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Peripersonal space representation in the first year of life: a behavioural and electroencephalographic investigation of the perception of unimodal and multimodal events taking place in the space surrounding the body.

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ABSTRACT

In my PhD research project, I wanted to investigate infants' representation of the peripersonal space, which is the portion of environment between the self and the others. In the last three decades research provided evidence on newborns' and infants' perception of their own bodies and of other individuals, whereas not many studies investigated infants' perception of the portion of space where they can interact with both others and objects, namely the peripersonal space. Considering the importance of the peripersonal space, especially in light of its defensive and interactive functions, I decided to investigate the development of its representation focusing on two aspects. On one side, I wanted to study how newborns and infants processed the space around them, if they differentiated between near and far space, possibly perceiving and integrating depth cues across sensory modalities and when and how they started to respond to different movements occurring in the space surrounding their bodies. On the other side, I was interested in understanding whether already at birth the peripersonal space could be considered as a delimited portion of space with special characteristics and, relatedly, if its boundaries could be determined. In order to respond to my first question, I investigated newborns' and infants' looking behaviour in response to visual and audio-visual stimuli depicting different trajectories taking place in the space immediately surrounding their body. Taken together, the results of these studies demonstrated that humans show, since the earliest stages of their development, a rudimentary processing of the space surrounding them. Newborns seemed, in fact, to already differentiate the space around them, through an efficient discrimination of different moving trajectories and a visual preference for those directed towards their own body, possibly due to their higher adaptive relevance. They also seemed to integrate multimodal, audio-visual information about stimuli moving in the near space, showing a facilitated processing of congruent audio-visual approaching stimuli. Furthermore, the results of these studies could help understand the development of the integration of multimodal stimuli

with an adaptive valence during infancy. When newborns' and infants were presented with unimodal, visual stimuli, they all directed their visual preferences to the stimuli moving towards their bodies. Conversely, their pattern of looking times was more complex when they were presented with congruent and incongruent audiovisual stimuli. Right after birth infants showed a spontaneous visual preference for congruent audio-visual stimuli, which was challenged by a similarly strong visual preference for adaptively important visual stimuli moving towards their bodies. The looking behaviours of 5-month-old infants, instead, seemed to be driven only by a spontaneous preference for multimodal congruent stimuli, i.e. depicting motion along the same trajectory, irrespective of the adaptive value of the information conveyed by either of the two sensory components of the stimulus. Nine-month-old infants, finally, seemed to flexibly integrate multisensory integration principles with the necessity of directing their attention to ethologically salient stimuli, as shown by the fact that their visual preference for unexpected, incongruent audio-visual stimuli was challenged by the simultaneous presence of adaptively relevant stimuli. Similarly to what happened with newborns, presenting 9-month-old infants with the two categories of preferred stimuli simultaneously led to the absence of a visual preference. Within my project, I also investigated the electroencephalographic correlates of the processing of unimodal, visual and auditory, stimuli depicting different trajectories in a sample of 5-month-old infants. The results seemed to provide evidence in support of the role of the primary sensory cortices in the processing of crossmodal stimuli. Furthermore, they seemed to support the possibility that infants' brain could allocate, already during the earliest stages of processing, different amounts of attention to stimuli with different adaptive valence. Two further studies addressed my second question, namely whether already at birth the peripersonal space could be considered as a delimited portion of space with special characteristics and if its boundaries could be determined. In these studies I measured newborns' saccadic reaction times (RTs) to tactile stimuli presented simultaneously to a sound perceived at different distances from

their body. The results showed that newborns' RTs were modulated by the perceived position of the sound and that their modulation was very similar to that shown by adults, suggesting that the boundary of newborns' peripersonal space could be identified in the perceived sound position in whose correspondence the drop of RTs happened. This suggested that at birth the space immediately surrounding the body seems to be already invested of a special salience and characterised by a more efficient integration of multimodal stimuli. As a consequence, it might be considered as a rudimentary representation of the peripersonal space, possibly serving, as a working space representation, early interactions between newly born humans and their environment. Overall, these findings provide a first understanding of how humans start to process the space surrounding them, which, importantly, is the space linking them with others and the space where their first interactions will take place.

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INTRODUCTION

In our everyday life we experience the space as a unitary, undivided environment in which we perform our actions and shape our interactions. However, a growing number of studies suggests that "that the brain constructs not one but various functionally distinct representations of space" (Di Pellegrino & Làdavas, 2015, p. 126), in particular separating the extrapersonal space from the peripersonal space. Several studies recently investigated how adults represent the peripersonal space (PPS), namely "the space immediately surrounding the body" (Canzoneri, Magosso, & Serino, 2012, p. 1), a "multisensory-motor interface between body and environment" (Teneggi, Canzoneri, di Pellegrino, & Serino, 2013, p. 1), which "mediates every physical interaction between the body and the external world, because it is within its boundaries that we can reach and act upon objects, as well as avoid looming threats" (Canzoneri et al., 2012, p. 1). These studies focused on several aspects characterizing this portion of space, from its functions to its neural underpinnings, through its main features, first of all its plasticity. The representation of the PPS is generally considered to be invested of two main, distinct functions, which obey to different principles and involve different sensory and motor processes (de Vignemont & Iannetti, 2015). On one side, the PPS has a defensive function, protecting the organism from dangerous or threatening stimuli (Graziano & Cooke, 2006); on the other side, it has a working function, which permits goal-directed actions within the portion of space where it is possible to interact with both objects and others (Brozzoli, Ehrsson, & Farnè, 2014; Brozzoli, Cardinali, Pavani, & Farnè, 2010). The extension of the PPS can be defined by the quality of the multisensory interactions that take place within it: in fact, enhanced audio-tactile and visuo-tactile interaction can take place within this portion of space, thanks to the particular spatial alignment that multimodal stimuli have with the body (Van der Stoep, Nijboer, Van der Stigchel, & Spence, 2015). In light of this, a few recent studies

investigated the PPS boundaries using a task based on the multisensory integration of tactile and auditory stimuli and highlighted, among other findings, the plasticity of the PPS dimension in social situations: the PPS was shown to be modulated both by the presence of others and by the quality of the interactions with them (Canzoneri et al., 2012; Teneggi et al., 2013). The PPS plasticity has been investigated also in relation to tool use, actions (like grasping or walking) and personality traits like anxiety and claustrophobia. With respect to tool-use induced plasticity, it was demonstrated that the use of a tool could extend the PPS (Bassolino, Serino, Ubaldi, & Làdavas, 2010; Canzoneri et al., 2013; Gamberini, Seraglia, & Priftis, 2008; Longo & Lourenco, 2006; Serino, Bassolino, Farnè, & Làdavas, 2007) and that the long-term experience of its usage can lead to a stable extension of the PPS dimensions (Serino et al., 2007). Concerning the reshaping of the PPS following voluntary actions, a recent study showed, for example, that the boundary of the PPS was perceived as farther away from the body when the participant was walking vs. standing (Noel et al., 2015). Finally, it has been shown that people with higher claustrophobia seem to represent the near space as larger compared to people with less anxiety of closed spaces (Lourenco, Longo, & Pathman, 2011) and that the size of the defensive PPS surrounding the face seems to be modulated by anxiety, as suggested by a positive correlation between the level of personal anxiety and the dimensions of the defensive PPS (Sambo & Iannetti, 2013).

Despite the importance of this portion of space for adaptive behaviour – especially with regards to body protection and goal-directed actions – not many studies have yet investigated the representation of the PPS space during infancy and– to my knowledge – none has tried to measure its boundaries in young infants. I thought that it would have been interesting and also important to investigate how the representation and the perception of the PPS develop during the early stages of postnatal life, especially given that this is the portion of space where the earliest interactions take place. These interactions could occur either between the infants and

other individuals or between the infants and the objects that are part of their environment. In both circumstances, the interactions could have either a positive or a negative valence: objects and people close to one's body could either attract attention and trigger goal-directed actions or represent a potential danger from which the infants would need to defend themselves. Therefore, I believed that it would have been important to investigate whether the precursors of the representation of the PPS might exist prior to significant postnatal experience. If this were the case, the PPS might be represented already at birth as a delimited portion of space characterised by, among other features, an enhanced processing of multisensory information within its boundaries. This rudimentary representation might then develop and evolve, in parallel with infants' increasing experience of the environment and with their structural and functional brain development, becoming more complex during infancy and childhood. At the same time, this low level, early representation of the PPS might in turn influence infants' consecutive development, both from a behavioural and a neural point of view, biasing them to pay attention to the space immediately surrounding their body, where the abovementioned interactions take place (interactive-specialisation approach, Johnson, 2000, 2001, 2011a, 2011b). Alternatively, the special salience and representation of this space might emerge at a later stage and, possibly, as a function of the interactions that take place within it.

Research in the last three decades provided evidence on newborns' and infants' perception of their own bodies as well as of other individuals. With regards to the first aspect, recent findings indicated that newborns in the first days of their life show a visual preference for temporally and spatially congruent visuo-tactile stimulation referred to their bodies (Filippetti, Johnson, Lloyd-Fox, Dragovic, & Farroni, 2013; Filippetti, Orioli, Johnson, & Farroni, 2015). In one study, the authors presented a group of newborns with an infant's face being stroked on his cheek with a paintbrush while they stroked the newborns' check with a similar paintbrush. The touch that the newborns perceived on their face was either temporally congruent or

incongruent with the one they could see (Filippetti et al., 2013). In a second study, they presented the newborns with an infant's face being stroked with a paintbrush either on his cheek or forehead and, at the same time, they stroked the newborns in a congruent or incongruent position with respect to the visual stimulus (Filippetti et al., 2015). In both studies, newborns showed a visual preference for the congruent vs. incongruent visuo-tactile stimulation. Remarkably, the results of the first study also showed that newborns' visual preference disappeared when they were presented with an inverted face, i.e. when the visual information was not body related. Taken together, these findings showed that newborns can detect intermodal temporal and spatial synchrony related to their own bodies, suggesting that already at birth humans could show the basic processes underneath body perception, which will allow them to form a representation of their bodies (Filippetti et al., 2013). Similarly, Zmyj and colleagues investigated the importance of visuo-tactile congruency to self-perception in infants aged 7 and 9 months (Zmyj, Jank, Schütz-Bosbach, & Daum, 2011). The authors presented the infants with two displays showing life-like baby doll legs, one of which was being stroked. The infants' own left leg was also stroked, in synchrony with only one of the two visual displays. They showed that infants could discriminate between temporally congruent vs. incongruent visuo-tactile stimulation, as demonstrated by their visual preference for the synchronous display. Most importantly, also in this study infants showed a visual preference only when the visual stimuli were body-related (i.e. life-like baby doll legs), suggesting an early sensitivity to body morphology in infants. With regards to the second aspect, namely humans' discrimination of faces since birth, several findings provided evidence for the discrimination of human faces already during the first days of life. In 1991, Johnson and Morton (Johnson & Morton, 1991; Johnson, 2005; Johnson, Senju, & Tomalski, 2015; Morton & Johnson, 1991) proposed a two-process theory for the development of face processing. They suggested that newborns might be predisposed to orient towards faces by a subcortical face detection mechanism ("Conspec"),

which biases the inputs that the cortical circuits receive during the first weeks of life. This mechanism may then decline during the second month of life and give way to an acquired cortical circuitry ("Conlern") that controls infant orienting preferences and face recognition and processing from 2 months of age onwards. Evidence for face detection in newborns was provided by several studies: for example, Johnson and colleagues showed newborns' visual preference for simple face-like patterns (Johnson, Dziurawiec, Ellis, & Morton, 1991), while Farroni and colleagues demonstrated that this preference occurred only if the contrast polarity of the naturalistic or schematic face stimulus was coherent with natural lighting conditions (Farroni et al., 2005) and that newborns visually preferred faces with a direct vs. averted gaze (Farroni, Csibra, Simion, & Johnson, 2002), but only in the context of an upright face with a straight head (Farroni, Menon, & Johnson, 2006).

As highlighted by these findings, there is some evidence about infants' perception of their bodies and about their ability of discriminating face-like stimuli. Conversely, not much is known about the way in which they represent the space between themselves and others. The fundamental motivation of my PhD research project was focusing on this "missing piece of the puzzle", investigating the early representation of the portion of the environment that links ourselves with the others.

I decided to investigate the perception of the PPS in infancy around two focuses of interest, starting from the very first hours of life: in fact, this could have given me the opportunity to investigate the ontogeny of the representation of the near space and the factors involved in it prior to the intervention of significant postnatal experience. On one side, I wanted to study how newborns and infants processed the space around them, if they differentiated between near and far space, possibly perceiving and integrating depth cues across sensory modalities and when and how they started to respond to different movements occurring in the space surrounding their bodies. On the other side, I was interested in understanding whether already at birth the

PPS could be considered as a delimited portion of space with special characteristics and, relatedly, if its boundaries could be determined.

In order to respond to my first question, I investigated newborns' behavioural responses to visual stimuli depicting trajectories moving towards different directions in the space immediately surrounding their body. Previous research focused on infants' discrimination of looming trajectories through the measurement of their defensive reactions in response to impending collision (Ball & Tronick, 1971; Bower, Broughton, & Moore, 1970; Kayed & van der Meer, 2000; Kayed & van der Meer, 2007; Náñez, 1988; Yonas et al., 1977; Yonas, 1981). The different groups of authors considered several behaviours as defensive, in particular eye widening, head and arm movements and eye blinks. However, Yonas and colleagues (1977) stated that the variables investigated by previous studies (i.e. eye widening, head movements and arm movements) should not be considered adaptive responses, but part of a tracking process. Conversely, they suggested that blinking of the eyes should be considered the best indicator of awareness to impending collision in early infancy (Yonas, 1981). Hence, they concluded that newborns are not sensitive to impending collision, as they do not respond to it with appropriate defensive or avoiding behaviours (Yonas et al., 1977). However, I thought that focusing on the lack of defensive responses could have masked young infants' ability to actually detect and discriminate among relevant moving trajectories. Moreover, taking into account only defensive reactions means interpreting the object approaching along a colliding trajectory only as a possible danger and not as an interesting stimulus to interact with (de Vignemont & Iannetti, 2015; Kandula, Hofman, & Dijkerman 2015; Van der Stoep et al., 2015). For these reason, I decided to use a preferential looking paradigm to investigate newborns' discrimination of different trajectories and their possible visual preference for those directed towards their bodies (i.e. those signalling impending collision). I measured the looking behaviour of newborns presented with uni and multimodal (congruent and incongruent), visual and audio-visual

trajectories moving towards different directions in the space immediately surrounding their bodies. I chose to investigate multimodal stimuli in light of their higher ecological validity in signalling the motion of an object in the space. Most importantly, studying the processing of multimodal cues referring to the direction of moving trajectories would allow to further investigate multisensory integration during the earliest stages of life, as well as the interplay between multisensory integration principles and the adaptive and behavioural importance of the stimuli. The development of multisensory integration abilities is a particularly relevant topic because integrating efficiently information coming from different modalities has important adaptive benefits, but, at the same time, it is a significant challenge with which humans are confronted during development (Bremner, Lewkowicz, & Spence, 2012). Multiple sensory modalities provide us with complementary information about the environment and, at the same time, the redundancy of information across different senses has a central role in disambiguating among competing information coming from the surrounding environment. However, the computational process behind the integration of multiple senses is highly complex and places relevant challenges to the developing organism: different senses convey information using different codes, both with regards to the space and the brain, leading to an important question on how humans develop the ability to integrate them (Bremner et al., 2012).

Subsequently, I wanted to investigate the development of the perception of different movements taking place in the near space during the first year of life. Specifically, I chose to study infants' visual preferences for visual and audio-visual (congruent and incongruent) trajectories in correspondence with two important milestones in their motor development, i.e. the emergence of reaching and grasping abilities. In fact, I thought that there might be a link between infants' ability to act voluntary and purposefully on the environment and their perception of events taking place within the same environment. Recent findings on adult participants showed activity of the sensorimotor areas responsible for reaching and grasping

actions during tasks in which the participants had to determine the expected time-to-contact of a looming stimulus (Field & Wann, 2005; Billington & Wilkie, 2011), further supporting the hypothesis of a link between reaching and grasping and the processing of trajectories taking place near the body. I also wanted to study the neural underpinnings of the perception of different trajectories during infancy, measuring the electroencephalographic correlates of the perception of visual and auditory trajectories moving in the near space in a group of 5-month-old infants. In this respect, I was particularly interested in two aspects. On one side, I wanted to study whether infants' brain allocates different amounts of attention to stimuli with different behavioural relevance since the earliest stages of processing, as it was recently found in adults (Vagnoni, Lourenco, & Longo, 2015). On the other side, I wanted to investigate in infants the recently hypothesised role of primary visual and auditory cortices in processing crossmodal information (Kayser, Petkov, & Logothetis, 2009; Murray et al., 2016).

Finally, having gained a first understanding of newborns' processing of trajectories in the space and of their perception of visual and auditory cues signalling the different positions of a moving objects with respect to the depth dimension, I investigated the existence at birth of the PPS as delimited portion of space, with clearly identifiable boundaries. To address this, I measured newborns' saccadic reaction times in response to synchronous audio-tactile stimulation delivered when the auditory stimulus was perceived at different distances from the body, i.e. either in the extrapersonal or in the peripersonal space (Canzoneri et al., 2012).

Overall, the studies conducted within my PhD research project provided a first understanding of newborns' and infants' representation of the space immediately surrounding the body and of their perception of movements taking place within it. In particular, the findings obtained in my studies suggested that newborns might be, already at birth, predisposed to focus their attention on the portion of space closer to their own body and on movements directed towards their body itself. Furthermore, my results provided additional information on how

humans process and integrate multisensory information early in life and, specifically, on the evolution of newborns' and infants' visual preferences for congruent vs. incongruent audio-visual cues signalling motion within the near space. Finally, the results of my studies suggested that already at birth the PPS might exist and might be already invested of a special salience as the portion of space where, in particular, social interaction will take place.

The next few paragraphs will give an outline of the upcoming chapters of this manuscript, which will summarise the theoretic and methodological aspects relevant for my thesis and describe the studies that I ran in order to investigate the representation of the PPS during the first year of life.

First of all, I will define and describe the concept of the peripersonal space, considered as a multisensory interactive interface between ourselves and the external world that surrounds the body immediately beyond it (Chapter 1). I will review previous findings highlighting its principal functions, defensive on one side and goal-directed on the other, and features. Among these, its typical plasticity: the PPS, in fact, has been shown to expand or contract depending on the actions that we are performing (e.g. tool use), on our personality traits (e.g. anxiety) and on social interactions. Furthermore, a few studies describing newly developed tasks capable of measuring the PPS dimensions will be reviewed. Finally, I will report a few findings on the neural underpinnings of the PPS representation in humans and non-human primates, along with some studies on infants' ability of localising tactile stimuli taking place within this portion of space. Next, I will focus on another fundamental topic for the studies conducted within this project, namely the perception and discrimination of the different trajectories of stimuli moving in the space, with a particular emphasis on looming ones, for their widely recognised behavioural relevance (Chapter 2). I will describe studies investigating the perception of unimodal and multimodal looming stimuli, depicted by visual and auditory stimuli. Both behavioural and neuroimaging studies conducted with non-human primates as well as human

adults and infants will be summarised. Altogether, the reviewed studies highlight the importance of looming information for behavioural outcomes and, relatedly, the existence of a perceptual and attentive bias capable of facilitating the processing of looming signals themselves.

Continuing, I will give an overview of the methodologies that can be used to shed light on the cognitive and functional development of preverbal infants (Chapter 3). Both behavioural and neuroimaging methods will be presented, with a focus on those used within this project, i.e. preferential looking paradigms on one side and electroencephalography on the other.

Finally, I will present the studies conducted during my PhD with the aim of shedding new light on newborns' and infants' representation of the space surrounding their bodies and of the multisensory events taking place within it (Chapters 4-7). In the first study I measured newborns' (14-95 hours of life) looking behaviour in order to evaluate their ability to discriminate between stimuli moving along different trajectories within the space surrounding their body and, in particular, to investigate the existence of a spontaneous preference for impending collision trajectories, directed towards their body itself (Chapter 4.3). In everyday life, though, information about the trajectories of moving objects is conveyed not only through visual information, but also through auditory information and through the combination of visual and auditory cues. For this reason, I ran a second study that investigated, once again measuring newborns' looking behaviours, the multisensory integration of audio-visual stimuli depicting approaching and receding trajectories in the first days of life (Chapter 4.4). Subsequently, I decided to track the development of the visual preferences for different unimodal and multimodal, congruent and incongruent, trajectories during the first year of life. To address this, I measured, using a paradigm similar to that employed in my previous studies, the looking behaviour of infants aged 5 and 9 months of life (Chapter 5). These specific ages were chosen as they corresponded to two milestones in infants' motor development, i.e. the achievement of the ability to reach and grasp, respectively. I thought, in fact, that the increasing

ability to act purposefully in the PPS might be related with infants' perception of the same portion of space. These data, other than on infants' perception of different trajectories, provided further insights into the development of the integration of stimuli coming from different modalities during the first year of life. In order to further study this aspect and especially its neural underpinnings, I started to investigate the electroencephalographic correlates of the perception of unimodal, visual and auditory, stimuli depicting different trajectories in a sample of 5-month-old infants (Chapter 6). This study specifically focused on two aspects: on one side, examining the existence of differences in the early stages of the processing of trajectories with a different behavioural relevance (i.e. approaching vs. receding trajectories); on the other side, investigating whether the recently hypothesised role of primary sensory cortices in processing crossmodal information might apply to infants as well (Murray et al., 2016). Finally, the last couple of studies involved once again newborn participants and specifically studied the existence, at birth, of the PPS as a delimited portion of space with clear boundaries, which could be determined (Chapter 7). For this study, I adapted a task recently used for determining the PPS boundaries in adults using multisensory audio-tactile stimuli and measuring the participants' reaction times (Canzoneri et al., 2012).

Overall, the results obtained so far provided a first insight on newborns' and infants' perception of the space immediately surrounding their body and of the events that take place within it, suggesting that already at birth and during the first year of life the peripersonal space could be considered as a portion of space that is invested of a special importance.

1. PERIPERSONAL SPACE

Although in everyday life we experience the space as a whole, growing evidence suggests the existence of different and functionally distinct representations of it (di Pellegrino & Làdavas, 2015). In particular, an accepted distinction is that between personal (near), peripersonal and extrapersonal (far) space.

The peripersonal space (PPS) can be defined as "the space immediately surrounding the body", which "mediates every physical interaction between the body and the external world, because it is within its boundaries that we can reach and act upon objects, as well as avoid looming threats" (Canzoneri, Magosso, & Serino, 2012, p. 1). It contains the objects with which it is possible to interact, specifies a "private area" during social interactions and encloses the possible dangers to which the organism should pay attention (Coello, Bourgeois, & Iachini, 2012; de Vignemont & Iannetti, 2015).

Rizzolatti and colleagues firstly introduced the term peripersonal space in 1981, describing the neurons that are activated by tactile and visual stimuli presented in the space immediately surrounding the body of a monkey (Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981; de Vignemont & Iannetti, 2015; di Pellegrino & Làdavas, 2015). However, the idea that the space immediately surrounding the body could be characterised by a special salience had been previously introduced by Hediger, director of the Zurich zoo, who noticed that animals' behaviour depended on the position of other animals, whose vicinity was tolerable only within a certain distance (de Vignemont & Iannetti, 2015).

Using the term "peripersonal space", Rizzolatti and colleagues (1981) wanted to highlight the close link between visual or auditory and somatosensory processing that pertains exclusively to the portion of space closest to the body (Làdavas, 2002; di Pellegrino & Làdavas, 2015). Most importantly, the PPS and its boundaries can be defined by the quality of the multisensory interactions taking place within it. In fact, enhanced audio-tactile and visuo-tactile

interactions occur within the PPS and can be explained by the particular spatial alignment that multimodal stimuli have with the body when they happen within this portion of space (Van der Stoep, Nijboer, Van der Stigchel, & Spence, 2015). the PPS is, coherently, conceived as a "multisensory-motor interface between body and environment" (Teneggi, Canzoneri, di Pellegrino, & Serino, 2013, p. 1), represented in premotor and parietal areas by neurons that integrate somatosensory information coming from the body and visual and auditory stimuli occurring next to the body (Noel et al., 2015; Teneggi et al., 2013).

The next few paragraphs will describe some of the recent evidence and theoretic reflections about the PPS and, in particular, its functions, dimensions, plasticity and neural underpinnings and correlates.

1.1 PERIPERSONAL SPACE FUNCTIONS

Traditionally, two main functions have been attributed to the peripersonal space: on one side, being a defensive space, where an individual would defend himself from an upcoming threat or danger; on the other side, being a working, action-directed space where it is possible to act upon objects.

Graziano and Cooke (2006) proposed that the representation of the space near the body has mainly a defensive function, considering self-defence as "the most important behaviour biologically" (H. Hediger, *cited in* Graziano, & Cooke, p. 845). In their paper, the authors reported their previous findings showing that "defensive-like" behaviours were triggered in monkeys by the electrical stimulation of the brain areas responsive to multimodal stimuli that occur close to the body (ventral intraparietal area − VIP − and polisensory zone − PZ − in particular). In light of this, they suggested that the major role of these areas is the construction of a safety margin around the body and the selection of the most appropriate defensive behaviours. However, they also suggested that these areas could, at the same time, have a variety of other functions and could participate in complex behaviours, such as those related to social interactions (Graziano & Cooke).

