants, but not of early/congenitally blinds. In the auditory target condition, the groups of blind participants showed an overall better performance than the sighted participants. Furthermore, when the auditory target streams were presented in temporal coincidence with the tactile distractors, the change of hand posture selectively affected the performance of the sighted participants, and not the one of the visually deprived participants. Taken together, these data suggest that the perception of tactile and auditory apparent motion, as well as the effect of the hand posture adopted while performing the task, is significantly modulated by the presence and the lasting of the visual experience.

Although preliminary, the data reported in the Experiment 11 suggest that the audiotactile ventriloquism effect differs as a function of the hand posture and the visual status of the participants. In sighted participants, auditory localization was biased biased toward the side of concurrent tactile stimuli, with larger absolute shifts in sound localization for auditory and tactile stimuli being separated by a large spatial discrepancy, as compared to when they were separated by a small spatial discrepancy or when they were spatially coincident. As just in Bruns and Röder’s study (in press), the effect was reduced when the task was performed in the crossed (vs. uncrossed) hand-posture, though still significant in the large spatial discrepancy condition. Furthermore, the audiotactile ventriloquism effect was shown to operate in an external coordinate system, rather than in a purely anatomically centered representation of space.

The group of visually deprived shows significantly higher capabilities in correctly localizing sounds presented simultaneously with tactile stimuli (i.e., a reduced audiotactile ventriloquism effect). Even more interestingly, the pattern of results reported in the crossed-hands condition seems to suggest a discrepancy in the frame of reference on which the two groups rely on, as indicated by the ventriloquism effect in the spatial coincidence condition, occurring in opposite directions in the two groups. Namely, whereas sighted participants tend to respond toward the external location of the tactile stimulus, visually deprived participants, tend to respond as according to an anatomical frame of reference.

Taken together, the results of the experiments here presented, far to constitute an exhaustive investigation of the crossmodal sensory interactions occurring between auditory and tactile, add to still partial evidence on this topic. However, the incongruity of the results and the limited array of paradigms used in the experimental investigations might suggest that, although the aspects characterizing audiotactile interactions are numerous and various in nature, they are still inadequately explored. Furthermore, to the best of our knowledge, there are issues, such as, for instance, the potential crossmodal congruency effects based on frequency similarities, which still remain to be fully assessed. All these cues would thus point to the necessity of further investigations to provide a more extended and satisfactory assessment of this topic.

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