Brozzoli and colleagues, instead, argued in favour of the hypothesis that the PPS representation might have evolved to guide voluntary, object-directed actions as well as motor behaviours leading to the interaction with other individuals (Brozzoli, Cardinali, Pavani, & Farnè, 2010; Brozzoli, Ehrsson, & Farnè, 2014). They reviewed previous findings highlighting the presence of bimodal visuo-tactile neurons in a parieto-frontal network that allows a body-centred coding of space, which would be useful for the execution of purposeful actions on the environment. Furthermore, they tested whether different modulation of the PPS multisensory coding would originate from different object-oriented actions, hypothesising more important modulations for more complex actions (Brozzoli et al., 2010). To address this, they compared the

visuo-tactile effects produced by complex (reach-to-grasp) vs. simple (reach-to-point) actions, under the hypothesis that during grasping the brain has to take into account not only the target spatial position (as during pointing), but also its shape, size and characteristics. The participants were asked to report the elevation of a tactile stimulus delivered on the acting hand and to ignore visual distractors appearing on the target object while performing one of the two actions. i.e. reaching or pointing. In this way, the authors could investigate the multimodal interactions that happen during the two actions measuring the "crossmodal congruency effect" (CCE), i.e. the performance difference between congruent and incongruent trials (Brozzoli et al., 2010). The results showed, during the execution phase, a higher CCE for grasping than for pointing, highlighting a different modulation of the visuo-tactile interplay during the two different actions, with stronger interactions triggered by grasping vs. pointing (Fig. 1.1.1, upper panel). In light of these results, the authors speculated about the possibility of a fast modulation of the PPS representation according to the ecological needs during actions execution. Analysing the movements kinematics, they also showed that the action dynamics affected the task performance, demonstrating a parallel between different kinematics and different interplay between visual and tactile stimuli in the execution phase (Fig. 1.1.1 bottom panel). This result strengthened their hypothesis about the existence of a link between the execution of voluntary actions and the multisensory representation of PPS. Although highlighting that their data are not incompatible with the defensive role of the PPS, the authors speculated that the multisensory-motor interface between the body and the events happening in the nearby space could have evolved in order to drive voluntary actions, like approaching movements (Brozzoli et al., 2010).
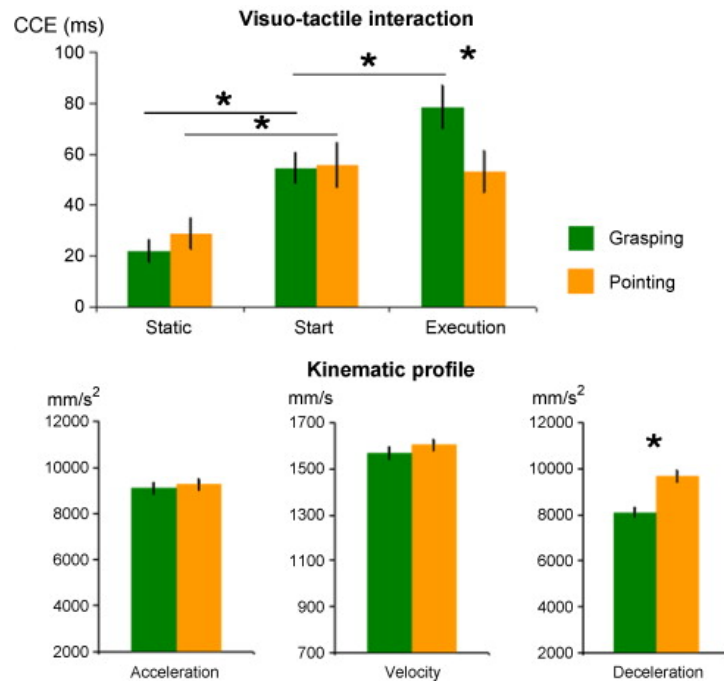
Figure 1.1.1 CCE and kinematic results (from Brozzoli et al., 2010). Upper panel: means and standard errors for the amplitude of the CCE as function of action phase. Lower panel: means and standard errors of the parameters of the reaching component for both actions: peaks of Acceleration (left part), Velocity (central part) and Deceleration (right part) .

Recently, de Vignemont and Iannetti (2015) tried to address the question on whether there is only one or multiple kinds of representations of the PPS and, particularly, on whether a single PPS can fulfil different functions. Their interrogation mainly derived from the complexity of this area and of its function. It was also motivated by the vague definition of this portion of space - both in terms of dimensions and functions - created by studies in cognitive and social psychology that referred to the same portion of space with greatly different descriptions (de Vignemont & Iannetti). In particular, they focused on the two main functions that have been attributed to the PPS representation: a defensive function, aiming to protect the body from potential threats, and a goal-directed function, which intervenes when we act on objects and interact with others within this portion of space. They reported that two models on the PPS representation have been suggested. On one side, the "Swiss army knife model" suggested the existence of a single cortical map of the PPS, which subserves both its functions. On the other side, the "Specialist model" hypothesised the existence of two different

representations, each subserving one of the two functions, which are alternatively activated depending on the nature of the situation. They also reported that, to date, no studies tried to understand how the different PPS functions are represented in the brain (de Vignemont & Iannetti). With regards to the motor domain, they reported that different amounts of attentional and motor resources are allocated to different parts of the body in relation to the two functions of the PPS: to the hand for the working space (e.g. when reaching or grasping) and to any part of the body for the defensive space. At the same time, while the working space seems to be more related to voluntary movements, the defensive space could be associated to automatic ones (such as defensive reflexes). They also suggested that the existence of a difference between working and protective PPS could be argued with reference to sensory processing: while the protective space might require rapid detection of threats, the goal-directed function should need a fine-grained recognition of the features of the stimulus in order to precisely guide movements towards it (de Vignemont & Iannetti). Finally, they suggested that, under certain conditions, the extension of the PPS could be differently modulated depending on its function. Anxiety, for example, could increase the extension of the defensive space and, at the same time, decrease that of the working space, whereas, conversely, tool use could extend the working space without altering the dimension of the defensive space (de Vignemont & Iannetti). In light of this evidence, the authors argued in favour of a "dual model of PPS, with a clear functional distinction between protection of the body and goal-directed action" (de Vignemont & Iannetti, p. 327), two functions that require different sensory and motor processes, obeying to different principles. They also argued against an "infinite multiplication" of peripersonal spaces, and suggested that a possible third function of the PPS, i.e. joint action, should be considered as part of the working space, in which more individuals act together on objects. They considered, in fact, the distinction between protective and working space to be "parsimonious and plausible"

(de Vignemont & Iannetti, p. 333), nevertheless acknowledging that it will need to be validated by empirical evidence.

The boundaries of the peripersonal space can be defined in two different ways (Costantini, Ambrosini, Tieri, Sinigaglia, & Committeri, 2010; Ferri, Tajadura-Jiménez, Väljamäe, Vastano, & Costantini, 2015). On one side, a metric criterion could be used, including within the PPS any object located within a certain distance from the body, usually the farthest distance at which a person can reach for the object. On the other side, a functional approach, currently receiving a good consensus, suggests that the PPS boundaries can dynamically change according to contingent factors (Ferri et al., 2015).

In line with the functional hypothesis, Canzoneri, Magosso and Serino (2012) recently implemented a dynamic audio-tactile integration task that measures the dimensions of the PPS and, specifically, assesses its extension in an ecologically valid situation. They measured the participants' reaction times (RTs) to a tactile stimulus delivered to their hand while a sound simulated the motion of a sound source either towards the participants' hand or away from it. They used a dynamic sound in light of the findings, both in humans and monkeys, indicating preferential responses for moving stimuli in the neural systems representing the PPS (Graziano, Yap, & Gross, 1994; Graziano, Reiss, & Gross, 1999; Makin, Holmes, & Zohary, 2007) and, at the same time, because dynamic stimuli are particularly relevant for the PPS, as it codes the spatial position of stimuli with which the body could possibly interact (Canzoneri et al.). Tactile stimulation was delivered at different delays from the onset of the auditory stimulus, hence occurring when the sound source was perceived at different distances from the hand. The participants were required to respond to the tactile stimulation verbally and as rapidly as possible, trying to ignore the sound (Canzoneri et al., Fig. 1.2.1). They hypothesised that stimuli coming from different modalities would interact more efficiently if presented within the same spatial frame and, hence, expected the RTs to decrease progressively as a function of the

perceived approach of the sound and, conversely, to increase as a function of its perceived

regression (Canzoneri et al.; Fig. 1.2.2).
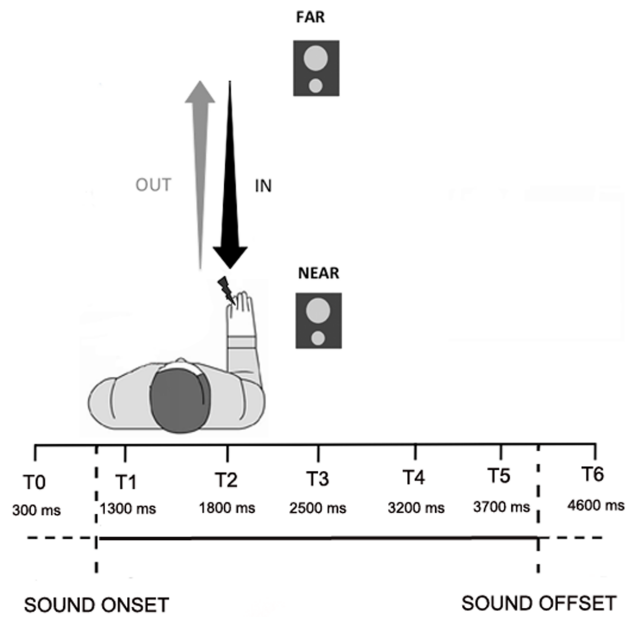
Figure 1.2.1 Procedure (from Canzoneri et al., 2012). The participants received a tactile stimulus at their hand while task-irrelevant sounds either approached to or receded from the hand. Tactile stimuli were delivered at different temporal delays from sound onset (from T1 to T5), so that they were processed when sounds were perceived at different distances from the hand.
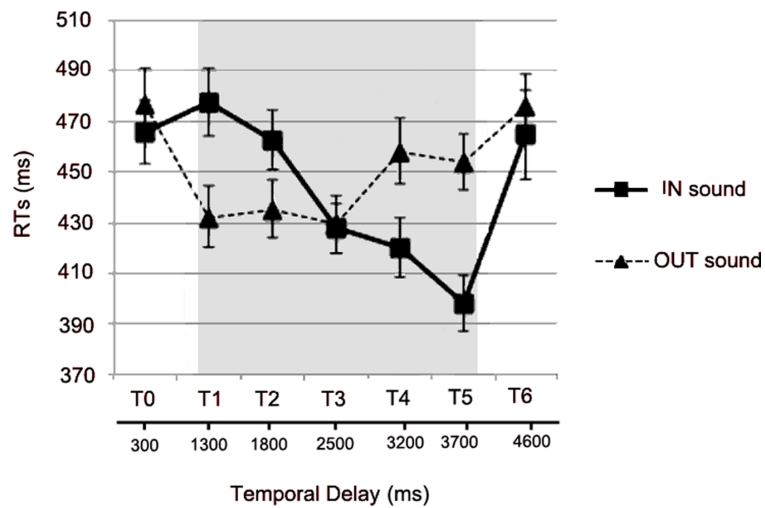
Figure 1.2.2 Effects of IN and OUT sounds on tactile processing. (from Canzoneri et al., 2012). Mean RTs (and S.E.M.) to the tactile target at different temporal delays (from T0 to T6) for IN (filled line) and OUT (hatched line) sounds. The shaded region indicates the duration of the sounds.

The data collected confirmed their hypothesis, but also highlighted a different shape of the

relationship between sound position and RTs depending on the perceived sound direction.

When the sound was approaching, the temporal delay (and thus the perceived sound position) showed a significant effect on the RTs, which resulted significantly shorter in the closest vs. farthest positions with respect to the body. When the sound was receding, instead, the differences between the RTs at the higher vs. lower temporal delays were not significantly different once they had been corrected for multiple comparisons. In light of these results, the authors claimed that dynamic sounds can modulate tactile processing depending on their perceived position in space and on the direction of their motion (the modulation being stronger for approaching vs. receding sounds). In particular, they showed that tactile RTs are speeded up by the presence of a simultaneous sound if this is perceived within a limited distance from the hand, supposedly thanks to the more effective integration of multisensory stimuli happening within the same spatial representation. They also suggested that the critical distance where the RTs are first speeded up should be considered as the estimated boundary of the representation of the PPS around the hand (Canzoneri et al.).

The PPS is the portion of space where interactions with others occur. However, little is known about the way in which it is modulated by social environment and social interactions (Teneggi, Canzoneri, di Pellegrino, & Serino, 2013). Teneggi and colleagues (2013), following up on the previous research from their group, which identified the boundaries of the PPS (Canzoneri et al., 2012), investigated how the presence of others and the interaction with them shaped the PPS representation of adults. To address this, they conducted two studies using their previously developed (Canzoneri et al., 2012) dynamic audio-tactile integration task.

The first study investigated the role of the sole presence of another person in the far space. The participants performed the task while facing either another person or a mannequin. The results showed a different modulation of the RTs depending on who the participants were facing. In particular, in the "other person" condition the PPS boundaries seemed to be located in a position closer to the body than in the "mannequin" condition (Fig. 1.2.3), showing that the

PPS representation shrank when the far portion of the space was occupied by another person, but not when it was occupied by a mannequin. This suggested that the PPS accommodates in the presence of others, probably in relation to its function as an interactive space where defensive and approaching behaviours should be triggered (Brozzoli, Pavani, Urquizar, Cardinali, & Farnè, 2009; Graziano & Cooke, 2006; Serino, Annella, & Avenanti, 2009; Teneggi et al., 2013).
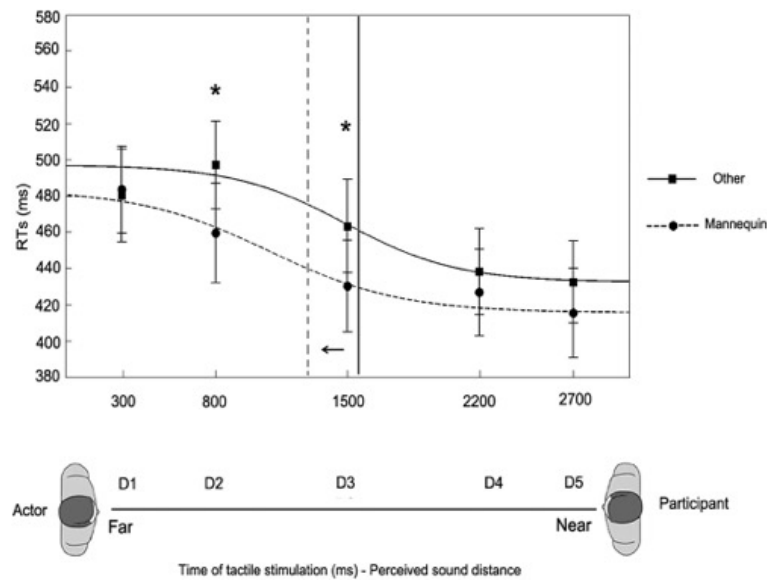
Figure 1.2.3 PPS boundaries as a function of others' presence (from Teneggi et al., 2013). The figure shows the mean RTs – fit with a sigmoid function – to tactile stimuli, at different perceived sound distances, corresponding to different delays of the tactile stimulus, when the participants faced the other person or the mannequin (error bars represent SEM). the PPS boundaries were closer to the participants when they faced the other person than when they faced the mannequin.

In the second study, the participants performed the audiotactile task before and after performing an economic game with the actor that they would be then facing during the task itself. During the game, the actor was instructed to behave in a cooperative or non-cooperative way, depending on the condition assigned to each participant. The participants also had to rate the perceived fairness of the actor's behaviour during the game. The results showed an interesting interaction between the perceived distance of the sound, the session and the game condition. When the actor behaved in a non-cooperative way, the RTs for all perceived distances were speeded up after the game as compared to before the game, but the critical point

where the sound affected the speed of the RTs did not change: both before and after the game, the PPS boundaries were located approximately in the same position as in the first experiment, when the participants were only facing another person. When the actor behaved in a cooperative way, instead, a different pattern of results was found. Before the game, the RTs varied as a function of the perceived position of the sound, as in the first experiment. However, after the game the boundaries of the PPS representation disappeared, as demonstrated by the absence of significant differences between the RTs at any Distance condition. This was due to faster RTs in response to the farthest sounds after vs. before the game, but not in response to the closest sounds (Fig. 1.2.4). In light of this result, the authors speculated that after a cooperative interaction there were no more detectable boundaries between the participants and the actor, suggesting that the participants' PPS extended and included the actor's PPS as well (Teneggi et al., 2013).
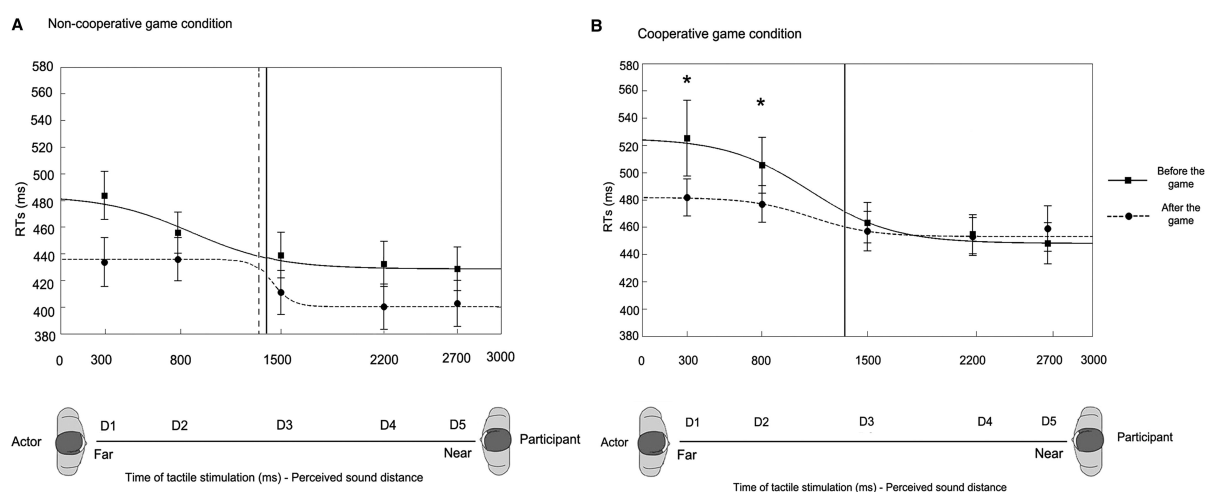
Figure 1.2.4 PPS boundaries after A) a non-cooperative interaction; B) a cooperative interaction (from Teneggi et al., 2013). The figure shows mean RTs to the tactile stimulus at different perceived sound distances, corresponding to different delays of the tactile stimulus delivery (error bars represent SEM). In the Non-cooperative game group, the RTs were generically faster at any sound distances after the game than before the game, but the PPS boundaries did not shift. In the Cooperative game group, the RTs were faster after the game than before the game only at the farthest sound distances (D1 and D2), that is in correspondence with the portion of space occupied by the cooperative other.

This interesting result was confirmed by a third study in which the sound depicted a wider spatial range. The results of this study confirmed that after a cooperative interaction the tactile RTs were speeded up when the simultaneous sound was perceived at the spatial position

occupied by the actor and that the critical spatial position where the sound first modulated the tactile RTs was located at a farther distance after vs. before the game (Fig. 1.2.5). Summarizing, after an unfair interaction, the participants were generally faster in processing tactile stimulation and this modulation likely depended on the socially unacceptable behaviour of their partner; after a fair interaction, instead, the PPS of the participants seemed to extend to include the space occupied by their partner (Teneggi et al., 2013).
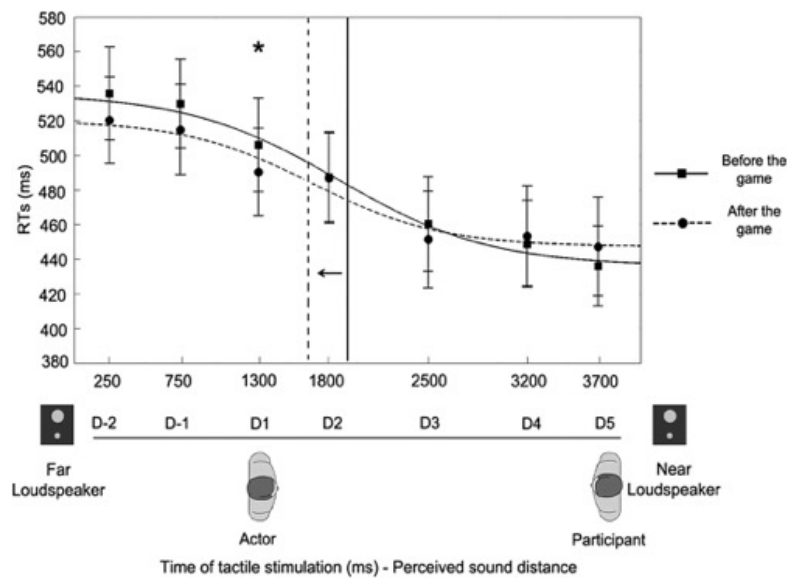
Figure 1.2.5 Shift of the PPS Boundaries after a cooperative interaction in the control experiment (from Teneggi et al., 2013). Mean RTs at the seven different perceived sound distances, before and after the game, are reported (error bars represent SEM). After a cooperative interaction, the PPS boundaries extended toward the space occupied by the cooperative other.

To sum up, the authors showed that the representation of the PPS is sensitive to the presence of others in the far space as well as shaped by the interactions with them and, more specifically, by the evaluation of other people's behaviour during such interactions. They proposed that their findings could highlight a relationship between sensorimotor functions, as physical and perceptual experiences, and complex social representations, suggesting that mental processes are "situated and embodied in our physical experiences" (Teneggi et al., 2013, p. 4).

Also Heed and colleagues investigated how the PPS is modulated by social interactions and, in particular, how others' actions influence multisensory integration within it (Heed,

Habets, Sebanz, & Knoblich, 2010). During social interactions, others often act within our own PPS, changing the relevance of events happening near the body for our own actions. Consequently, it is likely that also visuo-tactile integration will be affected as well (Heed et al., 2010). In Heed and colleagues' (2010) study, the participants performed a crossmodal congruency (CC) task, both alone and together with another person. As previously described (Ch. 1.1, Brozzoli, Cardinali, Pavani, & Farnè, 2010), the CC task is a visuo-tactile interference tasks in which the participants have to respond to the elevation of tactile stimuli ignoring visual distractors presented synchronously at the same or a different elevation. The participants' responses are usually faster and more accurate when the elevation of the tactile stimuli and the visual distractors is the same, revealing a so-called "crossmodal congruency effect" (CCE), which can be considered a "reliable measure of multisensory processing in the peripersonal space" (Heed et al., p. 1), as it quantifies the strength of the interaction between visuo-tactile stimuli (Brozzoli et al., 2010). In Heed and colleagues' study, when the participants performed the CC task together with a partner, they were told to focus only on the tactile stimuli, while the partner was responding to the visual ones. The results showed that the CCE was significantly reduced when the task was performed with a partner sitting within the participants' PPS vs. alone, but not when the partner was sitting outside the participants' PPS (Heed et al.). A control study showed that the CCE did not differ between the alone and the partner condition when the partner was sitting within the participant's PPS, but was not responding to the visual distractors (Fig. 1.2.6). Overall, the results demonstrated a social modulation of visuo-tactile integration only when the partner was performing a task within the participants' PPS. In this situation, the participants' performance was mainly improved in the incongruent trials, showing that the participants could ignore the incongruent stimuli more efficiently when their partner was acting upon them (Heed et al.). The authors speculated that this modulation could be due to a top-down influence of multisensory integration: representing the partner's task might have

"changed the relative contributions of the visual and tactile modalities to tactile judgements" (Heed et al., p. 3), in particular – in this specific situation – reducing the importance of visual information. This modulation could be interpreted in two different ways: on one hand, knowing that the partner was responding to the visual distractors might have decreased their potential threatening value for the participants, reducing the amount of attention that they allocated to them (PPS defensive function); on the other hand, it might have reduced the likelihood of the visual stimuli as potential action targets, reducing their interference (PPS goal-directed function) (Heed et al).
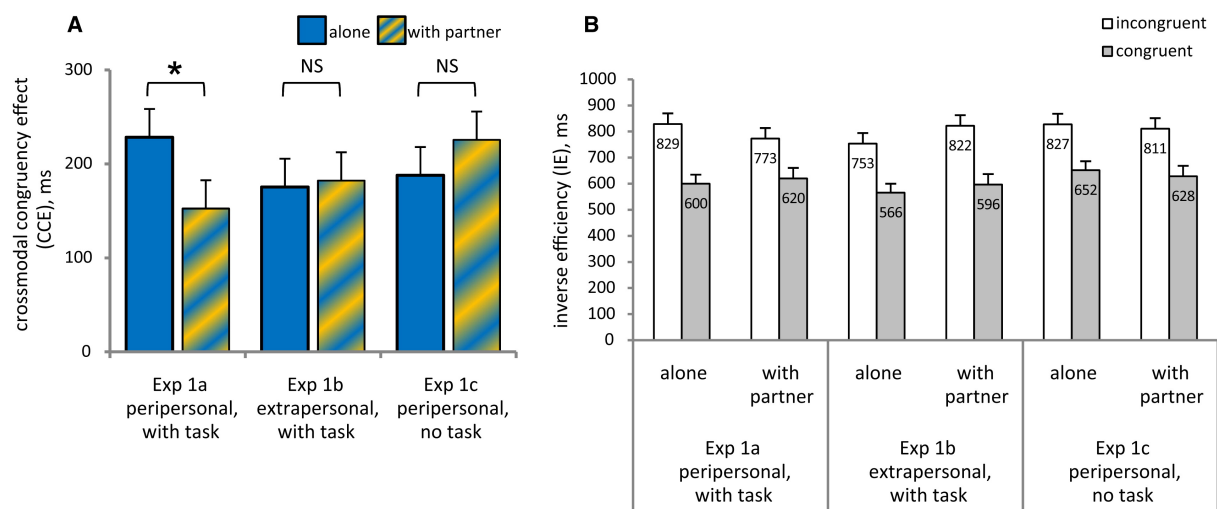
Figure 1.2.6 Results of the experiments (from Heed et al., 2010). (A) Crossmodal interference, assessed by the crossmodal congruency effect (CCE), i.e., the difference between incongruent minus congruent conditions (see B). The dependent measure is the inverse efficiency (IE, reaction time/percentage of correct responses) The CCE was lower when a partner performed a task involving the visual distractors, but only when she resided in the peripersonal space of the participant. *p < 0.05. Error bars denote standard error of the mean. (B) IE data, separately for incongruent and congruent conditions. Each bar in (A) results from subtracting gray bars from their neighboring white bars in (B). Note that changes in the CCE are due mainly to changes of performance in the incongruent trials.

The semantic content of the stimuli happening in the PPS could shape its boundaries as well, as demonstrated by Ferri and colleagues (Ferri et al., 2015). They investigated the impact of emotion-inducing approaching sounds on the PPS boundaries, asking their participants to detect tactile stimuli presented to their right hand while they were listening to task-irrelevant sounds that simulated the approach of a sound source (Canzoneri et al., 2012; Teneggi et al., 2013). The presented sounds elicited positive, neutral or negative emotional responses,

depending either on their physical properties or their content (i.e. "psychological associations to the sound producing source", Ferri et al., p. 469). The results showed that the PPS was larger when the presented sound (both artificial or ecological) had a negative vs. neutral valence: the PPS boundaries were farther away from the participant when the task-irrelevant approaching sound was negative. When the sounds had a positive valence, instead, the PPS was smaller compared to both the negative and neutral sound conditions (Ferri et al.; Fig. 1.2.7 and 1.2.8). The authors discussed the modulation of the PPS boundaries induced by task-irrelevant emotional information suggesting that it could be explained by the defensive function of the PPS itself. Our perceptual systems are meant to inform us about possible dangers in the environment in order to keep a spatial margin of safety around the body and, as a consequence, they constantly monitor the space around it, alerting us of any possibly dangerous event, like those possibly signalled by sounds with a negative valence (Ferri et al.).
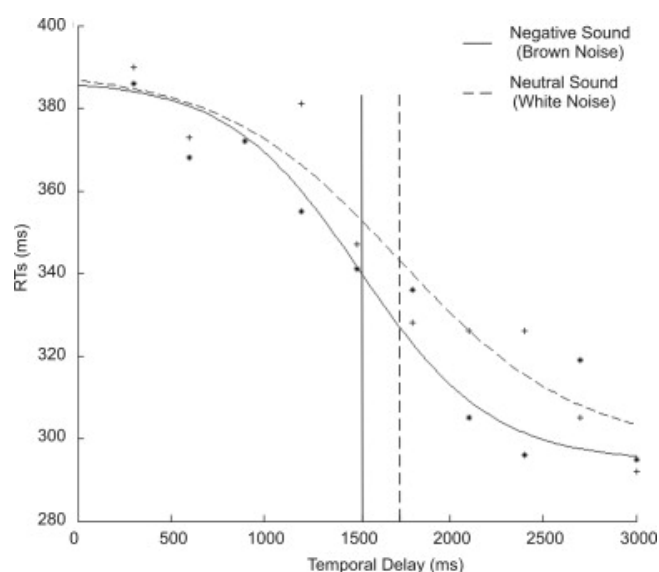
Figure 1.2.7 PPS boundaries during the presentation of a Negative vs. Neutral artificial sound (from Ferri et al., 2015). The solid and the dashed vertical lines represent the central point of the sigmoidal function of negative and neutral sounds, respectively, i.e. the supposed boundary of PPS in each sound condition.
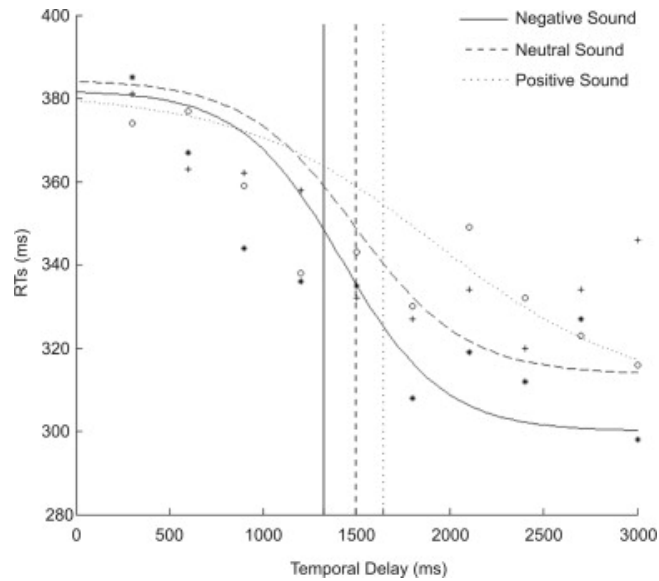
Figure 1.2.8 PPS boundaries during the presentation of a Negative, Neutral or Positive natural sound (from Ferri et al., 2015). The solid, dashed and dotted vertical lines represent the central point of the sigmoidal function of negative, neutral and positive sounds, respectively, i.e. the supposed boundary of PPS in each sound condition.

Teneggi and colleagues (2013) showed an expansion of the PPS boundaries after a positive interaction, but shrinkage of the same after a negative interaction. Conversely, Ferri and colleagues' (2015) findings highlighted an expansion of the PPS after a negative emotional stimulus. These two findings seem to be conflicting with each other, but Ferri and colleagues discussed them in light of the functional differentiation of the PPS recently described by de Vignemont and Iannetti (2015). In particular, Ferri and colleagues claimed that the study by Teneggi and colleagues targeted the working function of the PPS, whereas theirs focused on its defensive function. They consequently speculated that the same outcome – i.e. PPS expansion – can be elicited in opposite situations according to the PPS function that has been triggered (Ferri et al.).

One of the most important features of the PPS is its plasticity, as demonstrated by the abovementioned studies on the influence of social interactions on the PPS extension as well as by findings on tool- and action-induced modulations of its dimensions and on its changes in relation to trait anxiety and claustrophobic fear (Van der Stoep, Nijboer, Van der Stigchel, & Spence, 2015).

Several studies investigated, using different tasks, the plasticity of the PPS in relation to the use of tool. Serino and colleagues studied whether the PPS surrounding the hand could be extended by a short or long-term experience of tool-use in everyday life (Serino, Bassolino, Farnè, & Làdavas, 2007). They investigated the effect of the use of a cane for navigating in the space in blind, expert, and sighted, naïve, participants. They demonstrated that in sighted participants the hand PPS extended around the tool after a brief period of use and, similarly, contracted backwards after a resting period; conversely, blind participants' PPS extended around the cane as soon as they held it, but only if its length was the same of the cane that they normally used. These results demonstrated that the long-term use of a tool can induce a stable extension of the PPS to include the tool, suggesting that multiple representations of the PPS could simultaneously exist and could be "dynamically and functionally engaged depending on contextual demands" (Serino et al., 2007, p. 647).

Later on, the same group investigated whether the PPS around the hand could be extended using a computer mouse, whose actions have a distal effect on the computer screen, i.e. the far space (Bassolino, Serino, Ubaldi, & Làdavas, 2010). With this study, they wanted to investigate the effect of the extensive use of an everyday-life tool on the PPS representation of healthy participants. They showed that when the participants sat in front of the screen without using nor holding the mouse, they responded more quickly to audio-tactile stimuli presented near the hand vs. near the screen, whereas if they were either using or just holding the mouse,

they responded to audio-tactile stimuli near the hand or near the screen with the same speed, showing an extension of the PPS towards the far space (i.e. the computer screen). These findings suggested once again that the everyday use of a tool such as a computer mouse results in a lasting extension of the PPS representation, evoked not only by active usage but also by passive holding of the tool. As for blind cane users (Serino et al., 2007), the authors speculated that expert tool users can simultaneously hold different space representations, which can be dynamically and immediately triggered depending on the context (Bassolino et al., 2010).

More recently, Canzoneri and colleagues investigated how tool use could affect the representation of both the PPS and the body (Canzoneri et al., 2013). Using their previously developed dynamic audio-tactile integration task (Canzoneri, Magosso, & Serino, 2012) and a tactile distance perception task, they showed that even a brief usage of a tool induced plastic changes in the representation of the dimensions of the body part using it and of the space around it. In particular, it extended the PPS representation along the tool and, at the same time, it modified the representation of the body: after tool use, the participants perceived their forearm as longer and narrower, with a shape similar to the one of the tool. These results highlighted a strong overlap between the representations of the PPS and of the body, demonstrating that a tool extending the action space of the body can be incorporated into the body representation (Canzoneri et al., 2013).

A line bisection task was also used to investigate the effect of tool use on the PPS representations as well as the transition between near and far space in healthy adults (Gamberini, Seraglia, & Priftis, 2008; Longo & Lourenco, 2006). When performing a line bisection task in the near space, healthy adult participants show a slight leftward bias, known as "pseudoneglect". Conversely, in the far space the bias seems to be directed towards the right side (Longo & Lourenco, 2006). In the study by Longo and Lourenco, the participants were asked to bisect lines at four possible distances, using either a laser pointer or a stick. The authors

expected to find a gradual shift of the bisection bias from the left to the right while moving from near to far space when the participants used the laser. At the same time, they expected that using the sticks would expand the representation of the near space, leading to a constant leftwards bias in the bisection of the lines located both in the near and far space. The results confirmed their predictions: when a laser was used, the participants showed a gradual left to right shift in their bisection bias with the increased distance of the lines; when the stick was used, instead, they showed a constant leftward bias, not modulated by the distance of the lines, as if all the lines were perceived in the near space. The authors speculated that during laser use, the near space representations became gradually less active with the increased distance of the stimulus, reducing the rightward orienting tendency of the left hemisphere and hence biasing attention to the right. Conversely, when a stick was used the near space representations stayed active at every distance, maintaining the leftward bias and suggesting that the use of the tool extended the dimensions of the near space (Longo & Lourenco, 2006). The study run by Gamberini and colleagues (2008) used the same paradigm, both in a real environment and in virtual reality. Their results replicated the previous findings suggesting a shift from peripersonal to extrapersonal space when the laser was used and an extension of the PPS to the extrapersonal space when a stick was used, extending them to virtual reality as well (Gamberini et al., 2008).

The PPS could be modulated and remapped also by actions, like grasping (Brozzoli, Pavani, Urquizar, Cardinali, & Farnè, 2009) or walking (Noel et al., 2015). In the study by Brozzoli and colleagues (2009), the participants completed a crossmodal congruency task in which they were required to judge the elevation of a tactile stimulus in presence of visual distractors with congruent or incongruent elevation, either grasping the object embedding the visual distractors or not. When the participants were not grasping the object, they were faster in responding to congruent vs. incongruent trials, showing a classic CCE effect despite the distance of the distractors from the hand. In the grasping condition, the CCE became stronger

as soon as the grasping action was initiated, demonstrating that, from the very beginning of an action, "the task-irrelevant visual information located on the to-be-grasped object interacted more strongly with the tactile information delivered on the hand that will eventually grasp the object" (Brozzoli et al., p. 916). These results showed that tool use is not indispensable for the brain in order to remap the PPS, which can be reshaped also by voluntary actions (Brozzoli et al.).

More recently, Noel and colleagues investigated whether the PPS space dimensions changed while walking, showing for the first time a modulation of the PPS around the chest following whole body motion. The participants performed the dynamic audio-tactile integration task developed by the authors (Ch. 1.2; Canzoneri et al., 2012; Teneggi et al., 2013), responding to tactile stimulation on their chest either while walking or standing immobile. The authors hypothesised that the PPS dimensions would be expanded during walking, i.e. that the RTs to tactile stimulation would be speeded up by a simultaneous sound perceived farther away compared to when they were standing still. The results confirmed their predictions, showing an enlarged representation of the PPS in the walking vs. standing condition, shown by faster RTs to the tactile stimulation on the chest at each perceived distance of the sound (i.e. also when the sound was perceived in the far space). They also showed that the representation of the PPS was modulated by motor, kinaesthetic and proprioceptive cues, but not by visual cues, as demonstrated by the absence of any effect on the RTs of the presentation of optic flow during the task. The authors claimed that as the PPS is the portion of space where individuals interact with external stimuli, if these external stimuli and the body move faster towards each other their interaction must be anticipated, leading to the extension of the PPS boundaries themselves. They hence suggested that these results reinforce the conceptualization of the PPS as a "dynamic sensory-motor interface between the individual and the environment" (Noel et al., 2015, p. 375).

The plasticity of the PPS can be shown also in relation to anxiety and claustrophobic fear (Lourenco, Longo, & Pathman, 2011; Sambo & Iannetti, 2013). Lourenco and colleagues investigated the relationship between the PPS dimensions and claustrophobic fear, correlating the performance on a line bisection task (Longo & Lourenco, 2006) with trait anxiety for closed spaces and physically restrictive situations. As in their previous studies, they measured the size of the participants' individual PPS using the rate at which their bisection bias switched rightwards as an index of near space extension (with steeper slopes corresponding to a smaller PPS; Longo & Lourenco, 2006; Lourenco et al., 2011). They hypothesised that, considering the PPS in relation to its defensive function, objects in the near space could induce anxiety and, as a consequence, individuals with a larger PPS could be more likely to experience claustrophobia. They found a systematic, positive relationship between individual differences in the dimensions of the PPS and individual differences in non-clinical claustrophobic fear: people with higher claustrophobia seemed to represent the near space as larger compared to people with less anxiety of closed spaces. The authors speculated that claustrophobic fear might at least partially result from an over-projection of the near space representation related to the defensive purposes of the PPS itself (Lourenco et al., 2011). Sambo and Iannetti (2013) investigated the existence of a possible relationship between personality traits and the defensive PPS surrounding the face, considered as the portion of space where individuals react to potential threats, triggering efficient self-protective actions. Such actions are modulated by the degree of perceived danger represented by the stimulus, which in turn is modulated by anxiety and fear, as well as by the distance of threatening stimuli (Sambo & Iannetti). In order to investigate the relationship between anxiety and the defensive PPS, the authors measured the participants' "hand-blink reflex" (i.e. the blink elicited by hand stimulation) when the hand was located at different distances from the face. They inferred from it the boundaries of the participants' defensive PPS and correlated its extension with the participants' personality traits. They showed that the

defensive PPS around the face was clearly separated from the far space by a sharp boundary and demonstrated that trait anxiety, but not claustrophobic fear, was a significant predictor of size of the defensive PPS, with higher anxiety scores corresponding to a larger defensive PPS, whose margin was located further away from the body than in less anxious individuals (Sambo & Iannetti). The authors speculated that the different results on the relationship between claustrophobic fear and the extension of the PPS found in their study and in the one by Lourenco and colleagues could be related to the different tasks used: specifically, they suggested that their task, involving threat and risk perception, could be more closely related to anxiety than claustrophobia. Along the same line, they suggested that a paradigm focusing on body defence vs. multisensory integration and/or motor execution could be responsible of the different findings on the continuous vs. sharp transition between far and near space (Sambo & Iannetti).

1.4.1 Non-Human Primates

Singe-cell recordings in monkeys firstly revealed the discrete processing of the portion of space immediately surrounding the body, which involves several interconnected sensorimotor areas - including parietal and frontal premotor cortices - which are crucial for controlling body, head and arm movements (di Pellegrino & Làdavas, 2015; Graziano, Yap, & Gross, 1994; Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981). Neurons in these areas respond to both visual and tactile stimuli, under the condition that they are both presented within the same receptive field (RF), coded under a spatial register centred on the body (Làdavas, 2002).

Single-cell studies, reviewed by di Pellegrino and Làdavas (2015), demonstrated that a large group of neurons in the area F4, located in the caudal portion of the ventral premotor cortex, responds to both tactile and visual stimuli and, at the same time, has large tactile RFs, which are arranged to form a map of the body surface (di Pellegrino and Làdavas; Graziano et al.,1994). Particularly, these neurons are effectively triggered by three-dimensional objects moving in the portion of space nearest to the animal's body, namely its PPS. More recently, Graziano and colleagues provided evidence demonstrating that neurons in F4 integrate auditory information as well, holding F4 responsible for representing nearby space (Graziano, Reiss, & Gross, 1999). Most importantly, the visual RF of neurons in area F4 is not dependent on eye movements, but moves with the tactile RF on the body surface, regardless of eye gazes (Graziano et al., 1994). This demonstrates that these neurons code the location of visual stimuli on a body-centred reference frame, which would also be appropriate for visually guiding approaching or defensive movements in response to objects located within the PPS, as movements are programmed with respect to body-centred coordinates as well (di Pellegrino & Làdavas).

Several findings showed that monkey's PPS works in a highly plastic and dynamic way. The rapid and dynamic reshaping of the PPS according to sensorimotor experiences could be critical for preparing and executing actions in response to objects moving in the PPS itself (di Pellegrino & Làdavas, 2015). For example, Iriki and colleagues trained monkeys to retrieve food dispensed beyond reach using a rake and showed that neurons' RFs expanded along the rake as soon as the monkey started to use it purposefully, but shrank back to their original dimension when the monkey was only passively holding the rake (di Pellegrino & Làdavas, 2015; Iriki, Tanaka, & Iwamura, 1996).

As neurons encoding the PPS are located within brain areas adjacent to those containing mirror neurons, the relationship between these two systems has recently been investigated, particularly in order to find out if a mechanism similar to mirror neurons' one could encode the PPS of other individuals. Within this framework, Ishida and colleagues recorded the activity from monkey's VIP area, involved in the multisensory and body-centred representation of the near space (Ishida, Nakajiama, Inase, & Murata, 2010). They showed that bimodal neurons in this area were activated by visual stimuli presented near their tactile RF and, critically, also by visual stimuli presented near the corresponding body parts of another individual (the experimenter), which was outside the subject's PPS. However, these same neurons were not activated by visual stimuli presented close to different body parts of the other individual. Furthermore, these neurons exhibited strong responses only to stimuli happening within the PPS of any of the two individuals, but not between these regions. The authors speculated that "individuals might encode the body parts of others using a representation of their own body parts, a "matching" mechanism that is functionally similar to how mirror neurons encode one's own actions and the actions of others" (di Pellegrino & Làdavas, 2015, p. 128; Ishida et al., 2010).

1.4.2 Humans

The existence of a selective representation of the PPS, separated from that of the extrapersonal space, has been supported by neuropsychological studies, in particular on patients with spatial attention disorders. Patients with right-brain damage (RBD) can manifest tactile extinction in the left (contralesional) side of the body (Làdavas, 2002). Extinction is the clinical symptom in which patients, despite being able to detect a detect a single tactile stimulus both on the ipsi- or contra-lesional side of the body, cannot report a contralesional stimulus in presence of a simultaneous tactile stimulus on the ipsilesional side of the body. Làdavas and colleagues showed that RBD patients with tactile extinction presented the same symptom when the stimulus delivered to the contralesional hand was visual or tactile, suggesting the existence of a crossmodal visuo-tactile extinction, but only when the visual stimulus was presented in the near, peripersonal, space (Làdavas, di Pellegrino, Farnè, & Zeloni, 1998). It was demonstrated that the same crossmodal extinction mechanism can work for different body parts, for example the face (Làdavas, Zeloni, & Farnè, 1998). Supposedly, due to multisensory integration, a visual stimulus presented near a body part would activate the somatosensory representation of that body part. When two or more spatial representations are activated, the competition between them would lead to an extinction of the weaker one, which is the one in the contralesional side of the body. According to Làdavas (2002), these findings support the existence of a system integrating visual and tactile stimuli happening in the near space, i.e. the space immediately surrounding body parts, which is different from the mechanism responding to visual information in the far space. Furthermore, a study by Farnè and colleagues (Farnè, Pavani, Meneghello, & Làdavas, 2000) found strong crossmodal extinction effects in RBD patients when the visual stimuli were presented both close to the real hand of the patient or to a rubber hand arranged in a plausible posture. This demonstrated that visual information about the hand

position might be sufficient in order to process visuo-tactile stimuli in the PPS and could dominate over proprioceptive cues (Farnè et al., 2009).

More recently, the functional mechanisms of the PPS in healthy humans and their anatomical underpinnings, were investigated also with brain imaging techniques (di Pellegrino & Làdavas, 2015). These studies highlighted similarities between the cortical regions processing the space immediately surrounding the body in monkeys and in the human brain. For example, Makin and colleagues showed a robust activation of the intraparietal sulcus (IPS), the lateral occipital complex (LOC) and the premotor cortex for representing the visual space near the hand (Makin, Holmes, & Zohary, 2007). They ran a fMRI study that contrasted the response to a ball moving towards vs. away from the hands, manipulating both the distance of the stimulus and the proprioceptive feedback on the hand position coordinates. Furthermore, in order to disentangle the role of visual and proprioceptive information, they repeated their study both occluding the hand or substituting it with a dummy hand. They showed that: i) the occipital cortex represented visual information on hand position, regardless of proprioceptive cues; ii) conversely, the posterior IPS and the LOC represented proprioceptive information, regardless of visual aspects; iii) activity in the anterior IPS and the ventral premotor cortex was modulated by both visual and proprioceptive information (Makin et al., 2007).

Regions within the intraparietal and premotor cortices have also been shown to respond to multisensory stimuli presented within the PPS. Gentile and colleagues ran an fMRI study in which the participants were presented with uni and multimodal natural stimuli (visual, tactile and visuo-tactile) in the space immediately surrounding their hands, while they were gazing at them (Gentile, Petkova, & Ehrsson, 2011). They found enhanced BOLD responses for multimodal stimuli in the anterior IPS, the insula, the inferior parietal cortex, the postcentral sulcus, the parietal operculum, the premotor cortex and in the thalamus, the putamen and the cerebellum, showing the relevance of these circuits for the multisensory perception of the hand

in the space. Furthermore, they found non-linear, superadditive BOLD responses in the anterior IPS, in the cortex covering the postcentral sulcus, in the contralateral insula and in the ipsilateral operculum, in the dorsal premotor cortex, in the contralateral putamen and in the cerebellum (Gentile et al., 2011)

A recent study (Brozzoli, Gentile, Bergouignan, & Ehrsson, 2013) investigated whether the brain regions encoding one's own PPS could also code correspondent body parts of someone else, similarly to the "body-matching neurons" found in monkey's parietal cortex (Ishida et al., 2010). They measured BOLD adaptation (i.e. response reduction after repeated presentation) in order to identify neuronal populations showing selective activation to an object near to one's own hand as well as near to someone else's hand. During the task, the participants were presented with a moving object close to their hand for 3 seconds and, immediately after, close to another person's hand or to a dummy hand for another 3 seconds, or vice versa. The results highlighted the existence of populations of neurons in the human ventral premotor cortex that encode the space near the participant's own hand as well as near another person's hand, supporting the idea of a low-level "shared PPS representation", which could have a role in social interactions, coding events in a common reference frame (Brozzoli et al., 2013).

The relationship between the motor system and the PPS extension was also studied: Finisguerra and colleagues measured the boundaries of the PPS investigating the critical distance at which an auditory stimulus moving along a spatial continuum could affect the corticospinal excitability (Finisguerra, Canzoneri, Serino, Pozzo, & Bassolino, 2015). They delivered Transcranial Magnetic Stimulation (TMS) single pulses to the participants while they were presented with a sound perceived at different distances from their own body. At the same time, they measured the amplitude of the participants' motor evoked potentials (MEPs) as a proxy of the excitability of the motor system. They found that the amplitude of the MEPs was enhanced when the sounds were perceived within a certain distance from the hand, which could

be considered as the boundary of the PPS representation. Interestingly, and similarly to previous findings (Canzoneri, Magosso, & Serino, 2012), once the sound was perceived within the PPS, its relative position with respect to the body did not further influence the motor cortex excitability, suggesting that the PPS could be considered as a homogeneous portion of space. They also demonstrated that the direction of motion of the auditory stimuli (approaching vs. receding) did not modulate the MEPs, suggesting that both approaching and receding stimuli within the PPS could be relevant for the motor system in order to plan either defensive or object-directed movements. The authors speculated that these findings support the existence of a strict link between the multisensory representation of the PPS and the motor representation of actions (either interactive or defensive) that could take place in this portion of space (Finisguerra et al., 2015).

Recently, Longo and colleagues investigated whether the activation of the right hemisphere during tasks involving spatial attention is specific for stimuli presented in the near space, as suggested by the evidence supporting the right hemisphere specialization for spatial attention and the existence of separate representations of near and far space (Longo, Trippier, Vagnoni, & Lourenco, 2015). In this study, the participants were required to judge the position (left, centre or right) of a transector with respect to a line that was seen at four different distances ("landmark task"), while their brain activity was recorded with the EEG. Previous findings revealed a specific negative ERP component generated by line bisection over the right occipito-parietal cortex, between 170 and 400 ms after stimulus presentation (Foxe, McCourt, & Javitt, 2003; Waberski et al., 2008). Longo and colleagues measured this "line-bisection" component and confirmed that spatial attention induced a negativity over occipito-parietal electrodes on the right side of the brain. Most importantly, they demonstrated that the amplitude of the negative peak was inversely related to the distance of the line, with closer lines leading to more negative peaks (Fig. 1.4.1 and 1.4.2). They speculated that these results are suggestive of a

specialization of the right occipito-temporal cortex for orienting attention to the portion of space immediately surrounding the body (Longo et al., 2015).
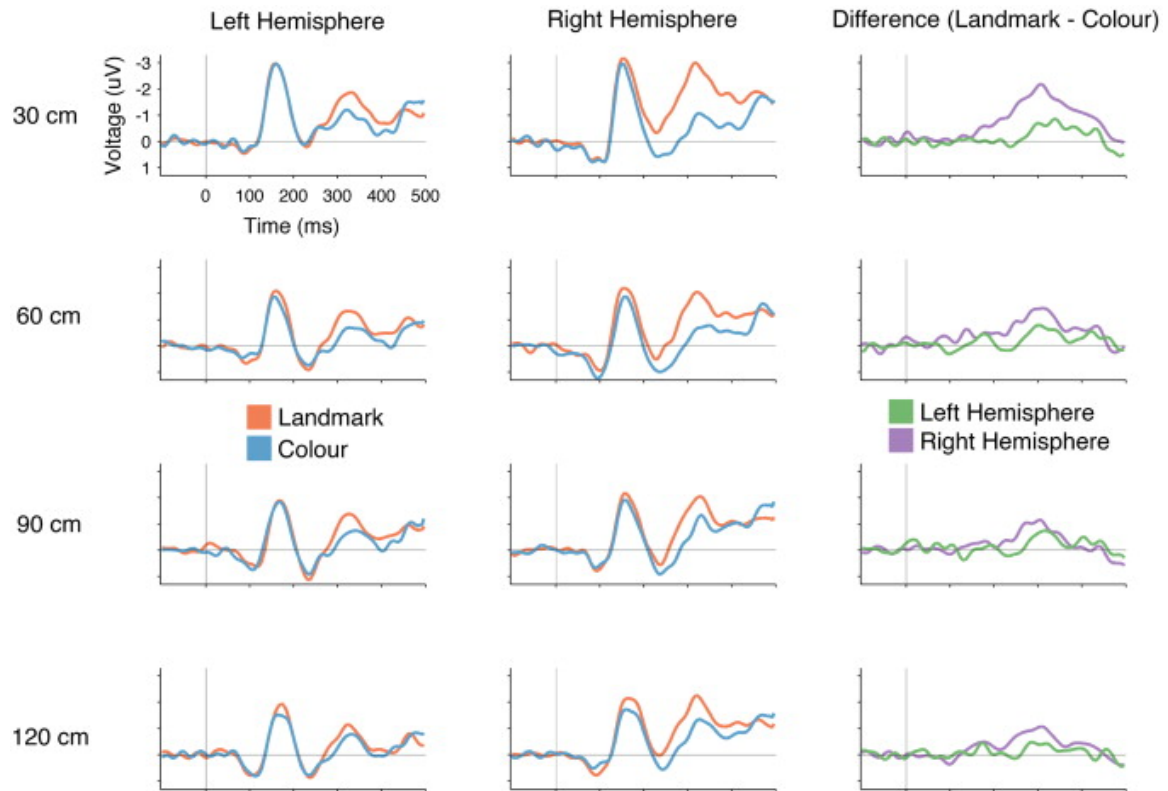
Figure 1.4.1 ERP results (from Longo et al., 2015). ERPs in the landmark and colour (control) tasks for each viewing distance in the left and right hemispheres, and difference waveforms (landmark − colour) in both hemispheres (right panel).
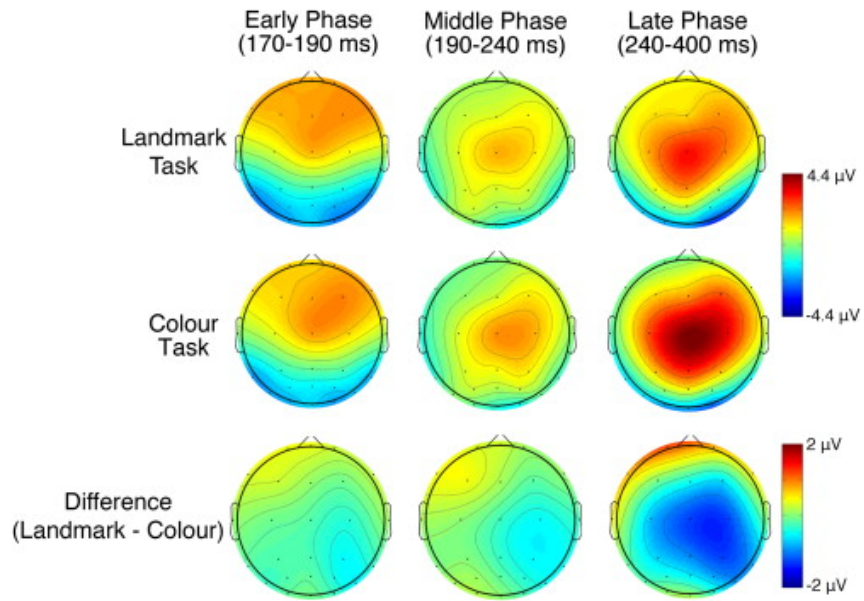
Figure 1.4.2 Scalp maps (from Longo et al., 2015). Scalp maps showing mean voltage across the scalp in the two tasks (and their difference) in each of the three phases.

Touch can be useful in order to discriminate which information signalled by vision and audition can denote any properties of the PPS, as confirmed by the findings demonstrating the importance of touch in its representation. Despite the importance of touch, little is known about the development of tactile localization abilities during infancy (Bremner, Mareschal, Lloyd-Fox, & Spence, 2008). Bremner and colleagues investigated the ability to localise tactile stimuli presented within the PPS in 6.5- and 10-month-old infants. They were particularly interested in shedding light on the development of tactile localization abilities as well as in the interplay between visual and tactile cues associated with spatial localization during infancy. In fact, the localization of tactile stimuli in space is challenged by postural changes, which can cause a misalignment between information coming from touch and the other senses, vision in particular (Bremner, Mareschal et al., 2008). In their experiments, the authors presented vibrotactile stimuli to either palm of infants' hands and compared their responses (i.e., their visual and manual behaviours) while the hands were in a crossed vs. uncrossed posture. This allowed them to determine infants' abilities to remap the spatial location of tactile stimuli in response to postural changes and to evaluate the influence of visual information on tactile localization. The results showed that 10-month-old infants could make accurate manual orienting responses to tactile stimuli both when their hands were in a crossed or uncrossed position and to adapt the direction of their visual orienting to tactile stimuli depending on their hands posture. Conversely, infants aged 6.5 months showed a predilection for manual vs. visual orienting responses and made more contralateral manual responses in both postural condition, hence responding on the appropriate side in the uncrossed, but not in the crossed-hands posture. Overall, the data showed for the first time that infants in both age groups were able to orient correctly to an invisible tactile stimulus when their hands were uncrossed (i.e. in a familiar position), suggesting that they can use unimodal tactile cues to locate a stimulus and, hence,

explore the space around it. Furthermore, the latency of these responses (both manual and visual) suggested that they should not be considered as reflexes, but as responses driven by cortical control. Moreover, the increase of visual responses with age is suggestive of the development of crossmodal links in the overt attentional responses to the spatial position of tactile stimuli. Despite the localization of tactile stimuli could – in principle – be achieved using a body-centred reference frame, regardless of visual information on limbs position, the higher occurrence of contralateral visual responses in the younger infants suggested that 6.5-month-olds used a visual framework to orient their manual responses, indicating that they perceived tactile sensations with respect to a visuo-spatial reference frame. Conversely, older infants seemed to have a greater capacity to remap the spatial location of tactile stimuli as a function of hands posture (Bremner, Mareschal et al., 2008).

Bremner, Holmes and Spence (2008) suggested that young infants' poor performances in spatial orienting tasks might be due to their difficulty in finding a correspondence between the location of the stimuli in the environment and the body-centred, proprioceptive coordinates necessary to orient towards them. In light of this, they suggested the existence of two independent mechanisms of multisensory integration that could account for the early development of spatial representations in the PPS. The first mechanism relies on visuo-spatial information: the position of the limbs is computed according to their normal location in the visual field. This mechanism can normally lead to accurate localization of the limbs, thanks to the great reliability of spatial information provided by vision, but also to errors, for example in body illusions like the "rubber hand illusion". The second mechanism, instead, allows to remap the correspondences between the position of the stimuli in the environment and the position of the limbs according to postural changes. This mechanism, thanks to its sensitivity to posture, permits to orient vision correctly when the location of the limbs is atypical. The authors speculated that the younger participants in their previous study (Bremner, Mareschal et al.,

2008) responded to the tactile stimuli relying on a visual mechanism, i.e. computing the typical position of their limbs in space, whereas the older infants had developed the ability of taking into account postural remapping while computing the correspondences between visual and proprioceptive information. In light of this, they suggested that the PPS representations might develop from these two separated mechanisms, the first being present already in the first six months of life and relying mainly on vision and previous experience, and the second emerging after 6.5 months of age and dynamically incorporating posture information. Finally, the authors highlighted how the emergence of these two mechanisms could be observed looking at the development of reaching and grasping, which happens within multisensory PPS representations (Bremner, Holmes et al., 2008).

Bremner and colleagues also investigated the neural bases of the localization of touches in the near space and their relationship with the computation of postural changes (Rigato, Begum Ali, van Velzen, & Bremner, 2014). They recorded the somatosensory evoked potentials (SEPs) following vibrotactile stimulation on the hands – in either uncrossed or crossed postures – in 6.5-, 8- and 10-month-old infants. A first study compared the electroencephalographic activity with respect to somatosensory processing in 6.5- vs. 10-month-old infants. Both age groups showed SEPs over central regions contralateral to the stimulated hand, but only the 10-month-old infants showed an influence of arms posture on the processing of tactile stimuli (Fig. 1.5.1). In particular, 10-month-olds showed an effect of arms posture over central sites in the early components of the SEPs, as in adults, suggesting that postural information modulated "the feed-forward stages of processing in somatosensory cortex" (Rigato et al., 2014, p. 1222). Furthermore, a second study showed that this effect was found only if the infants could see their hands, suggesting that visual cues are necessary for computing information about the postural remapping of limbs at this age and, hence, that visual information modulates somatosensory processing.
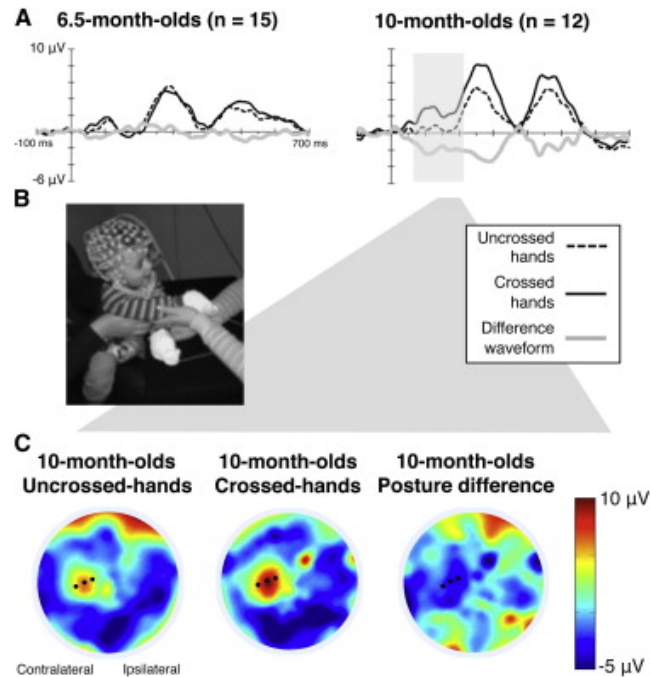
Figure 1.5.1 Somatosensory Evoked Potentials in Crossed- and Uncrossed-Hands Postures, in 6.5- and 10-Month-Old Infants (from Rigato et al., 2014). (A) Grand averaged SEPs in both posture conditions (and difference waveform) from central electrodes (C3, C4) contralateral to the stimulated hand in 6.5- and 10- month-old infants. The shaded area indicates the time course of statistically reliable effects of posture on somatosensory processing. (B) A 6.5-month-old infant adopting the crossed-hands posture during the experiment. (C) Topographical representations of the voltage distribution over the scalp in the 10-month-old infants from 150–200 ms after the tactile stimulus. Small black discs indicate the locations of the electrodes chosen for SEP analyses.

A third experiment investigated the influence of experience on the development of somatosensory remapping in infancy, repeating the previously described study with 8-month-old infants who could or could not yet perform spontaneous reaching movements across their body midline. The results showed an effect of posture over a wide range of brain areas in the mid latency SEP components, but only in the group of infants who performed spontaneous midline-crossing reaches (Fig. 1.5.2). These data suggested that at an earlier stage of development touch localization is modulated by posture beyond the initial feed-forwards stage of processing. In light of these findings, the authors speculated that the cortical networks

responsible for dynamically updating the location of a perceived touch regardless of the posture of the limbs become functional during the first year of life (Rigato et al., 2014).
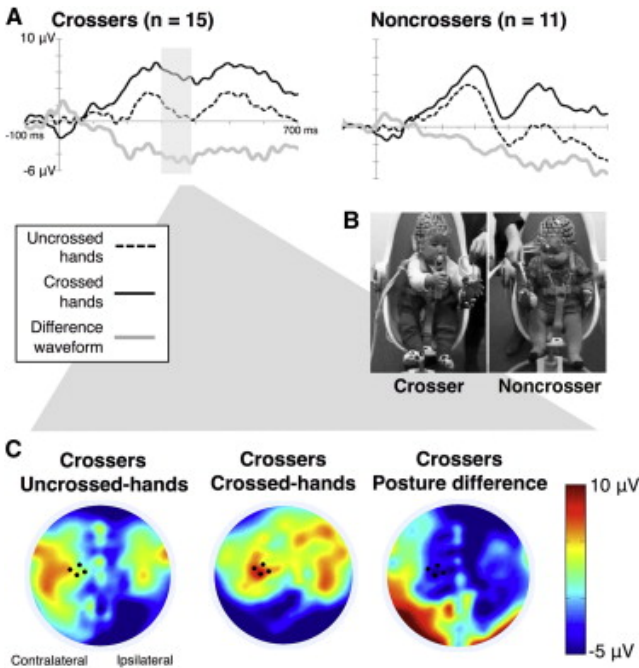
Figure 1.5.2 Somatosensory Evoked Potentials in Crossed- and Uncrossed-Hands Postures in 8-Month-Old Infants who did or did not perform midline-crossing reaches (from Rigato et al., 2014). (A) Grand averaged SEPs (and difference waveform) from central electrodes (C3, C4) contralateral to the stimulated hand in both "crosser" and "noncrosser" 8-month-old infants. The shaded area indicates the time course of reliable effects of posture on somatosensory processing. (B) A "crosser" and a "noncrosser" 8-month-old showing distinctive reaches in the reaching task. (C) Topographical representations of the voltage distribution over the scalp in the crossers from 340–390 ms after the tactile stimulus. Small black discs indicate the locations of the electrodes chosen for SEP analyses.

2. LOOMING

Looming signals, both in the visual and the auditory domain, indicate the approach of objects and provide salient warning cues about impending collision (Maier, Chandrasekaran, & Ghazanfar, 2008; Neuhoff, 1988; Schiff, Caviness, & Gibson, 1962). For these reasons, they are considered particularly relevant from a behavioural point of view (Maier et al., 2008) and, as a consequence, organisms would profit from being able to immediately differentiate them from other stimuli (Tyll et al., 2013). In fact, looming stimuli can signal the approach of a threat to be avoided or of a prey to be confronted, whereas receding stimuli can indicate a failed pursuit or a successful escape (Cappe, Thut, Romei, & Murray, 2009). Information conveyed by moving objects is ethologically meaningful, because it can contribute to an organism's evolutionary success: when encountering an approaching object, the observer has to decide whether to avoid it or confront it, whereas when encountering a receding one, the same observer could be either reassured of his safety or decide whether a pursuit would be worth or not (Cappe et al., 2009). These examples show how even simple sensory cues about motion in the space surrounding the body could provide adaptively relevant information, whose misinterpretation could potentially have a mortal cost (Cappe et al., 2009).

For these reasons, several studies investigated the responsiveness to looming and receding stimuli and proposed that it could be an evolved capacity (Cappe et al., 2009). Accordingly, these studies showed a privileged processing of looming signals, both when presented unimodally and multimodally. For example, they demonstrated that the time to arrival of a sound characterized by rising intensity is systematically underestimated (Rosenblum, Carello, & Pastore, 1987). Moreover, these studies found that an approaching sound was attended for longer periods of time and perceived as changing more in intensity level and as closer to the observer compared to a sound characterized by falling intensity, perceived as receding (Ghazanfar, Neuhoff, & Logothetis, 2002; Neuhoff, 1998; Neuhoff, 2001; Rosenblum,

Wuestefeld, & Saldaña, 1993). These findings have been interpreted according to the potential evolutionary benefit that looming signals could provide, helping to create and maintain a margin of safety around the body (Ghazanfar et al., 2002). Along the same line, looming sounds have also been shown to enhance the activity of the amygdala (Bach et al., 2008). It was also demonstrated that the processing of looming signals is significantly and selectively facilitated when looming is signalled by both auditory and visual cues, both in humans (Cappe et al., 2009) and in non-human primates (Maier, Neuhoff, Logothetis, & Ghazanfar, 2004). Furthermore, it was shown that multisensory looming stimuli are preferentially integrated also in the brain: non-linear interactions begin earlier in response to them (Cappe, Thelen, Romei, Thut, & Murray, 2012) and fMRI responses to their presentation are enhanced both in low-level visual cortices and in the superior temporal sulcus (Tyll et al., 2013).

Some of the studies on looming perception, performed both with unimodal and multimodal stimuli, and conducted on human adults and infants and on non-human primates using either behavioural or imaging methods will be summarised in the following paragraphs.

2.1 HUMAN ADULTS

2.1.1 Unimodal (visual or auditory) looming stimuli

A few studies investigated the importance of visual motion direction and onset to attract attention. A series of studies by Franconeri and Simons (2003, 2005) and Abrams and Christ (2005, 2006) alternatively highlighted the importance of either of these two components to attract attention, operationally defined "as speeded search performance when an otherwise non-predictive stimulus happens to be the target of a visual search" (Franconeri & Simons, 2003, p. 999). A first study (Franconeri & Simons, 2003) tested how different types of motion captured attention, suggesting that some dynamic events (like looming) might be behaviourally more urgent than others and consequently receive processing priority when there are no competing goals (behavioural urgency hypothesis). The results showed that looming stimuli indeed captured the participants' attention more than receding ones, because of their major behavioural significance. This result was criticised by Abrams and Christ (2005), who suggested that the onset of motion, rather than motion per se, captures attention. They speculated that motion onset could be suggestive of the presence of a possible predator or prey and, thus, ethologically relevant. They also speculated that Franconeri and Simons' (2003) receding stimuli did not capture attention because they were shrinking and not really receding in depth. Their position was in turn criticised by Franconeri and Simons (2005), who highlighted that if their receding stimuli did not capture attention because they lacked translation, then their looming stimuli should not have either. If this were the case, it would mean that only certain types of motion onset capture attention (i.e. looming onset). In a second study, they also demonstrated that motion alone can capture attention also in absence of motion onset and speculated that, however, some kinds of dynamic motion might capture attention more strongly than others (Franconeri & Simons, 2005). This position was eventually acknowledged also by

Abrams and Christ (2006), who concluded that motion in absence of motion onset might capture attention under specific circumstances. Von Mühlenen and Lleras (2007) further investigated this issue and demonstrated that every kind of motion onset can attract attention when it is abrupt, whereas when random motion gradually shifts to an oriented flow, only looming motion captures attention, in accordance with the behavioural urgency hypothesis. More recently, also Rossini (2014) demonstrated that both looming and receding stimuli are capable of attracting attention, but only looming stimuli produced globally shorter reaction times (RTs) when the participants were required to discriminate a target. Hence, he suggested that looming motion is in itself effective in enhancing visual processes, supporting the role of movement direction in attracting attention.

With regards to the monitoring of the space surrounding the body, the auditory system has a number of advantages over the other sensory systems, which suggest that its primary function is being a warning system (Ferri, Tajadura-Jiménez, Väljamäe, Vastano, & Costantini, 2015). Audition, in fact, provides us with a continuous flow of information, also when the eyes are closed, and provides information also about events occurring outside the visual field; furthermore, it's a powerful change detector, capable of quickly orienting towards potential threats (Ferri et al., 2015). Several studies investigated adults' perception of auditory looming signals, showing the existence of attentional biases and perceptual asymmetries towards looming stimuli in the auditory domain. Rosenblum and colleagues investigated how listeners judged the time of arrival of an approaching sound (the recording of a moving car) (Rosenblum, Wuestefeld, & Saldaña, 1993). They demonstrated that listeners can make anticipatory judgments of the time of passage of an approaching car, highlighting that acoustic signals provide information specifying the time to arrival of a looming source. They also showed that the listeners tended to consistently underestimate the time of passage and suggested that this anticipatory tendency would well fit with the warning role of the auditory system, as in the real

world it would trigger the appropriate avoidance behaviour, ensuring the listener's safety (Rosenblum et al., 1993). The authors also explored the role of experience in this task (previous evidence – Schiff & Oldak, 1990 – indicated better auditory looming judgement accuracy in blind individuals) by providing feedback to their participants and showed that providing graphical feedback significantly improved judgement accuracy (Rosenblum et al., 1993). In 1998, Neuhoff showed that listeners overestimated the intensity change of looming (rising) compared to receding (falling) sounds, especially at the highest intensity levels. He referred this bias to the behavioural valence of rising intensity sounds, which could signal movement towards the organism: selectively directing the attention towards these sounds could provide adaptive advantages. He reported this bias for both vowel sounds and sinusoids, but not for white noise, probably in relation to dynamic localization priorities in a natural environment, where meaningful broadband noise is less commonly produced by single relevant sources (Neuhoff, 1998; 2001). Later on, he further investigated this attentional bias and showed that looming sounds are perceived to change more in loudness than equivalent receding sounds and to start and stop closer to the observer than equidistant falling ones (Neuhoff, 2001). This effect was true for vowel sounds, but not for white noise, and was accentuated for louder sounds. He suggested that the asymmetry in coding rising intensity sounds can be considered an adaptive mechanism providing warning of looming sound sources. In fact, it would be more critical to detect approaching sources, especially if closer to the body, to signal incoming threats to the organism so that it could adequately prepare for contact or increase its margin of safety (Neuhoff, 2001). Along the same line, Grassi and Darwin (2006) investigated whether the sounds' amplitude envelopes influenced the perceived duration of sounds lasting up to 1 sec. The authors extended the results of a previous study (Schlauch, Ries, & DiGiovanni, 2001), conducted with sounds of 200-msec duration, which showed that rising (ramped) sounds are perceived as lasting longer than falling (damped) sounds, highlighting their higher salience also

within a temporal perceptual dimension (Grassi & Darwin). In particular, Grassi and Darwin showed that the duration of ramped sounds was slightly underestimated (compared to steady sounds), whereas the duration of damped sounds was underestimated substantially and that this pattern could not be explained by mere sensory factors. They speculated that the underestimation could be due to the fact that listeners could possibly and involuntary exclude the tails of damped sounds from the computation of subjective duration, suggesting a role for cognitive factors in the reported bias.

Behavioural studies showed a perceptual and attentive bias towards looming auditory (rising-intensity) stimuli (Grassi & Darwin, 2006; Neuhoff, 1998; Neuhoff, 2001; Rosenblum et al., 1993). Seifritz and colleagues (2002) studied the neural basis of this bias using fMRI and showed that dynamic sounds activated the right temporal plane more than static ones and that rising, but not falling, sounds activated a distributed neural network responsible for auditory motion perception, space recognition and attention. They also confirmed previous behavioural findings on auditory motion perception, showing that changing intensity is a good indicator of a moving sound source and that rising sounds are perceived to change more in loudness than falling ones. Overall, their results highlighted that the prioritization of rising sounds is associated with a distributed brain network modulating those processes that would provide adaptive advantages (Seifritz et al.). Later on, Bach and colleagues (2008) further investigated this topic, examining the intrinsic (not learned) warning value of rising sounds with fMRI as well as physiological and behavioural responses. They hypothesised that an intrinsically warning stimulus would enhance preattentive processes, prepare for action, increase phasic alert, shift attentional resources toward the auditory modality, and activate a phasic alertness network in the right hemisphere and the amygdala, as detector of intrinsically relevant events in the environment (Bach et al.). They showed that the Skin Conductance Response (SCR) and the deceleration of the heart rate (HR) were enhanced for rising compared to falling intensity

sounds, as it happens for orienting reflexes and that the right amygdala activation was increased by rising sounds. Furthermore, they reported that rising sound intensity facilitated autonomic orienting responses and accelerated RTs to subsequent acoustic, but not visual, stimuli. Overall, they demonstrated that intensity change in an auditory stimulus was capable of activating the amygdala, triggering autonomic reactions and driving the allocation of attentional resources and therefore suggested that rising intensity could reasonably be considered as a simple and intrinsic auditory warning cue indicating relevant events in the environment (Bach et al.). Their results suggested that the activation of the amygdala, along with the right intraparietal sulcus, the posterior part of the left superior temporal sulcus (STS) and the left temporal plane, by rising sounds could be considered as the neural correlate of the behavioural and attentional biases related to looming sounds in both humans and monkeys.

The behavioural aspects and neural mechanisms of looming processing have been investigated also with respect to the emotional valence of looming visual stimuli (Vagnoni, Lourenco, & Longo, 2012, 2015). Vagnoni and colleagues investigated whether the affective value of a looming stimulus influenced its perceived time-to-contact (TTC) (Vagnoni et al., 2012). They presented their participants with threatening (snakes and spiders) and non-threatening (butterflies and rabbits) visual looming stimuli and showed that the TTC was underestimated for the threatening ones. Also, they found a relationship between the magnitude of this effect and the self-reported fear of the animals depicted by the stimuli (Fig. 2.1.1). Overall, they demonstrated that the perception of looming is affected by the semantic content of the stimuli (other than by purely optical cues) and, therefore, that emotion can shape basic aspects of visual processing (Vagnoni et al., 2012).

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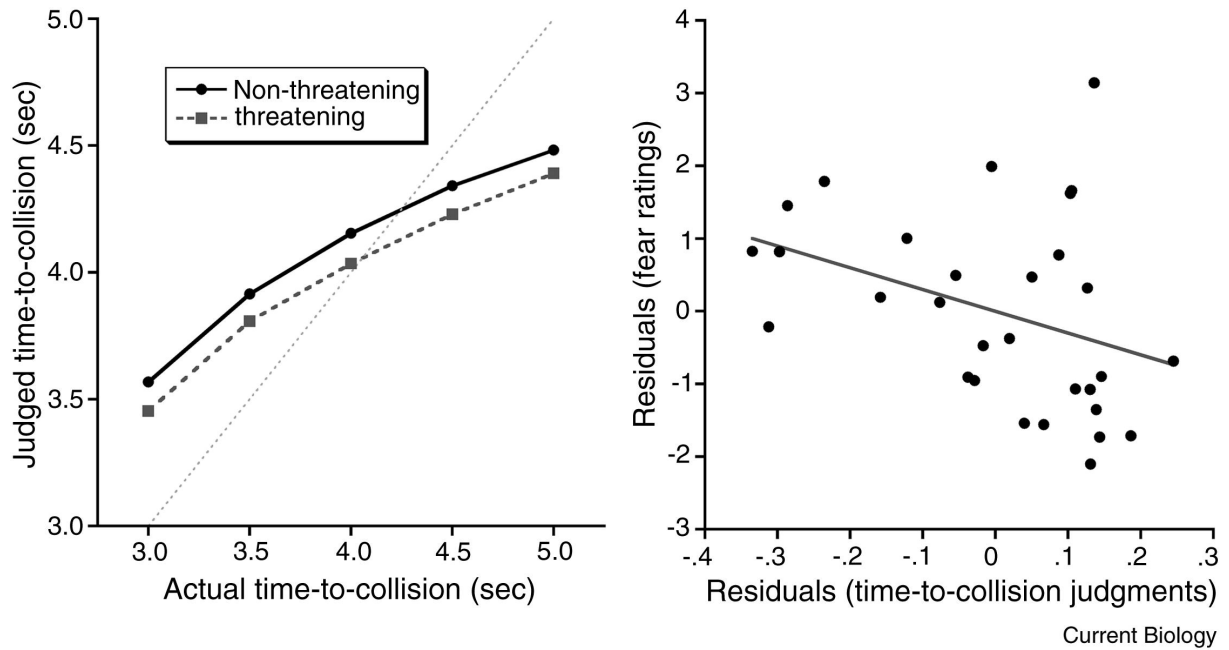
Figure 2.1.1 Experimental results (from Vagnoni et al., 2012).
Left panel: judged time-to-contact increased monotonically as a function of actual time-to-contact for non-threatening and threatening stimuli. The light grey dotted line indicates veridical judgments. There was a clear bias to underestimate time-to-contact for threatening compared to non-threatening stimuli.
Right panel: scatterplot showing relation of time-to-contact judgments and fear. These residuals were significantly negatively correlated, indicating that greater fear was associated with increased underestimation of time-to-contact.

Subsequently, the same authors measured visual-evoked potentials (VEPs) and oscillatory neural responses to threatening and non-threatening looming stimuli, in order to investigate the cortical mechanisms underlying this behavioural modulation. They found that the P1 was modulated by the affective content of the stimulus, showing a smaller amplitude for threatening stimuli (Vagnoni et al., 2015). This result is in line with other findings suggesting that positive and negative stimuli are discriminated by the brain since the earliest stages of processing and immediately receive different amounts of attention (Carretié, Hinojosa, Martín-Loeches, Mercado, & Tapia, 2004; Smith, Cacioffo, Larsen, & Chartrand, 2003). Nevertheless, the direction of the P1 modulation is less clear, with some findings suggesting larger amplitude for negative stimuli (Carrettié et al., 2004; Smith et al., 2003) and others for positive ones (Begleiter, Gross, & Kissin, 1967; Begleiter, Gross, Porjesz, & Kissin, 1969). They also reported effects of the emotional content of the stimuli on the early frontal N1 (decreased for threatening stimuli) and late occipital N1 (enhanced for negative content) and an effect of the speed of the

stimuli on the late parietal N1, whose amplitude increased as the speed did (Vagnoni et al., 2015). Moreover, threatening stimuli showed a less positive amplitude in the EPN (early posterior negativity) and a more positive amplitude in the LPP (late positive potential), two components thought to index the greater attention paid to emotional stimuli (Dolcos & Cabeza, 2002; Lang, Bradley, & Cuthbert, 1997; Olofsson, Nordin, Sequeira, & Polich, 2008; Schupp, Junghöfer, Weike, & Hamm, 2004; Schupp et al., 2000) (Fig. 2.1.2). Concerning stimulus-induced brain oscillations, they found more desynchronization in the alpha band during the presentation of threatening stimuli, as well as increased beta band desynchronization over posterior sites when the TTC decreased and greater desynchronization in the high gamma band over sensorimotor areas after the presentation of threatening stimuli (Vagnoni et al., 2015) (Fig. 2.1.3). Overall, their results suggested that both the speed and the affective value of the approaching stimulus modulated several aspects of the visual processing of looming stimuli, favouring an appropriate processing of threatening ones, in turn useful to engage in fast and adequate responses (Vagnoni et al., 2015).
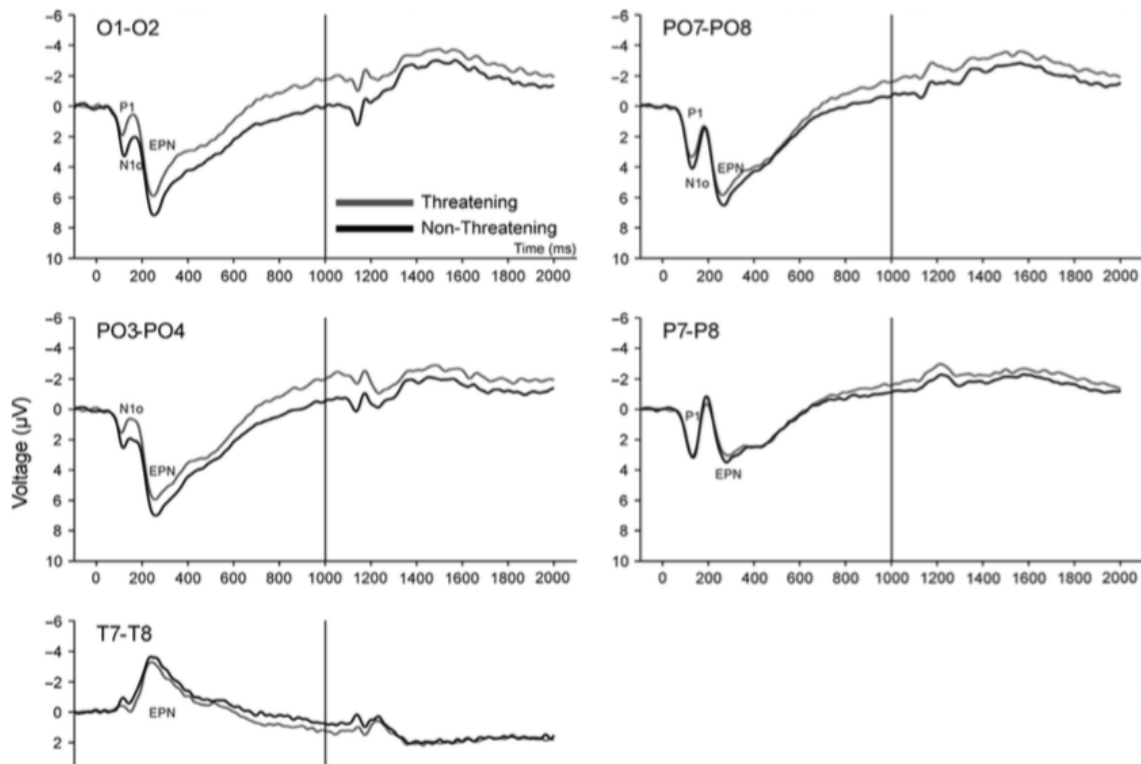
Figure 2.1.2 Averaged visual-evoked potential (VEP) waveforms at occipital (O1–O2), occipito-parietal (PO3–PO4; PO7–PO8), parietal (P7–P8) and temporal (T7– T8) electrodes (from Vagnoni et al., 2015). The earliest, positive, deflection is the P1, which is smaller for threatening vs. non-threatening stimuli. The difference is more marked on the occipital channels (O1–O2) relative to the occipito-parietal (PO7–PO8) channels. No difference was found on the parietal channels (P7–P8). The second, negative, deflection is the N1 occipital, which is less positive for threatening vs. non-threatening stimuli. The third one is the EPN, which is less positive for the threatening stimuli vs. non-threatening stimuli. The EPN is significantly less positive on all included channels apart from channels P7 and P8. These three components were clearly modulated by the emotional content of the stimuli. The black vertical line at 1000 ms represents the stimulus disappearance.
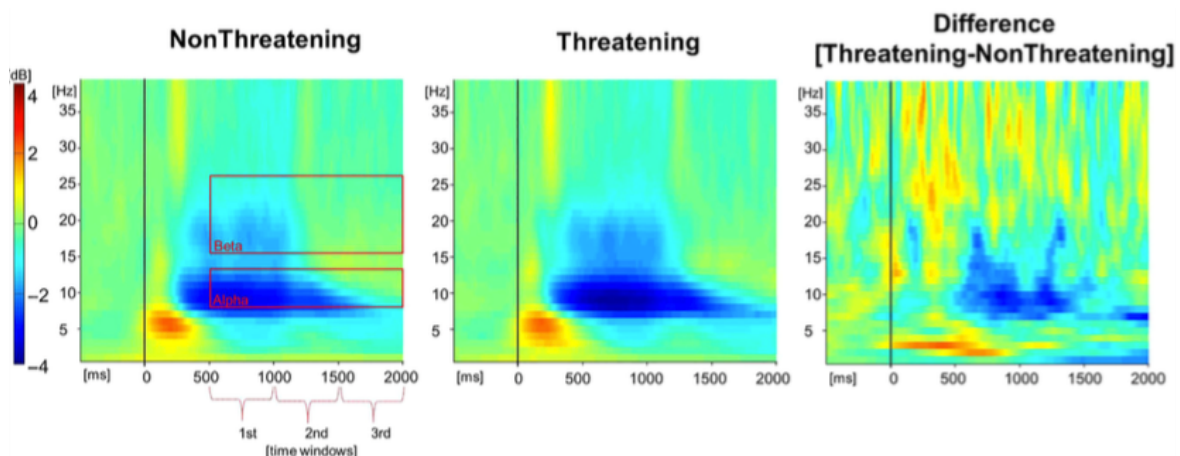
Figure 2.1.3 Brain oscillations in response to threatening and non-threatening stimuli (from Vagnoni et al., 2015). The colour maps represent the grand mean time–frequency representations of EEG spectral power over the occipito-parietal electrodes, during the three periods 500–1000 ms, 1000–1500 ms, 1500–2000 ms in the alpha (8–13 Hz) and beta (15–25 Hz) bands (The brackets specify the three different periods while the two red squares the frequency bands). Baseline-rescaled responses were averaged across all subjects. In the first panel the colour map on the left represents the grand mean for non-threatening stimuli, the second represents the grand mean for threatening stimuli, whereas the third one represents the grand mean of the difference between threatening and non-threatening stimuli.

Emotion involvement in looming perception was also investigated in relation to auditory stimuli, as salient events can evoke emotional responses that often elicit an automatic attentional shift towards these same events, modulating their perceptual processes (Tajadura-Jiménez, Väljamäe, & Vastfjall, 2008). To address this, the participants were presented with approaching or receding sounds followed by a photograph with a positive, negative or neutral valence and were asked to make a speeded forced choice judgement on their feeling when looking at the photograph. The authors measured the self–reported ratings, the RTs in making the same ratings, and the electrodermal activity (EDA) and the facial electromyography during the presentation of the sound. They hypothesised that a greater salience would evoke a greater increase in emotional arousal and, in turn, capture and hold attention. The results showed that the participants responded faster after being presented with a looming vs. receding sound and that this difference was more evident for negative vs. neutral photographs. Also, they were faster when presented with longer vs. shorter and with louder vs. softer sounds. Furthermore, the participants reported that approaching and longer and approaching and louder sounds were perceived as more unpleasant and arousing. Finally, approaching sounds led to a bigger activity of CS and ZM muscles and approaching longer and louder sounds showed a tendency to increase the EDA. Concluding, the authors highlighted that their data support the hypothesis of a greater biological salience of approaching sounds (Tajadura-Jiménez et al., 2008).

2.1.2 Multimodal looming stimuli

In 2009, Cappe, Thut, Romei and Murray investigated multisensory integration of visual and auditory looming and receding stimuli by humans, using movement detection and subjective ratings, and showed selective multisensory integration of looming stimuli. They investigated whether multisensory looming and/or receding signals are integrated to facilitate behaviour using a go/no-go motion detection paradigm with both unisensory (visual or

auditory) and multisensory stimuli. They measured the RTs for motion detection (irrespective of its direction and multisensory congruence) and subjective ratings of intensity and compared the performance between uni and multisensory conditions and across the multimodal ones, in order to investigate the existence and selectivity of any facilitative effects (Cappe et al.). They showed that the participants' RTs were significantly facilitated for multisensory compared to unisensory looming and receding stimuli (Redundant Signal Effect, RSE), granting evidence for multisensory integration of the audio-visual pairs of stimuli signalling motion in depth, irrespective of congruence (Fig. 2.1.4a). They also assessed, using Miller's race model inequality, whether the observed RSEs with RTs could be explained by probability summation or whether they were consistent with integrative processes. They demonstrated that all multimodal conditions exhibited facilitation in excess of probability summation, indicating that integrative processes contribute to the RSEs (Cappe et al.). Moreover, also the movement ratings were significantly higher for multisensory looming and receding stimuli, but only when the direction of visual and auditory stimuli was congruent. Furthermore, they demonstrated that the RTs were faster and the movement judgements higher for congruent audio-visual looming stimuli compared to all the other multisensory conditions, showing a selective facilitation of multisensory looming (Fig. 2.1.4b). Finally, they showed that the participants' RTs were significantly faster and movement ratings were reliably higher for audio-visual vs. unimodal (both visual and auditory) looming stimuli; conversely, the facilitation of the RTs and ratings for the receding multimodal stimuli were not significantly different from those measured when a receding visual stimulus was paired with a static auditory one. Overall, then, only for multisensory looming the performance was enhanced due to the presence of multisensory congruent movements and not simply due to multisensory stimulation. They discussed how their findings on the selective integration of multisensory looming could have implications on how multisensory integration principles are integrated with ethologically salient stimuli as

looming ones. They suggested that the conceptualization of the rules that govern multisensory integration should carefully consider the complexity of stimuli that vary in location (e.g. the "spatial rule" should be extended to include depth), dynamics, effectiveness and ethological value (Cappe et al.).
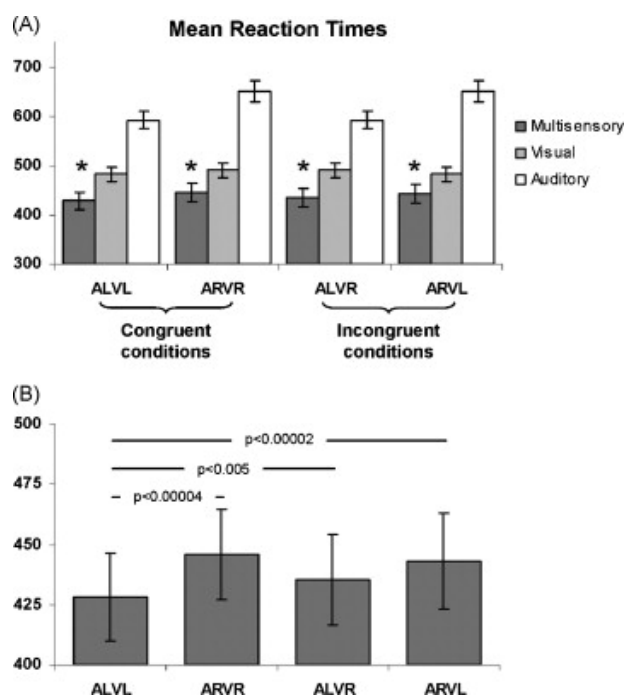
Figure 2.1.4 Multisensory facilitation of reaction times (from Cappe et al., 2009). Group-averaged reaction times (RTs) and S.E. are plotted for each experimental condition. (A) In all multisensory conditions reaction times were significantly faster than in either of the constituent unisensory conditions (asterisks). This was the case both when the movement direction was congruent or incongruent between the senses. (B) Direct comparison of RTs to multisensory conditions revealed that the performance with multisensory looming stimuli (ALVL) was selectively facilitated beyond that for other multisensory conditions.

In 2012, the same group of researchers investigated the neurophysiological underpinnings of the already demonstrated selective behavioural facilitation for multisensory looming stimuli (Cappe, Thelen, Romei, Thut, & Murray, 2012). They emphasised that determining how multisensory integration principles operate when the stimuli show dynamic variations should help understand the relationship between the same principles and higher-order signals used for communication and motor planning. They suggested that multisensory

looming stimuli are ideal to investigate these relationships as they integrate covariance of information in space (depth specifically), time and effectiveness and, at the same time, could signal either a threat or the successful acquisition of a goal or object. They used the same go/no-go task described in a previous study of their group (Cappe, Romei, Thut, & Murray, 2009), which investigated the existence of a behavioural facilitation for multisensory vs. unisensory looming or receding stimuli, and recorded continuous EEG on 160 channels. Their study provided the first demonstration that the human brain preferentially integrates multimodal stimuli: the authors provided evidence for selective superadditive interactions of responses to audio-visual (AV) looming stimuli during early post-stimulus onset periods. Concerning the timing of non-linear, multisensory interactions, they showed that they began earlier for congruent AV looming than for congruent AV receding or incongruent conditions (Fig. 2.1.5).
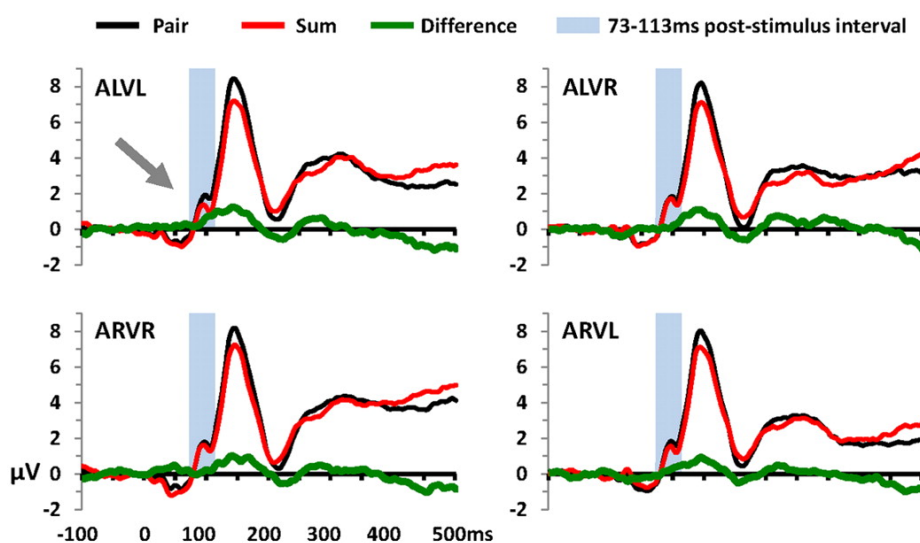
Figure 2.1.5 Group-averaged voltage waveforms and ERP voltage waveforms analyses (from Cappe et al., 2012). Data are displayed at a midline occipital electrode site (Oz) for the response to the multisensory pair (black traces), summed unisensory responses (red traces), and their difference (green traces). The arrow indicates the modulations evident for the multisensory looming conditions that were not apparent for any other multisensory combination over the ~70–115 ms post stimulus interval.

With respects to source estimation, instead, they described subadditive effects for multisensory looming conditions in the right claustrum and insula, the interior inferior temporal lobe and amygdala and the bilateral cuneus. In particular, they highlighted that the effects within the

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claustrum/insula were limited to multisensory looming conditions, showing a particular sensitivity to them and/or suggesting their own involvement in the processing of motion direction and multisensory congruence. Taken together, these findings suggested that multisensory interactions can facilitate the perception and processing of adaptively salient stimuli as those approaching the observer along a colliding pathway and highlighted the behavioural relevance of early and low-level multisensory interactions in humans (Cappe et al., 2012).

In order to explore the link between multisensory interaction mechanisms and human behaviour, Romei and colleagues tested whether the visual cortex excitability would be selectively modulated by looming sounds (Romei, Murray, Cappe, & Thut, 2009). The authors presented their participants with static, rising and falling sounds or noise while applying transcranial magnetic stimulation (TMS) over the occipital pole and quantified the amount of TMS-induced visual perceptions (phosphenes). They showed that only looming sounds significantly enhanced the visual cortex excitability and that this modulation started from very short sound durations (80ms), significantly below the perceptual discrimination threshold, providing the first evidence of stimulus-selective crossmodal interactions in the low level visual cortex. They concluded, then, that "visual perceptions are rapidly and efficiently boosted by sounds through early, preperceptual and stimulus-sensitive modulation of neuronal excitability within low-level visual cortex" (Romei et al., p. 1799). The early crossmodal effects triggered by looming sounds on the low-level visual cortices were investigated also by a case study on a patient with bilateral occipital lesion and spared residual portions of V1 and V2 (Cecere, Romei, Bertini, & Làdavas, 2014). The authors tested the effects of static, looming and receding sounds on line orientation discrimination and visual detection abilities in the preserved and blind portions of his visual field. They found that line orientation was significantly improved when the patient was presented with looming sounds, but only for lines presented in the partially

preserved visual field; conversely, in the visual detection experiment they showed that sounds induced a generalised improvement in both the intact and blind portions of the visual field. Their results provided evidence of the involvement of primary visual cortices in early crossmodal modulation of visual orientation sensitivity by looming sounds, but not of basic visual abilities such as detection, which could be mediated by alternative visual pathways bypassing V1(Cecere et al., 2014). The same improvement of orientation discrimination in presence of looming sounds had been reported by a previous behavioural study (Leo, Romei, Freeman, Làdavas, & Driver, 2011) on healthy participants, which however could not rule out the possible role of subcortical multisensory structures or higher associative cortices.

The neural network underlying multisensory looming processing was recently investigated using fMRI (Tyll et al., 2013). The authors analysed the brain activity during the processing of uni or multimodal looming or receding stimuli that required the participants' attention, but not their motor responses. Their results highlighted enhanced fMRI-responses to audio-visual looming (compared to receding) signals in low-level visual and auditory areas and in the multisensory cortex, namely within the superior temporal sulcus (STS) as well as parietal and frontal structures. With regards to the multisensory response profiles within these looming sensitive areas, they found multisensory responses larger than the mean of unisensory ones in almost all the areas, larger than the maximum of the unisensory responses in the left STS, in parts of the bilateral auditory regions and occipital cluster and superadditive responses (i.e. responses larger than the sum of the unisensory ones) in the left calcarine gyrus and the left superior parietal lobe. The authors speculated that the selective enhancement of neural signalling for looming multimodal stimuli could be considered as a mechanism capable of informing humans about possible dangers in the environment and, in turn, allowing them to avoid potential collisions or threats (Tyll et al., 2013).

The subjective duration of audio-visual looming stimuli was also investigated, following up on the previous findings about the difference in the perceived duration of looming vs. receding visual and auditory unimodal stimuli (Grassi & Pavan, 2012). The authors asked their participants to estimate the subjective duration of looming, receding and stationary auditory, visual and audio-visual stimuli. They calculated a direct estimate of each participant's point of subjective equality and showed that the subjective duration of receding sounds was shorter than that of looming sounds, but that there was no asymmetry in the perceived duration of visual looming and receding stimuli and that the result for audio-visual stimuli was intermediate between those of the auditory and visual ones. However, the amount of difference in the subjective duration of looming and receding stimuli seemed to vary according to the real duration of the stimuli, creating a possible confound. A further experiment was run in order to disentangle the role of duration and speed of the moving stimuli and showed that the temporal asymmetry in audition and audio-vision decreased with increasing durations and increased with increasing simulated speeds. The authors suggested that their results support a model proposed by Ernst and Banks (2002) that predicts that audio-visual estimates of duration should be driven by audition, as it is generally better than vision at estimating duration itself (Grassi & Pavan, 2012). Finally, the authors speculated that the overestimation of looming stimuli might be advantageous in audition, but not in vision: they suggested that whereas audition is a reliable alerting sense that can inform us about events that are not visible, an overestimation of looming by vision might become disadvantageous. In fact, according to them vision requires a more veridical representation of the world, because visual looming stimuli could arise from the motion of an object towards the observer or of the observer towards a still object and hence, a distorted perception of looming duration may lead to wrong time-to-contact estimates. Finally, they suggested an alternative explanation of the looming-receding asymmetry, hypothesising that "it is not looming that is special, but receding to be negligible" (Grassi & Pavan, 2012, p. 1331) and

supported it highlighting that the duration of the looming stimulus was not overestimated in comparison to the duration of the stationary one and that the asymmetry arose mainly from the underestimation of the duration of the receding stimulus (Grassi & Pavan, 2012).

2.2 Non-Human Primates

2.2.1 Behavioural studies

Schiff and colleagues investigated responses to visual looming in infant and adult rhesus monkeys, with the aim of discovering which visual stimuli signalling biologically salient situations are sufficient for triggering avoidance and escape responses during different stages of development (Schiff, Caviness, & Gibson, 1962). They presented their subjects (eight 5- to 8-month-old monkeys and 15 adolescent or adult ones) with the expanding or contracting shadow of a rubber ball that moved along a track perpendicular to the screen. Two hidden observers judged the behaviour or the animals, scoring several categories of response. They found that the vast majority of both infant and adult animals withdrew abruptly or "ducked" in response to the looming stimulus and that these behaviours were sometimes accompanied by alarm calls in the younger animals (Schiff et al., 1962). Also, the animals did not show any evidence of habituation when presented with series of looming stimuli. On the contrary, the contracting stimuli did trigger exploratory responses in most animals. The authors speculated that the similarity between infants' and adults' behaviour suggests that the role of past experience of collisions helps discriminating them already at the earliest stages of development (Schiff et al., 1962).

Vision, despite being really important in notifying incoming danger, may be sometimes ineffective, especially if looming objects are out of sight. Most animals evolved parallel auditory warning systems able to provide information about hidden incoming objects that could be dangerous (Ghazanfar, Neuhoff, & Logothetis, 2002). Ghazanfar and colleagues (2002) investigated whether non-human primates showed a bias towards auditory looming stimuli and whether this possible bias was dependent on the sound spectrum. They measured head rotation responses to unseen sound sources, expecting longer orienting responses to rising intensity

sounds if they were a salient environmental signal capable of indicating a looming source. The results confirmed their prediction, showing that their subjects oriented for longer periods of time after rising tones (but not white noise), suggesting that these are more salient than equivalent falling ones. The authors then concluded that rhesus monkeys, as well as humans, show an adaptive bias for perceiving biologically relevant sounds, like looming ones (Ghazanfar et al.).

Maier and colleagues investigated multisensory integration of looming and receding audio-visual stimuli in rhesus monkeys, using a preferential looking paradigm (Maier, Neuhoff, Logothetis, & Ghazanfar, 2004). They presented the monkeys with videos of a rapidly expanding (looming) or contracting (receding) disc matched to either a rising (looming) or falling (receding) intensity complex tone and measured their looking behaviour. They chose to present artificial stimuli in order to exclude any prior experiences of the subjects, as they were also interested in understanding whether any possible multisensory integration ability was experience dependent. When presented with a rising sound, the subjects looked longer to the matching, looming video; conversely, when presented with a falling sound, they did not show any visual preference. The preference shown by monkeys when presented with the rising sound could be due to a preference for visual looming stimuli, independent of the sound; however, if this were the case, the same pattern of looking times should be found when the falling sound was played. On the contrary, if the sound had an influence on looming perception, when presented with a falling sound the subjects should either look longer to the congruent, receding movie or show no visual preference at all, as it happened. Only the presence of a looming complex sound, then, biased the rhesus monkeys looking behaviour towards the congruent video display, demonstrating their ability to integrate multisensory information about looming, but not receding, audio-visual signals (Maier et al., 2004). The authors speculated that their monkey subjects made an arbitrary association between the rising sound and the looming visual

stimulus due to their immediate salience and that they were therefore able to extract relevant looming cues irrespectively of their arbitrary features (Maier et al., 2004).

2.2.2 Imaging studies

Maier and Ghazanfar (2007) recorded the local field potential (LFP) and the multiunit spiking activity (MUA) in the lateral belt auditory cortex of rhesus monkeys presented with auditory looming and receding signals. They presented two rhesus monkeys with samples of rising and falling intensity sounds: dynamic intensity change is considered the most effective cue for detecting the motion of a sound source in depth (Rosenblum, Carello, & Pastore, 1987), as intensity at the ears rises or falls when a sound source approaches or recedes. They showed that the magnitude of the activity in the auditory cortex was bigger for looming compared to receding stimuli, suggesting an important role of the lateral belt auditory cortex in the neural network supporting looming perception and responses to warning cues (Maier & Ghazanfar). In particular, they found a sustained increase in gamma-band power (45-90 Hz) in response to looming stimuli, but not to receding ones. This pattern was observed both in single cortical sites and across a population of 50 cortical sites. Also MUA responses recorded from an unbiased sample of cortical sites showed the same pattern (Fig. 2.2.1). In order to control for the possibility that the reported differences in activity were due to adaptation to the receding sounds (whose intensity fades progressively out) the authors repeated the experiment using white noise stimuli with identical characteristics, which did not elicit behavioural perceptual biases. This control condition did not reveal any differences in response to looming vs. receding stimuli and thus confirmed that the already hypothesised asymmetry in auditory cortical activity was specifically dependent on the direction of intensity change of complex, structured – and therefore naturalistic – sounds (Maier & Ghazanfar).
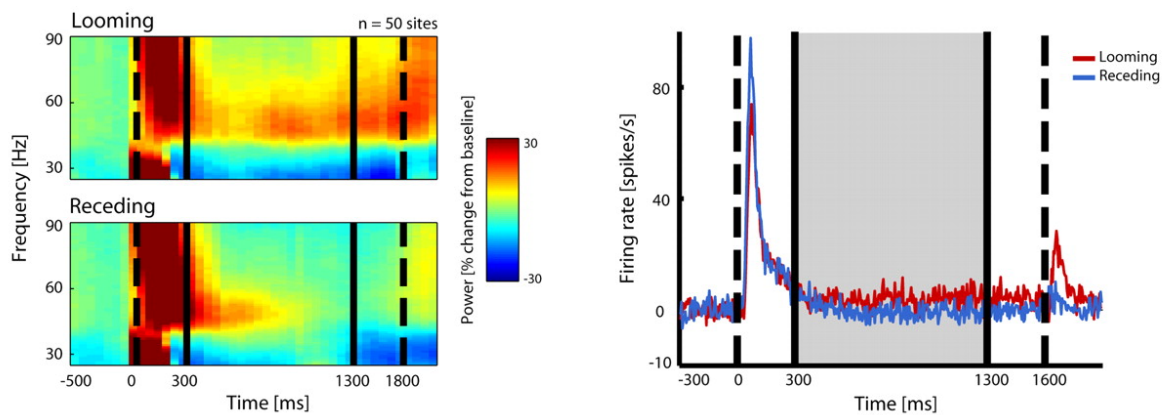
Figure 2.2.1 Experimental results (from Maier & Ghazanfar, 2007).
Left panel: Population LFP spectrograms in response to looming and receding stimuli (complex tone condition), normalized to baseline, averaged across 50 cortical sites.
Right panel: Population multiunit activity (MUA), normalized to baseline, averaged over 50 cortical sites in response to looming (red) and receding (blue) stimuli.

Maier, Chandrasekaran and Ghazanfar (2008) further investigated the neural correlates of looming perception in rhesus monkeys, studying the integration of bimodal looming signals in the temporal lobe. Integration across sensory systems has several behavioural advantages and requires, at the neural level, fast and flexible interaction between different brain regions, each conveying information from a different sensory modality. The authors investigated the role of the intercortical synchronization of neuronal activity in the auditory cortex and in the superior temporal sulcus (STS), recording LFP activity while rhesus monkeys were attending visual, auditory and audio-visual (congruent or incongruent) looming and receding stimuli. They found a sustained increase of oscillatory activity (most pronounced in the gamma frequency range) for looming stimuli, which probably reflects their greater behavioural relevance. Auditory looming signals elicited an increase in the auditory cortex activity, whereas visual ones in the activity of the STS (Fig. 2.2.2). Multimodal stimulation did not lead to different modulation compared to unimodal stimulation: also in multimodal situations, sustained activity was modulated by auditory looming signals in the auditory cortex and by visual looming stimuli in the STS. However, within single trials the authors observed multiple periods of highly correlated gamma activity in the two areas (Fig 2.2.3). They measured the strength of these correlations measuring

coherence and showed that it was significantly increased by congruent AV looming stimuli and that the observed increases were at least partially independent from power changes in the two areas. They suggested that neuronal coherence might help establish fast and selective functional connections between those populations of neurons that represent signals from different sensory modalities, which in turn might result in ameliorated behavioural responses to looming stimuli (Maier et al.).
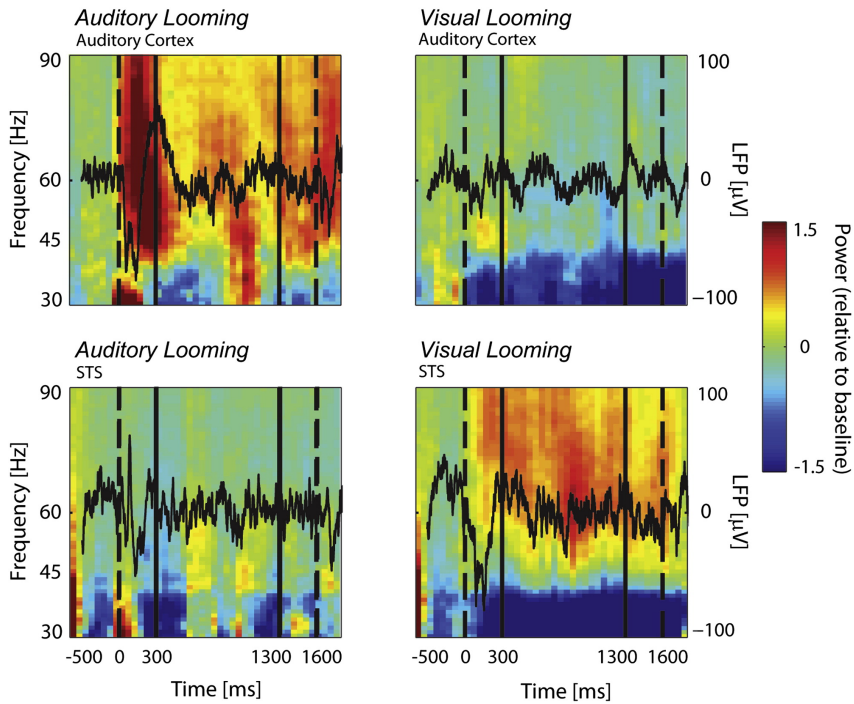
Figure 2.2.2 Looming Signals Evoke Sustained Oscillatory Activity in the Gamma Band in Auditory Cortex and the STS (from Maier et al., 2008). Time-amplitude representation of raw LFP signals (black traces), overlaid on corresponding spectrograms, simultaneously recorded from example cortical sites in auditory cortex and the STS, in response to auditory and visual looming stimuli. Traces and spectrograms represent the mean response over 32 trials per condition.
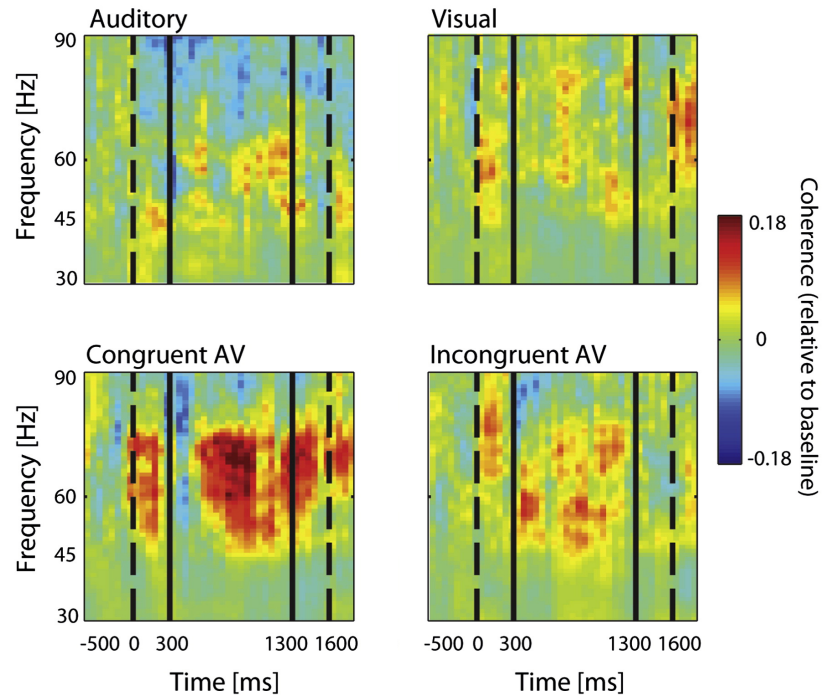
Figure 2.2.3 Gamma-band coherence is selectively increased during congruent auditory-visual stimulation (from Maier et al., 2008). Coherence, relative to baseline, between LFP signals recorded from one example pair of cortical sites in auditory cortex and the STS, in the auditory, visual, congruent AV, and incongruent AV conditions. Coherograms represent the mean across 32 trials per condition.

2.3 INFANTS

Research in infancy focused mostly on visual looming and, in particular, on infants' sensitivity to impending collision trajectories, investigated through the analyses of defensive reactions.

In 1970, Bower, Broughton and Moore investigated the responses of infants aged 6 days and over to approaching objects of high ecological validity, whose motion produces complex visual changes along with air pressure changes. A first experiment focused on discovering newborns' responses to approaching objects and led to the identification of an adaptive response comprising three components, namely "1) eyes wide open; 2) head goes back; 3) both hands come up between object and face" (Bower et al., p. 193). The authors also noticed occasional blinking after this response, but they did not consider it as an integral part of the same response and instead linked it to the process of recovering from that response itself. However, they found such a complete response only when the newborns were in a very specific position and acknowledge that, depending on the position of the participant, components 2 and 3 could be prevented from happening. In a second experiment the authors investigated if this response was modulated by the perceived distance of the approaching object, but had to renounce because of the violent upset that a near approaching object caused in their participants. Two further experiments were conducted in order to disentangle the relative contributions of visual changes and air pressure. Eight out of 9 infants showed partial avoidance responses when presented with the reduced visual presentation of the looming stimuli (i.e. they were presented with a projected expanding pattern, so they could see the object moving, but were prevented from feeling the air pressure change). Newborns' responses in this condition were described as less intense than in the first experiment and the authors suggested that this might have been due to the absence of air pressure changes. In their last experiment, they investigated the responses of 4 newborns to an increase of air pressure and found a response which was almost the opposite of the one

recorded so far (Bower et al.). They discussed that their data show that neonates display a functionally appropriate avoidance response to approaching objects, which is controlled by visual changes alone. One year later, Ball and Tronick (1971) followed up on Bower and colleagues' results and investigated how infants (2- to 11-week-old) responded to symmetrically expanding shadows, optically specifying an approaching object, asymmetrically expanding shadows, signalling approach on a miss path, or contracting shadows, signalling a receding object. They showed that infants moved their head back and brought their arms towards their faces during the hit sequences, turned their heads or eyes along the path of the shadow in the miss sequences and showed no response during the recession ones. They reported the difference in head movement (backwards vs. tracking) to be statistically significant and concluded that their data support the idea that infants can detect the direction of both real moving objects and their optical equivalents (Ball & Tronick).

However, Yonas and colleagues suggested that the abovementioned adaptive responses – considered defensive by the authors – could instead be part of a tracking process (Yonas et al., 1977). Yonas and colleagues highlighted that adaptive, defensive reactions – like eye-blinks – are expected to happen when an observer perceives an object rapidly approaching and reported previous findings placing the onset of blinking responses to real approaching objects either around 2 or between 2 and 4 months of life (Yonas et al.). The authors underlined the contrast between these results and those obtained by Bower and colleagues (1970) and by Ball and Tronick (1971), which suggested that younger infants could show defensive or avoidant responses other than an eye blink. They suggested that – apart from the equivocal violent upset sometimes reported – the postural changes reported by them could be considered of a tracking – rather than defensive – nature (e.g. eye widening). In order to test their hypothesis, the authors ran three experiments aiming at studying the development of sensitivity to information specifying impending collision and at investigating the nature of the postural responses

previously reported. In the first study, they presented infants aged from 1 to 9 months with three shadow projections: a symmetrically expanding display signalling collision, an asymmetrically expanding display specifying an object moving on a miss path and a non-expanding, rising contour display. Blinking was recorded in response to the 42% of colliding trials in 8- to 9-month-old infants and less frequently in response to miss and contour conditions; the same pattern of results occurred in 4- to 6-month-olds (20% of colliding trials), but not in the younger participants: infants aged between 1 and 2 months of life blinked rarely and with a similar frequency across conditions. In infants aged between 1 and 4 months, upward arm movement occurred in all three conditions, with no significant differences; in infants aged between 8 and 9 months, it occurred more often in the collision condition and the performed movement appeared as a reaching attempt. All three groups of infants showed head rotation in all three conditions, especially in the contour one: the higher occurrence of head rotation in the contour condition suggested that this response may not be considered as an avoiding or defensive behaviour. Head withdrawal occurred as well in all three conditions, in the older group slightly more in the collision one, whereas in the two younger groups it was more pronounced in the contour condition; in any case, though, the differences were not big enough to reach statistical significance. Tracking – defined as "a slow rotation of the head and eyes which followed the expanding contour of the display during at least half of the stimulus motion" (Yonas et al., 1977, p. 100) – was greater in the miss than the colliding condition and in the two older groups it was also greater for the contour than the collision condition. Fussing and vocalization were both really rare. The authors discussed how their findings indicate an extended developmental course of the avoidance response to impending collision, which is absent from 1 to 2 months after birth, begins to emerge between 4 and 6 months of life and is present at 8 and 9 months of age. They also suggested that as in the group of younger infants the head rotation was the only response being greater in the contour vs. collision and in the collision vs. miss comparisons, it should be

more correctly attributed to tracking rather than self-defence. A second experiment investigated this specific issue, trying to disentangle whether head rotation was due to tracking or avoidance. A group of young infants was presented with looming (colliding and non-colliding) stimuli, whose top contour stayed at the eye level throughout the trial. The authors hypothesised that head rotation could be interpreted as a defensive response only if it occurred also in this situation. Head rotation was similar between the hit and miss conditions in this experiment, further suggesting that it should be considered as part of an orienting, but not avoiding, response. The only difference in the two conditions was a greater amount of tracking in the miss vs. hit conditions. Again, no avoidance responses were detected, despite the speed of the looming object was slower than in the previous experiment. Finally, a third experiment investigated whether presenting a real looming object – instead of an expanding visual pattern – could be more effective in eliciting an avoiding behaviour in young infants. Once again, the only difference between the hit and miss conditions was in the amount of tracking, being major for the miss condition. The authors concluded that these findings show – in disagreement with previous studies – that young infants are not sensitive to information specifying impending collision until at least 4 months of age, as they do not respond to it with appropriate defensive or avoiding behaviours, which undergo an extended development (Yonas et al.).

Since then, several studies further researched sensitivity to impending collision information investigating defensive reactions to that which was considered a dangerous or threatening stimulus, interpreting the absence of avoiding behaviours as a lack of ability to distinguish impending collision information itself. Náñez (1988) further investigated the ability of distinguishing between presence and absence of impending collision in 3- to 6-weeks-old infants, again measuring their defensive behaviours (in particular blinking and backward head rotation). In a first study, the author presented the infants with the symmetrical expansion or contraction of a silhouette on a screen, at different speeds, and found a higher rate of blinking

on the looming vs. receding trials, in both speed conditions, particularly at the end of the trial, when the information for collision was maximal. Also backwards head movements seemed to be more frequent at the end of expansion trials. These results showed that infants' visual system is flexible and capable of processing optical events irrespective of their speed. A second study investigated whether the same responses would appear when the looming shadow was lighter than the background and showed no significant differences between expanding and contracting conditions in terms of blinking or backward head movements. The author attributed this result to the fact that infants interpreted the expanding light object as an expanding aperture and hence not as a threat. A final study had the aim of understanding whether the responses reported in the first experiment could be labelled as defensive, investigating if they could be elicited by a simple and instantaneous changes in the screen illumination. He reported that a sudden change of the screen illumination triggered the same number of blinks regardless of the direction of the change (light to dark or vice-versa) and that the rate of blinking was significantly higher in the first compared to the third experiment. Náñez concluded that his results provided strong evidence in favour of an earlier sensitivity for impending collision, if high-contrast visual information is provided and defensive reactions are measured. He reported, in fact, that the percentage of blinking found in his studies was significantly higher than that found by previous studies (Yonas, Pettersen, & Lockman, 1979) because the latter failed to maximise the contrast between the shadow and the background in their stimuli (Náñez, 1988).

More recent studies investigated the timing strategies of defensive blinking in infants, identifying a shift from an angle based to a more sophisticated time based strategy around 6 months of age (Kayed & van der Meer, 2000, 2007). The authors reviewed previous literature on the perception of looming stimuli and highlighted how blinking reactions are considered to be the more appropriate defensive reactions to expanding stimuli and the best indicators of awareness of the collision course of a stimulus in early infancy (Kayed & van der Meer, 2000;

Yonas, 1981). They also reported that previous findings consistently reveal the absence of defensive blinking in the first weeks of life and, hence, the absence of sensitivity for impending collision.

A study from Schmuckler and colleagues investigated how the path of approach and the type of imminent contact, i.e. a hit versus a miss, influenced infants' perception of looming (Schmuckler, Collimore, & Dannemiller, 2007). The authors highlighted the critical role, for survival, of perceiving kinetic information arising from the motion of objects in depth and reported once again that previous research demonstrated that young infants showed sensitivity to looming information displaying avoidance responses or defensive behaviours (such as blinking) (Schmuckler et al., 2007). Their research took the move from Yonas and colleagues' (1977) findings showing that infants older than 4 months responded more to symmetrical expansion (hit path) vs. asymmetrical expansion (miss path). Schmuckler and colleagues (2007) criticised the terminology used by this study, suggesting that an asymmetrical expansion does not necessarily refer to an approach along a miss path: if an object is approaching from the side, in fact, it could as well move along a trajectory targeting the infant face. They speculated that it is unclear whether the decreased reactions reported by Yonas and colleagues (1977) should be attributed to the nature of the imminent contact (hit vs. miss), the path of approach (front vs. side) or both and, therefore, they ran a further study to disentangle between these hypotheses. They presented 4- to 5-month-old infants with the motion of a real object (air pressure changes were blocked by a barrier positioned between the infant and the approaching object) and coded their eye blinks in response to the looming stimuli. The object could either approach the infant or withdraw, either from the centre or the side and move either along a hit or a miss path (Fig. 2.3.1).
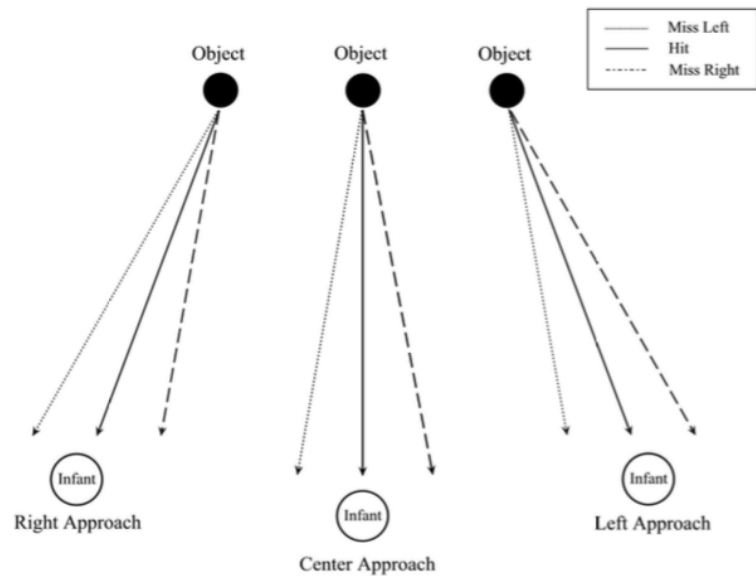
Figure 2.3.1 Schematic representation of the path of approach and type of contact variables (from Schmuckler et al., 2007).

The results highlighted that infants blinked significantly more in response to approaching vs. withdrawing motion and that, among approaching trials, movements approaching from the centre tended to trigger more blinks, especially if signalling a hit. Among trials showing an approach from the side, the frequency of blinks seemed to depend on whether the object crossed in front of the infant or not, with crossed misses producing greater responses than hits and uncrossed misses (Fig. 2.3.2). The authors discussed their results highlighting that infants aged between 4 and 5 months responded more strongly to objects expanding symmetrically from the centre (and hence moving along a hit path) compared to all other paths and types of contact and that asymmetrical non-collisions elicited more blinking than asymmetrical collisions if the looming object crossed the line of sight (Schmuckler et al.). They speculated that the latter, unexpected result implies that "infants cannot discriminate asymmetrical hits from asymmetrical misses" and that "true discrimination of hits vs. misses needs to be indicated by symmetrical vs. asymmetrical expansions" (Schmuckler et al., p. 113). The authors suggested that the most likely explanation for this result is the possibility that infants underperceived the absolute distance or size of the object (if they used monocular information rather than

binocular), yet acknowledging that it might be also due to some potential limitations of the study (e.g. head orientation).
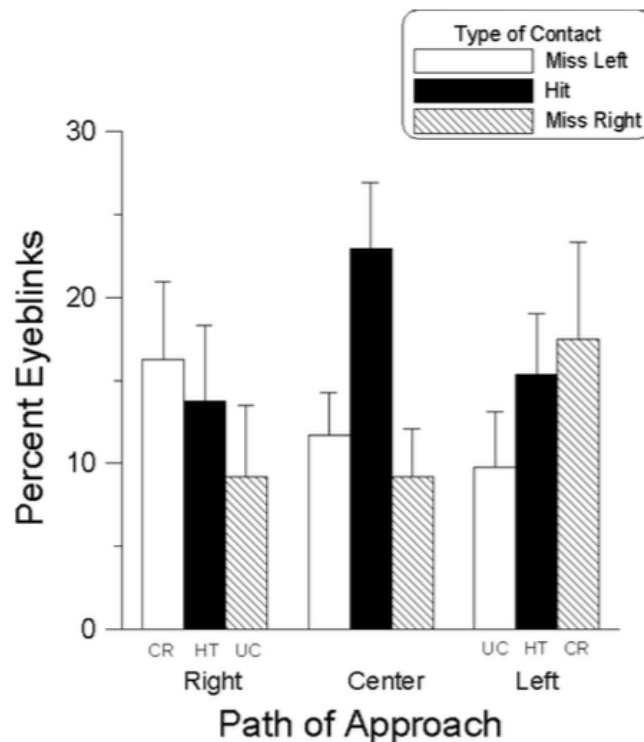
Figure 2.3.2 Experimental results (from Schmuckler et al., 2007). Percent eye blinking for approach trials, as a function of the path of approach and type of contact variables. "CR" refers to crossed misses, "HT" refers to hits, and "UC" refers to uncrossed misses, respectively.

Infants' integration of multisensory information specifying distance and direction of movement was also investigated (Walker-Andrews & Lennon, 1985). In a first experiment, 5-month-old infants saw a filmed event depicting a car either approaching or driving away, paired with a soundtrack with congruent or incongruent direction. The different events were presented successively and the looking times were recorded. The authors hypothesised that – if infants could detect the invariant relationship between sight and sound, they should look longer to the congruent audio-visual presentation. The results highlighted a comparable amount of looking times across conditions. In a second experiment, the two films were presented simultaneously, side-by-side (paired preference technique), paired once with one soundtrack and another time with the other one. This time, the results showed a visual preference for the movie depicting the

same direction of the sound played: the approaching movie was attended significantly longer when paired with a rising sound and the receding film when paired with the falling sound. However, within sessions, the proportion of looking time to the sound matching film was significantly longer than the proportion of looking time to the unmatched film only when the approaching soundtrack was presented. Moreover, the preferential looking seemed to be completely dependent on sound manipulation: the average of the proportions of looking time to each film in the two sound conditions did not differ from each other (Walker-Andrews & Lennon, 1985). These data demonstrated 5-month-old infants' ability to detect the spatial invariants of audio-visual stimulation depicting information on the direction of a movement, at least in a paired preference paradigm.

Table 2.3.1 Looming research in infancy. The table summarises data about the participants, aim, stimuli and variables investigated in the studies described in Ch. 2.3. The studies are reported in the same order as they are described through the text.

Year	1st Author		Participants		Aim	Stimuli	Dependent Variables
			N	Age			
1970	Bower	Exp 1	21	6-20 days	Discovering what infants do when objects approach them	Variety of moving objects	Infants' posture and movement
		Exp 2	5	8-17 days	Investigating the relationship between "nearness" of the approach and response	Foam-rubber cubes (different sizes) moving along a wooden table	Infants' posture and movement
		Exp 3	9	10-20 days	Disentangle the relative contribution of visual changes	Expansion pattern projected onto a screen	Infants' posture and movement
		Exp 4	4		Disentangle the relative contribution of air-pressure changes	Air pressure	Infants' posture and movement
1971	Ball	Exp 1	24	2-11 weeks	Further specifying infants' perceptual capacities when presented with approaching objects	Symmetrically or asymmetrically expanding or contracting shadows (cube, 5x5x5 cm) (12 cm/s)	Head backward, arms upwards, head tracking, fussing
		Exp 2	7	3-6 weeks	Further specifying infants' perceptual capacities when presented with approaching objects	Approach of a real object on a hit or miss path (30x30x5cm) (17 cm/s)	Head backward, arms upwards, head tracking, fussing
1977	Yonas	Exp 1	93	1-9 months	Studying how responses to information for impending collision change with age	Shadow of a diamond (6.5 x 6.5 cm) moving (17.3 cm/s) on a hit, miss or receding path	blinking, upward arm movement, head rotation, head withdrawal, tracking, fussing and heart rate
		Exp 2	18	28-57 days	Investigating the nature (tracking vs. avoidance) of head rotation observed in young infants in experiment 1	Optical expansion pattern (inverted triangle, 7 x 10 x 7 cm) which top contour stayed at eye level throughout the trial	blinking, upward arm movement, head rotation, head withdrawal, tracking, fussing and heart rate
		Exp 3	28	1-2 months	Investigating young infants' sensitivity to the impeding collision of a real object	Foam square (28x28x3.2 cm) moving towards the infant (on a hit or miss path) at a rate of 18.2 cm/s	blinking, upward arm movement, head rotation, head withdrawal, tracking, fussing and heart rate

Year	1st Author		Participants		Aim	Stimuli	Dependent Variables
			N	*Age*			
1988	*Náñez*	Exp 1	40	3-6 weeks	Testing Bower and colleagues' (1970) hypothesis that infants are inefficient processors of rapidly occurring events	Looms and zooms of a rear-projected diamond shaped silhouette (7x7 cm) moving at either 48 cm/s or 6 cm/s	Blink and backward head movement
		Exp 2	20	3-6 weeks	Investigating if infants distinguish between stimuli representing an approaching solid object vs. approaching large aperture	Approach or withdrew of a 7x7 cm diamond-shaped aperture (moving at 6 cm/s)	Blink and backward head movement
		Exp 3	20	3-6 weeks	Investigating infants' response to a rapid change in environmental illumination within stimulus expansion or contraction	Opening or closing of a shutter, producing an instant brightening or darkening of the screen	Blink and backward head movement
2000	*Kayed*		9	5-7 months	Investigating which strategies 5- to 7-month-old infants use when timing defensive blink	Virtual object (black circle with four small blue and red circles rotating within it) looming (at different speeds) and projected onto a white sheet	Eye blink
2007	*Kayed*		11	22, 26 and 30 weeks	Obtaining a longitudinal perspective on infants' defensive blinking to a virtual colliding object, attempting to identify a switch in timing strategies	Virtual object (black circle with four small blue and red circles rotating within it) looming (at different speeds) and projected onto a white sheet	Eye blink
2007	*Schmuckler*		24	4-5 months	Investigating the impact of the path of approach and the type of imminent contact with an object on young infants' perceptions of looming objects	Suspended black and orange soccer ball, adjusted to eye level, which moved along a track, towards or away from the infant, on different paths,	Eye blink
1985	*Walker-Andrews*	Exp 1	16	135-170 days	Investigating 5-month-olds sensitivity to audio-visual specification of distance and direction of movement	Two filmed events representing an automobile approaching or driving away, played along with a soundtrack moving in a congruent or incongruent direction	Preferential looking (sequential paradigm)
		Exp 2	16	144-166 days	Investigating 5-month-olds sensitivity to audio-visual specification of distance and direction of movement	Two filmed events representing an automobile approaching or driving away, played along with a soundtrack moving in a congruent or incongruent direction	Preferential looking (parallel paradigm)

3. METHODS

Both behavioural and imaging techniques can be used in order to shed light on the cognitive and functional development of preverbal infants. While the latter include the more recently developed electrophysiological and neuroimaging techniques, the former are based on a well-established tradition of tasks, which have been continuously improved and extended.

Behavioural methods help gather information about psychological change in infants without involving verbal instructions or complex responses and taking into account the short attention span and the limited cooperation of infants. Therefore, they focus on infants' natural tendencies, measuring for example their looking and sucking behaviours or their heart rate (Johnson, 2011a). Among behavioural techniques there are also the so-called "marker tasks", which investigate infants' performance at a specific task at different ages and in different contexts, gathering "evidence about how the observed behavioural change is accounted for by known patterns of brain development" (Johnson, 2011a, p. 19). Imaging methods, instead, "enable us to look at the living brain at work, and thus provide us with tools to investigate the neural underpinnings of developmental behavioural change" (Csibra, Kushnerenko, & Grossmann, 2008, p. 247). They include the recording of spontaneous or event-related electrical brain activity through electroencephalography (EEG) and event-related potentials (ERP) and the measurement of the oxygenation and deoxygenation of different brain areas using the functional MRI with children and the Near Infra-Red Spectroscopy (NIRS) with infants (Lloyd-Fox, Blasi, & Elwell, 2010).

The following two paragraphs will focus on the techniques used to run the studies described in the next chapters, i.e. looking behaviour paradigms – preferential looking in particular – and electroencephalography (EEG).

The employment of looking behaviour paradigms proves useful for gathering evidence on infants' development, building on their natural tendencies to look at discriminable and novel visual stimuli (Johnson, 2011a). Two main groups of techniques can be used and they are the "habituation-dishabituation" technique and the "preferential looking" technique.

Habituation is one of the simplest forms of learning and consists in the decline of fixation time to a repeatedly presented visual stimulus and in the subsequent recovery of attention to a novel one (Slater, 2002). Habituation was first demonstrated in young infants in the early 70s, in studies showing the creation of visual memories and, hence, suggesting that the visual cortex was already functioning at birth (Friedman, 1972; Slater, 2002). The procedure involves the presentation of a visual stimulus until the infant has created an internal representation of it, demonstrated by the diminished attention s/he directs towards it. Supposedly, the decrease of the fixation time directed to the stimulus parallels the creation, by the infant, of a mental representation of the stimulus itself (Wetherford & Cohen, 1973). Consequently, the successful habituation to a stimulus paired with the preference for the novel one in newborns and young infants could be considered as "the most consistently reported demonstration of visual memory at birth" (Slater, 2002, p. 70), for the success of habituation procedures is critically dependent upon the infants' ability to remember what they have seen.

However, habituation can be influenced by factors in the modality of measurement, as well as in the infant and in the stimuli themselves (e.g. complexity) (Bornstein, 1985). In particular, it could be influenced by infants' spontaneous preference for a stimulus over the other one: a strong spontaneous preference would not easily decline and, therefore, infants would possibly not show any novelty effect, even if they had habituated to the stimulus with which they were familiarised.

To overcome this problem, preferential looking paradigms can be used, to identify which stimuli are spontaneously preferred by young infants. Colombo and Mitchell (2009) review research from the first half of the 20th century reasoning that if infants were presented with different stimuli and showed a reliable visual preference for one of them, it could be deduced that they were capable of discriminating the visually preferred stimulus from the other stimuli presented. In the same way, the reviewed researches suggested the possibility of inferring which stimulus properties infants used to make these discriminations by carefully controlling the characteristics of the stimuli presented to them (Colombo & Mitchell).

The preferential looking paradigm, firstly introduced in the first half of the 20th century, eventually proliferated with Fantz's research (Colombo & Mitchell, 2009). In the late 1950s, Fantz demonstrated the tendency of various organisms to pay attention to some stimuli more than to others. He described the paradigm (Fantz, 1956) and proved its efficacy with chicks (Fantz, 1957; 1958a), infant chimpanzees (Fantz, 1958b) and human newborns (Fantz, 1958c). He showed that young infants responded differently to various visual patterns, demonstrating that simple discriminative abilities exist already early in life (Fantz, 1961a; 1961b; Fantz & Ordy, 1959), along with other researchers showing newborns' and young infants' perceptual abilities in relation to brightness, colour and shape perception (Berlyne, 1958; Hershenson, 1964; Spears, 1966).

Preferential looking studies revealed, among others, newborns' preference for face-like stimuli (Morton & Johnson, 1991). In 1991, Johnson and colleagues studied the visual tracking of 10-minute-old newborns presented with face-like, scrambled and blank stimuli and showed greater head and eye turning in response to the face-like stimuli vs. both the other stimuli (Johnson, Dziurawiec, Ellis, & Morton, 1991). According to the authors, this preferential tracking is likely to be consistent with the existence, in the brain, of a "unit of mental architecture in any species that […] contains structural information concerning the visual characteristics of

conspecifics" and "is available without the organism requiring exposure to specific stimuli" (Morton & Johnson, 1991, p. 170).

Preferential looking was also used to measure young infants' visual acuity, through the comparison of images with different spatial frequencies. Spatial frequency is a characteristic of any structure and is periodic across positions in space. It is expressed by the number of cycles of alternating sinusoidal components (i.e. dark and light bars) per degree of visual angle on the retina. It was hypothesised that if infants could discriminate the dark and light bars, they will spend more time looking at them vs. to a grey patch (Fantz & Ordy, 1959; Fantz, Ordy, & Udelf, 1962). Systematically changing the width of the bars permitted to identify the smallest bar width that can be resolved by the participants and hence to estimate the visual acuity at any specific age (Fantz et al., 1962; Slater, 2002).

In a preferential looking task, two different stimuli are simultaneously presented to the infant and the looking time towards each stimulus is recorded, either online or offline. The stimuli are presented on the left and the right side of a screen, consistent with young infants' tendency to orient more readily towards stimuli in the temporal vs. nasal visual hemifield, supposedly guided by subcortical control (Johnson, 1990; 2011a). At the same time, the positioning of the stimuli in the periphery of the screen helps in identifying overt shifts of attention towards one stimulus, signalled by the saccades made to orient the eyes towards it. In order to balance out the possible positions (side) preferences that some infants might show, stimuli are presented for two consecutive periods of time, with reversed positions on the screen (Fantz et al., 1962).

3.1.1 Setting

The experimental room where all the newborns and infants were tested in the behavioural studies was located within the Paediatric Unit of the Hospital of Monfalcone (GO – Italy), where they were all born. Newborn participants were recruited at the hospital during their and their mother's stay (which in Italy is usually 3 days after birth). In agreement with the medical and nursing staff, the experimenters approached the parents at least 12 hours after delivery and only if the newborns were healthy and their mothers receptive to visitors. The researchers briefly explained the research topic, the methods used and the paradigm, seeking for parents' agreement to participate in the study. If the parents decided to participate, they agreed to take their child with them to the experimental room, whenever s/he was awake. Hence, the paradigm was explained again and the informed consent for the participation in the study was signed. Details of potential infant participants were obtained through the Hospital database (following approval by the medical staff). The parents of the infants in the appropriate age group were contacted over the telephone and the research topic, the methods used and the paradigm were introduced to them. If they decided to participate in the study, they would book an appointment for a suitable day and time, when they would bring their child to the Lab within the Paediatric Unit of the Hospital of Monfalcone.

In the experimental room, the newborns and the infants sat on the experimenter's lap and attended to the stimuli presented on a monitor (24") in front of them. If present, auditory stimuli were conveyed from two loudspeakers positioned underneath the monitor, one under the left and one under the right halves of the screen. Black cardboard and black curtains covered the area around the monitor to prevent external stimuli to engage the infants' attention. The black curtain surrounding the monitor had a luminance of 0.2 cd/m^2 and the room was poorly lit in order to ensure that the infants' attention was focused on the screen (average walls luminance was of 30 cd/m^2; average ceiling luminance was of 15 cd/m^2). All measures were

taken from the infants' position and the ambience lightning while measuring was the same as the average lighting of the room during testing.

During the testing, the distance between the participants' face and the monitor was about 30 cm for newborns, distance at which visual acuity at birth is better (Fantz, Ordy, & Udelf, 1962; Slater, 2002), and about 90 cm for older infants. The participants' eye level was aligned to the centre of the screen.

A video camera located on top of the screen recorded the participants' eyes, allowing subsequent offline coding of their eye movements (Fig. 3.1.1). An additional small screen, placed outside the participants' view, allowed the experimenter to monitor their head position throughout the experiment. The experimenter who was holding the infants was always unaware of the ongoing trial and, additionally, was instructed to constantly focus on the monitor showing the participants' mirrored head position and was then unable to see the stimuli.

Figure 3.1.1 Newborns' looking behaviour. Example of a newborn's looking behaviour, showing the eyes oriented to the left, centre and right of the screen (from an experimental session in the Lab within the Paediatric Unit of the Hospital of Monfalcone).

3.2 Imaging techniques: Electroencephalography (EEG)

Electroencephalography (EEG) is the continuous, non-invasive recording of the ongoing electrical brain activity, measured through electrodes positioned on the scalp (Csibra, Kushnerenko, & Grossmann, 2008). EEG records the ongoing brain activity with an excellent time resolution and permits to link the recorded brain activity with the cognitive processes in which the participants were engaged during the recording (Csibra et al., 2008).

The electrodes positioned on the infants' scalp record the voltage changes that happen when a group of neurons close to each other are simultaneously activated. These voltage changes reflect the summated postsynaptic depolarization of the dendrites and, in order to be measurable, have to occur on many aligned synapses. Furthermore, they are more likely to be recorded if they are closer to the surface of the cortex (Csibra et al., 2008).

This technique is popular for studying brain activity during development because it records a robust signal, because it is less sensitive to motion artefacts than fMRI, hence more suitable for studying awake infants, and because it has a great time resolution, which can precisely reveal information about the timing of neurocognitive processes happening during the recording (Csibra et al., 2008; de Haan, & Thomas, 2002). Infant studies typically use high-density electrode systems comprising 64 or 128 electrodes, like for example the Geodesic Sensor Net (GSN), which are useful in studies with infants or special populations because, allowing the quick application of a large number of electrodes on the scalp, they favour a better spatial sampling of the head surface (Csibra et al., 2008; Johnson et al., 2001; Tucker, 1993).

The majority of studies using EEG in infancy try to link brain activity and cognitive processes through the measurement of brain activation in response to different stimuli, which require different cognitive processes (Csibra et al., 2008). The paradigms used while recording EEG with infants generally repeat the same stimuli (and thus the same related cognitive processes) several times, in order to isolate the brain activity involved in the processing of those

stimuli from other ongoing neural activity. The effect of non-related brain activation is reduced by averaging the EEG signal time-locked to the stimulus onset (Csibra et al., 2008).

Electroencephalographic studies in infancy have used mainly three approaches: they analysed event-related potentials, resting EEG and event-related oscillations (Csibra & Johnson, 2007).

Event-related potentials (ERPs) are time-locked averages of the EEG signal, reflecting the brain activation preceding or following a specific event (Csibra et al., 2008). They comprise a series of negative and positive waves, defined in terms of their peak latency and maximum amplitude from the pre-stimulus baseline (Taylor & Baldeweg, 2002). They have been traditionally divided into exogenous and endogenous components: the former ones represent the brain response to the appearance of any detectable stimulus, occur within the first 200 ms after stimulus onset and are sensitive to its physical characteristics; the latter ones, instead, reflect the cognitive processing of the stimuli, occur later and depend both on the physical features of the stimuli and on the paradigm and task. However, more recent studies suggested that top-down processes could modulate also the early ERP components and, hence, this distinction seems to be less meaningful now (Csibra et al., 2008). ERP waveforms are believed to reflect the synchronous activity generated by excitatory and inhibitory post-synaptic potentials and, as a consequence, the developmental changes in their morphology might reflect the changes in synaptic organization occurring during development (Csibra et al., 2008). It has been showed that young infants show less well-defined ERP peaks than adults and greater slow wave activity, probably due to reduced synaptic efficiency (Csibra et al., 2008).

Event-related oscillations (EROs) are recorded when a large number of neurons fire synchronously at the same frequency and can be interpreted in relation to the cognitive processes that were happening while the EEG was recorded (Csibra et al., 2008). They are considered to reflect the oscillatory activity related to a specific task or to the processing of a

specific stimulus because they are approximately time-locked to that task or stimulus presentation (Csibra & Johnson, 2007). Due to their specific nature, i.e. being restricted in both time and frequency, they can be highlighted performing a so called "time-frequency analysis", which tracks how amplitude changes over time at different frequencies (Csibra et al., 2008). Event-related oscillations are particularly useful for studying infants' cortical responses for several reasons and in particular, because they are less sensitive to latency variability than ERPs and because they can reflect sustained activation when the cognitive processing is not well time-locked to the event (Csibra & Johnson, 2007). However, as well as ERPs they are sensitive to electrical and behavioural (eye movements or motion) artefacts.

3.2.1 Setting

The study using EEG was run in the InfantLab at Goldsmiths, University of London. The infants who could possibly participate in the study were shortlisted from the InfantLab database. The experimenter contacted their parents over the telephone and briefly introduced to them the research topic, the methods used and the paradigm. If they decided to participate in the study, they would book an appointment for a suitable day and time, when they would bring their child to the InfantLab.

During the experiment, the electrical brain activity was recorded continuously via a Hydrocel Geodesic Sensor Net (GSN) (Electrical Geodesic Inc.), consisting of 128 silver-silver chloride electrodes evenly distributed across the scalp. In the GSN, the channels are arranged in an elastic tension structure that allows a quick application of the net on the infants' head (Hoehl & Wahl, 2012, Johnson et al., 2001). Before being applied, the net has to soak in warm electrolyte solution. The solution dries quickly on infants' heads, decreasing the risk of reducing the impedance due to the presence of bridges between the electrodes (Hoehl & Wahl, 2012). The most important advantage of the GSN system is its high spatial resolution, which may allow more accurate source localization. In fact, a 128 electrodes GSN can yield to a sampling density of less than 3 cm on the head of a 6-month-old infant (Johnson et al., 2001). Furthermore, being arranged in an elastic tension structure, the electrodes of GSN can be evenly distributed on a wide variety of different head shapes. However, due to its high impedance design and as it is not rigidly fixed on the scalp, the GSN is more prone to movement artefacts (Johnson et al., 2001).

When families arrived at the InfantLab, the infants' head circumference was measured and the appropriate EEG net was selected. While the net was soaking in warm electrolyte solution, the researchers interacted with the parents and tried to make the infants feel comfortable in the lab environment. They also explained the research topic and the paradigm

to the parents and asked them to fill in the consent form. After having soaked in electrolyte solution for about 10 minutes, the net was placed on the infants' head and the infants and their parent moved into the experimental room.

In the experimental room, the infants sat on their parent's lap and attended to the stimuli presented on a monitor (24") in front of him/her. During the testing, the distance between the participants' face and the monitor was about 90 cm and the infants' eye level was aligned to the centre of the screen. The walls of the room were covered with black curtains in order to prevent external stimuli to engage infants' attention. For the same reason, the room was dimly lit. A video camera located on the corner of the room recorded the whole experimental session, allowing subsequent offline coding of the infants' eye movements, which was performed to make sure that each participant was looking to the screen during all the included EEG segments.

4. DISCRIMINATION OF TRAJECTORIES IN NEWBORNS (STUDIES 1 AND 2)

4.1 RATIONALE

The ability to discriminate the trajectories of moving objects is highly adaptive, being fundamental for physical and social interactions. This ability becomes essential when objects move towards the observer, as an object perceived as approaching is predictive of communication and/or physical contact, and might represent a threatening or dangerous situation (Ch. 2). Therefore, it is reasonable to expect that soon after birth infants could be already sensitive to objects approaching their own body along a colliding pathway, in light of the important adaptive features of their trajectory.

Previous research investigated infants' sensitivity to impending collision trajectories through the analysis of defensive reactions to looming stimuli (Ball & Tronick, 1971; Bower, Broughton, & Moore, 1970; Kayed & van der Meer, 2000, 2007; Náñez, 1988; Yonas et al., 1977; Yonas, 1981, Ch. 2.3). Several behaviours were considered as defensive, in particular eye widening, head and arm movements (Ball & Tronick, 1971; Bower et al., 1970) and eye blinks (Kayed & van der Meer, 2000, 2007; Náñez, 1988; Yonas et al.; Yonas, 1981). Bower and colleagues identified in newborns, under certain setting conditions, an adaptive response comprising eye widening, a withdrawal of the head and a movement of the hands between the colliding object and the face. They also showed that this response was modulated by the visual components of looming stimuli and not by the concomitant air pressure changes (Bower et al., 1970). Ball and Tronick assessed newborns' sensitivity to impending collision too, showing backward head movements in response to hit looming sequences, head turning during miss looming sequences and no response during receding sequences (Ball & Tronick, 1971). However, Yonas and colleagues (1977) discussed how the variables investigated by previous studies (i.e. eye widening, head movements and arm movements) should not be considered as

adaptive responses, but as part of a tracking process. They suggested, instead, that blinking of the eyes should be considered the best indicator of awareness to impending collision in early infancy (Yonas, 1981) and concluded that young infants (1-2 months) do not show sensitivity to impending collision, as they do not respond to it with appropriate defensive or avoiding behaviours, which they argue undergo an extended development (Yonas et al.). Since then, studies investigating sensitivity to impending collision considered only defensive reactions, in particular blinking, to that which was considered a dangerous or threatening stimulus, interpreting the absence of avoiding behaviours as lack of the ability to discriminate impending collision itself (Ch. 2.3).

Most importantly, focusing on the lack of a defensive response could have masked infants' ability to actually detect and discriminate among relevant moving trajectories. In particular, I think that the presence (rather than the absence) of a defensive reaction may not be the most informative variable to be investigated in very young infants. As there is no evidence of humans' ability to recognise stimuli as dangerous right after birth (Farroni, Menon, Rigato, & Johnson, 2007; Johnson, Senju, & Tomalski, 2015), I suppose that the blinking reflex may not be elicited by impending collision in newborns because they may fail to categorise it as a possible danger in the first place. Crucially, taking into account only defensive reactions means interpreting the object approaching along a colliding trajectory only as a possible danger and not as an interesting stimulus to interact with (de Vignemont & Iannetti, 2015; Kandula, Hofman, & Dijkerman 2015; Van der Stoep, Nijboer, Van der Stigchel, & Spence, 2015). Furthermore, evidence in human adults as well as non-human primates highlighted that the perception and the processing of looming stimuli (which specify impending collision) are facilitated, due to their ethological relevance (Cappe, Romei, Thut, & Murray, 2009; Ghazanfar, Neuhoff, & Logothetis, 2002; Maier, Neuhoff, Logothetis, & Ghazanfar, 2004; Neuhoff, 1998; Neuhoff, 2001; Seifritz, 2002). Based on these considerations, I thought that a

preferential looking paradigm could have been more appropriate to evaluate if newborns are able to differentiate between different pathways of moving objects and if they pay more attention, as it would seem likely, to adaptively important ones (i.e. by showing a visual preference for approaching and colliding stimuli).

To address this (Study 1, Ch. 4.3), I measured newborns' looking behaviour in order to evaluate their ability to discriminate between stimuli moving along different trajectories within the space surrounding their body and, in particular, to investigate the existence of a spontaneous preference for impending collision trajectories. To address this, I designed a preferential looking study comparing an approaching and colliding trajectory (AC) with a receding one (R). I expected the newborns to be more attracted by the AC trajectory, which is adaptively more salient as it is directed towards their bodies. To generalise this hypothesis to other trajectories and to test whether this hypothesised preference could be specifically related to the impending collision depicted by AC or more generally to an approaching movement or to expansion in optical size, I included a sequential looking session comparing two different approaching trajectories, one colliding (AC) and one non-colliding (ANC). Again, I expected the newborns to look longer at the trajectory where the moving object directly approached their body, i.e. AC. This additional session also offered the opportunity to investigate whether newborns could discriminate between two trajectories both moving towards the same portion of space (i.e. the PPS) and differing only in their specific target (i.e. the body vs. the space around it).

In everyday life, though, moving objects convey information about their trajectory from different sensory modalities, in particular vision and audition. Indeed, the auditory system has a number of advantages over other sensory systems and can therefore be considered as the most efficient warning system we can rely on (Ferri, Tajadura-Jiménez, Väljamäe, Vastano, & Costantini, 2015), in particular as it is able to use several physical cues to determine the location and movement of a sound source (Hall & Moore, 2003). Several studies investigated the

sensitivity to auditory looming signals – i.e. those sensory stimuli signalling approach of objects – in both humans and non-human primates, revealing the existence of attentional biases and coding asymmetries for looming stimuli in the auditory domain (Bach et al., 2008; Ghazanfar, Neuhoff, & Logothetis, 2002; Grassi & Darwin, 2006; Maier & Ghazanfar, 2007; Neuhoff, 1998; Neuhoff, 2001; Rosenblum, Wuestefeld, & Saldaña, 1993; Seifritz et al., 2002; Ch. 2.1 and 2.2). Previous research also demonstrated the existence of a perceptual bias for multisensory looming stimuli in primates and selective integration of multimodal looming stimuli in human adults (Cappe et al., 2009; Cappe, Thelen, Romei, Thut, & Murray, 2012; Maier et al., 2004). Maier and colleagues, in particular, adopted the preferential looking technique in order to test rhesus monkeys' natural capacity to match visual and auditory looming cues. They presented simultaneous looming and receding visual stimuli paired with either looming or receding auditory stimuli and measured the monkeys' looking time to the matching video. They found a visual preference for the approaching visual stimulus when it was paired with the approaching sound, but no preference at all when the visual stimuli were presented together with the receding sound. Thus, only the looming sound biased their looking behaviour to the congruent visual stimulus (Maier et al., 2004).

In a similar way (Study 2, Ch.4.4), I measured newborns' looking behaviour in order to investigate the multisensory integration of audio-visual stimuli depicting approaching and receding trajectories in the first days of life. The newborns were presented with approaching (AC) and receding (R) visual trajectories, paired with sounds changing in intensity that simulate either the approach (increasing intensity) or the recess (decreasing intensity) of the sound source. In this way, I have been able to compare the looking behaviour to Congruent vs. Incongruent multimodal stimulation conveying adaptive information and to test for the existence of any facilitative effect of multisensory vs. unisensory stimulation in this context. This study also offered the opportunity of investigating the integration between the principles underneath

multisensory stimulation and the ethological meaning of the presented stimuli, which I thought

would have been higher for the stimuli that moved towards the newborns' body.

4.2 STIMULI

4.2.1 Visual Stimuli

The newborns have been presented with videos previously recorded in an ecological fashion, which showed the movement of a black-and-white-striped ball. The three stimuli presented during the sessions could be described as follows:

- AC: an approaching and colliding stimulus where a striped ball moved from the background towards the newborns' body along a linear colliding pathway;

- R: a receding (hence non-colliding) stimulus, consisting in the time-reversed AC stimulus, whereby the ball moved from near the newborns' body towards the background;

- ANC: an approaching but non-colliding stimulus, where the ball moved from the background towards the newborns along a linear but non-colliding trajectory (i.e. missing the head laterally).

On the screen the infants could see two peripheral black areas (i.e. "frames") on a grey background. Both frames were 24.4 cm wide and 20.4 cm high, they were both 0.85 cm apart from the nearest edge of the screen and 1.6 cm apart one from the other; they were both 6 cm apart from the top and the bottom of the screen. At the beginning of the AC and ANC stimuli and at the end of the R one the ball had a diameter of 7.2 cm and subtended a visual angle of 23.54° x 23.54°; on average, the stripes were 0.9 cm wide (2.94°). The ball was 3.2 cm apart from the nearest edge of the frame and 14 cm apart from the farthest and it was 6.6 cm apart from the top and the bottom of the frame. At the end of the AC stimulus and at the beginning of the R one, the ball had a diameter of 13.8 cm and subtended a visual angle of 37.70° x 37.70°; on average, the stripes were 1.7 cm wide (4.71°). The ball was 5.3 cm apart from both edges of the frame and it was 3.3 cm apart from the top and the bottom of the frame. At the end of the

ANC stimulus, the ball had a diameter of 10 cm and subtended a visual angle of 34.70° x 34.70°; on average, the stripes were 1.3 cm wide (4.33°). The ball was 3.2 cm apart from the nearest edge of the frame and 11.2 cm apart from the farthest and it was 5.2 cm apart from the top and the bottom of the frame. A generally accepted estimate of visual acuity at birth is 1 cycle per degree (Atkinson & Braddick, 1989): this ensures that the balls and their striped pattern could be detected by the newborns for the whole duration of each repetition of the stimuli.

The luminance of the display was 0.5 cd/m^2 for the black frames and 54 cd/m^2 for the grey background; it was instead 78 cd/m^2 for the white stripes of the moving ball and 108 cd/m^2 for the lightest part of them. High contrast stimuli were used in order to enhance newborns' attention towards them: Michelson contrast between the black frames and the grey background was -0.982, between the white stripes of the ball and the black frames was 0.987, and between the highlight of the ball and the black frames was 0.991.

The motion of every stimulus lasted 3.33 s and was preceded and followed by 10 frames (= 333 ms) where the ball stood still (during the last frame the contrast was reduced, favouring a fading effect), summing up to an overall stimulus duration of 4 s. Every stimulus was repeated 8 times, with a 1-second interval between two subsequent stimuli and 4 s of blank screen before the first one, for an overall trial duration of 44 s. In the AC and R stimuli, the speed of the ball was 10.6 cm/s, whereas in the ANC one it was 9 cm/s. The speed of the stimuli resulted from the combination of the length of the path that the ball had to travel (during the recording) and a display time long enough to ensure that the newborns' attention could be engaged. I was not particularly concerned of the effect the speed of the moving stimulus could have on the discrimination of the different trajectories, as previous studies are not consistent about the speed of the stimuli and, most importantly, because previous research (Náñez, 1988) indicated that even wide variations in the looming velocity (i.e. from 6 to 48 cm/s) do not impact on looming reactions in infancy.

The recorded ball had a diameter of 8 cm and a pattern of vertical black and white stripes, 1 cm wide, and moved at constant speed in 3D space. The recording structure was chosen accordingly to monitor size (24"). The camera was placed where the newborns' head would be positioned during the study, i.e. pointing towards the centre of the recording structure (both horizontally and vertically) at 35 cm from it. The start point of AC and ANC trajectories was 35 cm away from the camera, with a lateral displacement of 19 cm, and the end point was 5 cm away from the camera. In this way it was possible to ensure that the AC stimulus was not conveying the impression of hitting the newborns' face. In the AC stimulus the ball moved along a diagonal trajectory, i.e. from the start point towards a point 5 cm before the newborns' face position, in front of it. The R stimulus was the AC video played backwards (the video was edited using the software "Final Cut Pro X"). In the ANC stimulus, instead, the ball moved along a straight trajectory (i.e. both its start and end points had a lateral displacement of 19 cm from the camera).

4.2.2 Auditory Stimuli

In order to convey the impression of a sound source either approaching to or receding from the participants, I decided to modulate the intensity of the sound, as intensity is proven to be the sound feature that better accounts for the movement of the sound source in the space (Canzoneri, Magosso, & Serino, 2012; Maier & Ghazanfar, 2007; Middlebrooks & Green, 1991; Neuhoff, 1998; Rosenblum, Carello, & Pastore, 1987; Seifritz et al., 2002). A study investigated infants' (4-to-6-month-olds) sensitivity to intensity as an auditory distance cue using looming stimuli and measuring the amount of backward body pressure in response to looming vs. receding stimuli and demonstrated that infants can respond to the specific direction information provided by changes in the sound pressure level (Freiberg, Tually, & Crassini, 2001).

The auditory stimuli were two samples of a sinusoidal waveform of 4000 ms duration with constant frequency (8000 Hz) and presenting a variation in intensity of 15 dB SPL. Specifically, the sound simulating the approach of the sound source (increasing intensity sound) increased from 55 to 70 dB, whereas the sound simulation the recess of the sound source (decreasing intensity sound) decreased from 70 to 55 dB. The intensity was measured from the newborns' position at the average conditions of the room during testing (environmental noise and set up). The intensity interval chosen (i.e. 55-70 dB) was the same used in previous studies (e.g.: Canzoneri et al., 2012; Teneggi, Canzoneri, di Pellegrino, & Serino, 2013) that investigated the dimensions of the peripersonal space (PPS) in adults. I decided to replicate this variation in the intensity of the sound to convey the impression of a sound source moving within the portion of space that contains the boundary of adults' PPS (Ch. 1.2). I chose to present a sinusoidal waveform as there is evidence that complex sounds trigger facilitative effects and multisensory integration of looming signals more than samples of noise (Maier, Neuhoff, Logothetis, & Ghazanfar, 2004; Neuhoff, 1998; Romei, Murray, Cappe, & Thut, 2009). The frequency of the auditory stimuli (8000 Hz) was chosen in order to be reasonably sure that newborns could hear and discriminate the variations in intensity that were presented to them. A few studies tried to investigate the absolute hearing threshold in very young infants (Olsho, Koch, Carter, Halpin, & Spetner, 1988; Tharpe & Ashmaed, 2001; Trehub, Schneider, Thorpe, & Hudge, 1991; Weir, 1976, Weir, 1979; Werner & Gillenwater, 1990; Werner, 2002; Werner, 2007), although they highlighted the difficulty of studying intensity processing in such population, because i) there is no measure able to distinguish intensity coding from other factors, such as attention and memory, ii) their responses are exclusively non-verbal and iii) there are frequent changes in their arousal state (Weir, 1979; Werner, 2007). Among these studies, Weir (1976, 1979) found spontaneous motor responses to octave-band noises in the order of 75 dB SPL over frequencies ranging from 125 to 4000 Hz in full-term newborns aged less than 9 days

of life, although these values seem unreasonably high and might be related to the methods employed (Werner, 2002). Werner and Gillenwater estimated that 2- to 4-week-old infants' behavioural thresholds to pure tones are about 45 dB higher than adults' at 500 Hz and about 35 at 4000 Hz (i.e. roughly 54 dB SPL at 500 Hz and 30 dB SPL at 4000 Hz). By 3 months of age, the same thresholds improve to 40 dB SPL at 500 Hz, 24 dB SPL at 4000 Hz and 30 dB at 8000 Hz (Olsho et al., 1988; Tharpe & Ashmaed, 2001; Trehub et al., 1991; Werner, 2002). Also, physiological measures showed how thresholds measured in the inner ear or auditory nerve at term birth are no more than 15 dB higher than adults' ones (Werner, 2007).

4.3 STUDY 1: UNIMODAL TRAJECTORIES

In this first study, I investigated, through the analysis of their looking behaviour, newborns' ability of discriminating between different trajectories and the possible existence of a spontaneous visual preference for those approaching their bodies.

4.3.1 Participants

Twenty newborns (7 female) aged from 14 to 95 hours of life at time of test took part in the study. Ten additional newborns participated in the study but were excluded due to fussiness (n = 4), sleepiness (n = 2) or because of a strong side bias (they oriented more than 80% of their looking time to the same side, n = 4). All the newborns that participated in the study met the screening criteria of normal delivery, birth weight > 2500 g, gestational age > 37 weeks and had an Apgar index score between 8 and 10 at the fifth minute of life. No abnormalities were present at birth. The 20 newborns included in the final sample had a mean age of 46.53 hours (SD = 22.16) at testing, a mean birth weight of 3358.5 g (SD = 443.43) and a mean gestational age of 40.50 weeks (SD = 0.92).

Testing took place when babies were awake and alert, usually during the hour preceding feeding time. Parents were informed about the procedure and provided written informed consent to their child's participation. The local Ethical Committee of Psychology Research (University of Padua) approved the study protocol.

4.3.2 Method and procedure

The study was conducted with a preferential looking paradigm, as described in Chapter 3.1, using visual stimuli described in this chapter, par 4.2.1.

The experiment consisted of two sessions. Each newborn took part in both sessions of the experiment, each one including two trials. The two sessions and the two trials within each session were presented in counterbalanced order across participants.

The experiment began as soon as the newborns were seated and were attending to the centre of the screen. In session A, the newborns were presented with an approaching and colliding stimulus (AC) compared to a receding stimulus (R), whereas in session B the stimuli depicted two different approaching trajectories, moving either along a colliding (AC) or non-colliding pathway (ANC). In both sessions the newborns were presented with two simultaneous videos, one on the left and one on the right of the screen. Stimuli were located in the peripheral area of the screen to ensure that the newborns' attention was engaged. Session A used a parallel preferential looking paradigm, thus the newborns were presented with two different videos on the two sides of the screen, with counterbalanced positions across trials. Session B, instead, used a sequential looking paradigm, hence the newborns were presented with the same stimulus on both sides of the screen in each trial, and the looking times to the different stimuli were compared between trials (Fig. 1). In session B I decided to use a sequential looking paradigm, in which the visually presented trajectories were always symmetrical with respect to the body midline, in order to obtain an absolute measure of visual preference, controlling for those aspects that could affect the relative attractiveness the stimuli themselves. In fact, the recorded image of the ANC ball resulted to be slightly smaller at the end point than the image of the AC one because of the different distance from the viewpoint. Moreover, to keep constant the stimulus duration (4 s), the speed of the ANC ball (= 9 cm/s) was slightly lower than the speed of the AC or R ball (= 10.6 cm/s).
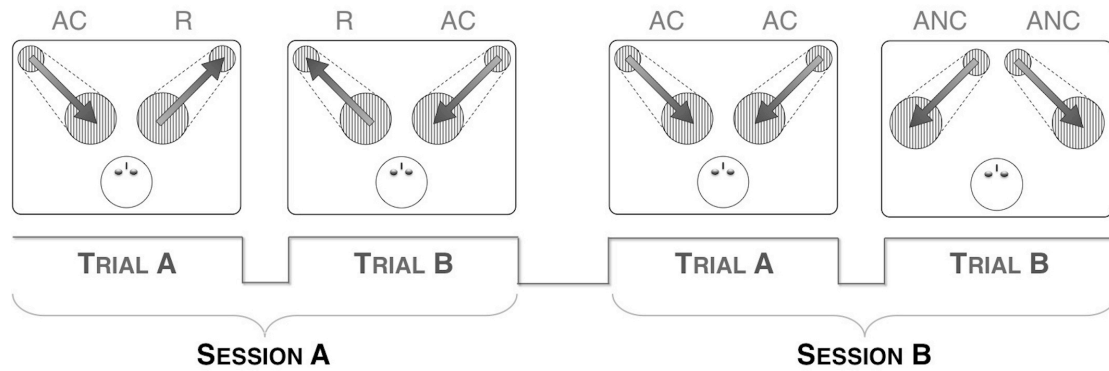
Figure 4.3.1 Description of the experimental procedure. The experiment consisted of two sessions (A and B), each including two trials (A and B). The two sessions and the two trials within each session were presented in counterbalanced order across participants. In session A, I compared in each trial AC and R stimuli (8 repetitions); positions of the two stimuli were counterbalanced across trials. In session B, in trial A I compared two simultaneous AC stimuli (8 repetitions), whereas in trial B I compared two simultaneous ANC stimuli (8 repetitions).

4.3.3 Hypotheses

In session A, AC and R stimuli were presented simultaneously, with counterbalanced positions across the two trials (AC on the left and R on the right in trial A, and vice versa in trial B). I expected the newborns to pay more attention to the AC trajectory, adaptively more salient as – if continued – it would result in a collision between the approaching ball and their body. Longer looking times at the AC (rather than R) stimulus could be explained by a visual preference either for impending collision or more generally for approaching movements. However, this hypothesised visual preference could also be simply related to the increase (rather than decrease) of the optical size of the stimuli rather than to their different trajectory. To control for such confound, in session B I presented the newborns with two stimuli both showing a ball moving along an approaching trajectory and both involving an increase of optical size. However, only one stimulus showed a ball moving along a colliding trajectory. More specifically, I showed two pairs of identical stimuli, in both trials: during trial A I showed two AC stimuli, whereas during trial B two ANC ones. Therefore, as both trials presented stimuli approaching the newborns and both stimuli increased in optical size, longer looking times in trial A than in trial B would be attributed to the newborns' ability of discriminating the actual

trajectory of each stimulus and to their preference for the one moving along a colliding trajectory, i.e. a trajectory specifically targeting their own body.

I hypothesised that the evidence derived from the looking times in the four trials would provide information about an implicit and rudimentary differentiation of the space surrounding the newborns' body. I expected to find a visual preference for stimuli that – if continued – would result in a collision between the moving ball and the newborns' body. In fact, I thought that these stimuli could be more interesting and adaptively more relevant than those directed somewhere else as they would lead to an interaction, either positive or negative, between the newborn and the moving stimulus.

Concerning defensive reactions, I expected to replicate previous findings (Náñez, 1988; Yonas et al., 1977) in terms of absence of consistent blinking to impending collision at birth. The lack of blinking in presence of visual discrimination and of a spontaneous visual preference would provide evidence of the appropriateness of a preferential looking paradigm for investigating newborns' sensitivity to colliding trajectories.

4.3.4 Data Analysis

Video recordings of the newborns' eye movements were analysed offline separately by myself and another observer. The second coder was unaware of the hypotheses and both coders were blind to sessions and trials order. The observers coded how long each newborn looked at each side of the screen during both sessions. In this way, I obtained a measure of the time that the newborns spent looking at each stimulus in each session.

Two interrater reliability analyses were performed: Pearson's *r* correlation analysis and the Interclass Correlation Coefficient (ICC). The Pearson's *r* correlation was performed on the total sample (n = 20) and revealed a score of *r* = 0.90. The ICC was performed for 20% of the sample (n = 4), and showed an agreement between coders = 0.94.

4.3.5 Results

For each newborn I calculated the proportions of looking time (P(LT)) dividing the LT to each stimulus by the total exposure time of that stimulus. Differences in the P(LT) to each pair of stimuli were normally distributed (Kolmogorov-Smirnov test, all *p* > 0.5). The results are summarised in Table 4.3.1. The data from each session were analysed using two paired planned comparisons.

Session	Stimulus	average LT (ms)	Exp (ms)	P(LT)	SE
A	AC	17332	64000	.2708	.0127
	R	12770	64000	.1995	.0157
B	AC	18204	32000	.5689	.0282
	ANC	14853	32000	.4642	.0278

Table 4.3.1 Looking time results. The table shows the average raw looking time (LT) to each stimulus in the two sessions, the total exposure times (Exp), the proportions of looking time P(LT) and their Standard Error (SE).

During session A, the newborns looked significantly longer at the AC stimulus compared to the R stimulus [$t(19) = 3.062$, $p = .006$, $d_z = 0.68$] (Fig. 4.3.2), showing a visual preference for the trajectories directed towards their own body vs. away from it.
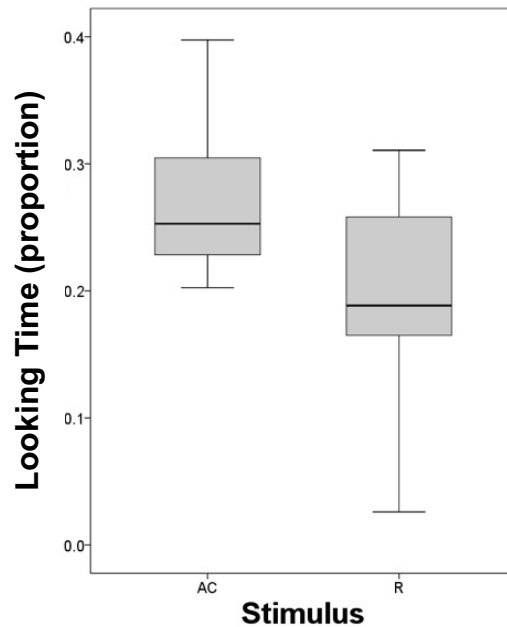
Figure 4.3.2 Proportions of looking time during session A. Distribution of the proportions of looking time (P(LT)) directed to AC and R visual stimuli during session A. The P(LT) were calculated dividing the LT to each stimulus by the total exposure time of that stimulus.

I ran an additional ANOVA on the P(LT) to AC vs. R stimuli in the first vs. second half of each of the 8 repetitions included in each trial (i.e. LT from 0 to 2000 ms vs. LT from 2000 to 4000 ms) in order to investigate whether this visual preference was affected by a preference for the bigger stimulus (i.e. the R ball in the first half of the presentation and the AC ball in the second half). The results showed a main effect of the Stimulus [$F(1, 38) = 4.744$, $p = .036$; $\eta^2 = .108$], but no effect of the Presentation half [$F(1, 38) = .246$, $p = .623$; $\eta^2 = .006$] nor of the Interaction [$F(1, 38) = .032$, $p = .860$; $\eta^2 = .001$]. This showed that the AC stimulus was attended for a longer proportion of time compared to the R one in both in the 1st and in the 2nd halves of the presentations and that the amount of looking time directed to each stimulus in the 1st vs. 2nd half of the presentations was not significantly different (Fig. 4.3.3). Crucially, the visual

preference for AC shown in this session did not depend on the dimension of the stimuli, but rather on their trajectory, as demonstrated by the fact that the newborns looked longer to the AC stimulus since its very beginning, when its optical size was smaller than that of the R stimulus.
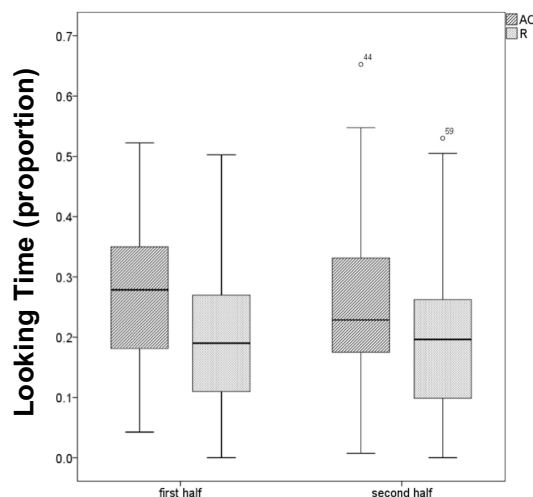
Figure 4.3.3 Distribution of the P(LT) to AC and R stimuli during the first and the second halves of the presentation (session A).

Session B was introduced in order to generalise the investigation to different trajectories, as well as to rule out the possibily that the hypothesised preference for approaching stimuli in session A was determined by a preference for expanding vs. contracting stimuli, which would not necessarily imply taking into account either motion in depth or impening collision intormation. In this session as well, the newborns showed a visual preference for the AC stimulus compared to the ANC stimulus [$t(19) = 5.139$, $p < .001$, $d_z = 1.15$] (Fig. 4.3.4), demonstrating: i) their ability to discriminate the specific target of an approaching trajectory and ii) a visual preference for the stimuli on a collision course with their own body. This result confirmed the visual preference for AC found in session A, suggesting that newborns' preference for trajectories directed towards their bodies was due to a real preference for impending collision information rather than to a preference for increasing optical size or approach in general. Most importantly, it also showed newborns' sophisticated ability of visually discriminating between

two trajectories both moving towards the space immediately surrounding their bodies, i.e. the peripersonal space.
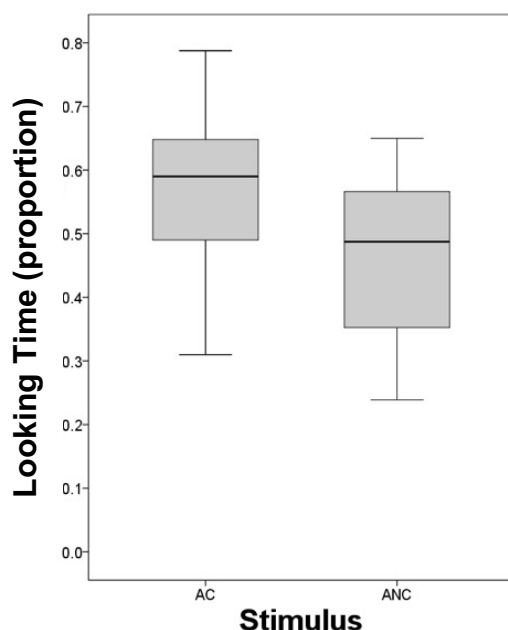
Figure 4.3.4 Proportions of looking time during session B. Distribution of the proportions of looking time (P(LT)) directed to AC and ANC visual stimuli during session B. The P(LT) were calculated dividing the LT to each stimulus by the total exposure time of that stimulus.

Prior research investigating newborn infants' perception of object trajectories in relation to themselves has focussed on their defensive behaviours. In order to examine these, the number of blinking manifested by this sample of newborns were also coded, according to the definition of blink stated by Yonas (1977, p. 99): "a rapid closing of the eye-lids, regardless of whether this was followed immediately by a reopening of the eyes". Following Yonas (1981) and Schmuckler, Collimore, and Dannemiller (2007), all the eye closures happening within the 2" time window surrounding the end of the stimulus were coded. Only trials showing at least one colliding stimulus were included (session A: trials A and B; session B: trial A only). Over a total of 480 colliding stimuli (seen by the whole sample of newborns), only 18 blinks were coded (4%). Moreover, only in 9 cases over 18 the newborns were looking at the screen immediately before the appearance of the blinking and, among these 9, only in 6 cases they were looking at the

colliding stimulus before closing their eyes. Two independent judges coded blinks for the 20% of the sample. The two judges agreed on the presence or absence of blinking in 123 over 128 trials, i.e. on the 96.09% of the total. Other reliability analyses (e.g., Cohen's K) were not performed due to the high degree of negative agreement (judges agreed on the absence of blink in 120 over 128 trials). This result confirmed the absence of consistent defensive blinking at birth, as previously showed by Yonas (1981).

4.3.6 Discussion

The results of this study have shown that newborn infants can discriminate between the trajectories of moving objects, showing a visual preference for those directed towards their own bodies, not only when they move in different directions (approaching vs. receding), but also when they both approach their peripersonal space. Previous studies on impending collision perception concluded that newborns are unaware of the colliding course of an object, since they do not show adaptive responses or defensive behaviours and, in particular, since there is no evidence of eye-blinks in reaction to an approaching stimulus (Yonas et al., 1977). But here, as these findings do not rest on claims about defensive reactions but, rather, on newborns' visual preferences, it was possible to show that right after birth infants are able to make quite sophisticated perceptual discriminations of objects approaching their bodies, vs. objects either receding from them or approaching the space around their bodies (the peripersonal space), but not on a direct collision course.

I thought that the focus on defensive responses could have masked infants' ability to detect and discriminate among relevant moving trajectories and hence I used a different method to test it. My decision was supported by previous findings in both adults and non-human primates revealing the facilitated processing of looming stimuli, irrespective of defensive reactions (Cappe, Romei, Thut, & Murray, 2009; Ghazanfar, Neuhoff, & Logothetis, 2002; Maier & Ghazanfar, 2007; Neuhoff, 1998; Neuhoff, 2001; Seifritz, 2002). For these reasons, I implemented a looking behaviour experiment in order to investigate newborns' ability to discriminate between different trajectories and – in particular – to discriminate approaching and colliding ones. The results showed that newborns seem to be able to discriminate between different trajectories taking place in the space immediately surrounding their own body. In particular, the newborn participants showed a visual preference for approaching and colliding stimuli, directed towards their bodies, when compared with both receding and approaching but

non-colliding ones. These results suggest that newborns are able to detect and discriminate colliding trajectories, as revealed by their visual preference for them, despite the lack of defensive reactions to impending collision, as shown by the absence of consistent blinking in this sample of newborns as in previous studies (Yonas et al., 1977). I speculate that the inconsistency between the existence of visual preference for the colliding trajectory and the lack of defensive behaviour to impending collision at birth could be due to the fact that newborns may lack the experience of dangerous stimuli necessary to elicit defensive responses. In fact, newborns might fail to categorise impending collision stimuli as dangerous or generally negative, but nonetheless their trajectory might award them a special salience (as suggested by their visual preference).

The visual preference for the approaching and colliding stimulus was found in both sessions of the experiment, consistent with the hypothesis that newborns are truly able to discriminate the actual trajectory of moving stimuli with respect to the body, even when trajectories are both approaching the peripersonal space, and show a visual preference for those targeting their body. In session A, I compared AC and R stimuli and showed that newborns looked longer at AC ones. On the basis of the findings of session A alone, it could be argued that the visual preference that was found could be attributed to a general preference for approach and not to the presence of collision information. At the same time, it could be referred to a preference for the increasing optical size of the approaching object, rather than to its trajectory. In session B, however, I compared two different approaching trajectories: this time, both stimuli approached the newborns and displayed an increasing optical size throughout the presentation, but only one specified impending collision. The visual preference for AC rather than ANC stimuli in session B suggests that newborns looking behaviour in session A was not due to a generic preference for approach (relative to recess) or to growth or expansion (relative to shrinkage or contraction), but to a specific discrimination of the actual trajectory of the

stimulus. Furthermore, the specific direction of the preference indicates that newborns seem to have a particular interest in objects directly approaching their own body.

Taking a different stance, it could be argued that the visual preference for the AC-AC stimulus pair in session B depended on the expected collision between the two symmetrically moving stimuli. However, the results of session A indicated that one AC stimulus alone is enough to elicit the visual preference.

The results of the two sessions support the hypothesis that already at birth humans are able to discriminate between different trajectories and show a visual preference for approaching and colliding ones, i.e. those directly targeting their own bodies.

I think that the preference for the visual stimulus depicting an approaching and colliding trajectory could be ascribed to the major adaptive salience of stimuli that, moving along a collision course, could come into direct contact with the newborn. The stimulus could either have a positive (interaction) or negative (danger) value, but in both instances it appears to be worth being looked at. Preferential looking paradigms cannot provide any information about the positive or negative valence of the shown stimuli, or the reason why one stimulus is visually preferred over the other (Banks & Ginsberg, 1985). As a consequence, based on the present data, it is not possible to draw a definite conclusion on whether the longer looking time directed to the stimulus approaching along a colliding trajectory was due to interest or threat. Additional developmental studies using physiological measurements are needed in order to shed further light on the valence of a stimulus approaching along a colliding trajectory in infancy. At the same time, the alternatively positive or negative salience of a stimulus moving into the space that surrounds the body could be directly linked to the two alternative functions that characterise this space itself (de Vignemont & Iannetti, 2015). De Vignemont and Iannetti recently differentiated between two specialist models of the PPS, based on a clear functional distinction. In particular, the authors distinguished between the definition of the PPS as a

protective and defensive space or as a working space, where goal-directed actions take place. They suggested that, although these two kinds of PPS spatially overlap one another, they require distinct sensory and motor processes that follow different principles (de Vignemont & Iannetti, 2015).

Concluding, this study suggests that at birth human infants seem to be already equipped with visual mechanisms that permit them to perceive the space surrounding their body, through the discrimination of different moving trajectories within the space immediately around their bodies and through the spontaneous visual preference for those moving directly towards them. These visual mechanisms might in turn predispose newborns to perceive their presence in the environment and to adaptively focus their attention on the PPS and their bodily self.

In Study 1 I demonstrated newborns' ability to discriminate between different trajectories of moving visual stimuli and their preference for those moving specifically towards their bodies. These findings suggest that newborns may be predisposed to focus on behaviourally relevant stimuli present in their environment right after birth. However, as in real life the motion of objects is perceived through different senses, I wanted to further study newborns' perception of relevant trajectories when specified by different sensory modalities, in particular vision and audition. In this second study, then, I investigated the looking behaviour of newborns presented with audio-visual stimuli depicting congruent and incongruent trajectories. This study gave me the opportunity of investigating the interplay between the principles underneath multisensory integration and the ethological meaning of the presented stimuli, which, based on my previous findings (Study 1) and on previous literature, I hypothesised being higher for those stimuli that moved towards the newborns' body.

4.4.1 Participants

Twenty newborns (11 female), aged from 19 to 90 hours of life at the time of testing, were included in the final sample. Ten additional newborns participated in the study but were later excluded due to sleepiness (n = 4), experimental errors (n = 1) or because of a strong side bias (they oriented more than 80% of their looking time to the same side of the screen, n = 5). All the newborns that participated in the study met the screening criteria of normal delivery, birth weight > 2500 g, gestational age > 37 weeks and had an Apgar index score between 8 and 10 at the fifth minute of life. No abnormalities were present at birth. The 20 newborns included in the final sample had a mean age of 54.93 hours (SD = 18.73) at testing, a mean birth weight of 3310 g (SD = 360.85) and a mean gestational age of 40 weeks (SD = 1.09).

As in Study 1, testing took place when babies were awake and alert, usually during the hour preceding feeding time. Parents were informed about the procedure and provided written informed consent to their child's participation. The local Ethical Committee of Psychology Research (University of Padua) approved the study protocol.

4.4.2 Method and procedure

The study was conducted with a preferential looking paradigm, as described in Chapter 3.1, using the visual stimuli described in this chapter, par 4.2.1 and the auditory stimuli described in par 4.2.2.

The paradigm included two sessions, each corresponding to a different audio-visual condition and each comprising two trials. Each newborn took part in both sessions. The order of presentation of the sessions and of the trials within each session was counterbalanced across participants.

The experiment began as soon as the newborns were seated and attending to the centre of the screen. In all trials the newborns were presented with multimodal stimuli, constituted by two simultaneous visual stimuli and a simultaneous sound. The two visual stimuli were displayed one on the left- and one on the right-hand side of the screen: they were located in the peripheral areas of the screen to ensure that the newborns' attention was engaged. The sound was conveyed by two loudspeakers positioned under the monitor, one under the left and one under the right halves of the screen. In each condition, the newborns were presented with two different visual stimuli on the two sides of the screen: on one side they could see an approaching visual stimulus (AC), whereas on the other side they could see a receding visual stimulus (R). The side of presentation of each stimulus was counterbalanced between the two trials. In the Increasing sound condition, the visual stimuli were accompanied by an increasing sound, depicting a trajectory congruent with the approaching visual stimulus (AC); on the contrary, in the

Decreasing sound condition they were paired with a decreasing sound, congruent with the receding visual stimulus (R) (Fig. 4.4.1). Stimuli were presented using E-Prime 2.0.10.
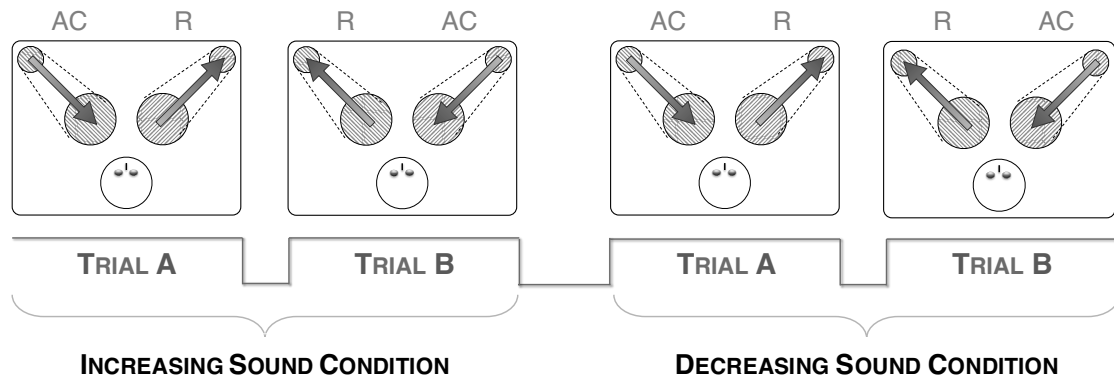
Figure 4.4.1 Description of the experimental procedure. The experiment consisted of two sessions, each representing a different audio-visual condition and each including two trials. The two sessions and the two trials within each session were presented in counterbalanced order across participants. In each trial of both sessions I compared AC and R stimuli (8 repetitions); positions of the two stimuli were counterbalanced across trials. In the Increasing sound condition, stimuli were paired with an increasing sound, congruent with the AC visual stimulus, whereas in the Decreasing sound condition they were paired with a decreasing sound, congruent with the R visual stimulus.

4.4.3 Hypotheses

For this study, I hypothesised two possible outcome scenarios. On one side, newborns might not integrate the audio-visual stimuli and the auditory stimulation could play a role solely as an attention getter. If this were the case, I would expect the looking behaviour pattern not to change if compared to the one found in the unimodal study (Study 1): the newborns would look longer at the approaching visual stimulus, irrespective of the sound, and possibly for overall longer periods of time than in the unimodal study as their attention might be enhanced by the mere presence of a simultaneous sound, irrespective of the perceived direction of the sound movement.

On the other side, as suggested by the literature, they might be able to integrate the multimodal stimuli and they might be more attracted by the audio-visual pair of stimuli depicting a congruent direction (Bahrick & Lickliter, 2000, 2012; Bahrick, Lickliter, & Flom, 2004; Filippetti, Lloyd-Fox, Dragovic, Johnson, & Farroni, 2013; Filippetti, Orioli, Johnson, & Farroni, 2015; Lewkowicz & Ghazanfar, 2006, 2009; Lewkowicz, Leo, & Simion, 2010; Lewkowicz, 2014). If this were the case, I would expect them to look longer at the approaching visual stimulus when paired with the increasing sound and at the receding visual stimulus when paired with the decreasing sound. At the same time, anyway, due to the adaptively relevance of looming stimuli, I could also expect to find a visual preference for congruent approaching audio-visual stimuli in the Increasing sound condition and the absence of any visual preference in the Decreasing sound condition. This last hypothesised result would closely resemble that obtained by Maier and colleagues with rhesus monkeys (Maier, Neuhoff, Logothetis, & Ghazanfar, 2004). If this were the case, I could anyway speculate on newborns' ability to integrate multimodal stimulation as – if they did not – I would expect to find a visual preference for the approaching visual stimulus also in the Decreasing sound condition.

Moreover, should newborns integrate audio-visual stimuli, I would expect a facilitative effect of multimodal vs. unimodal stimulation in the processing of stimuli with congruent direction (Cappe, Thut, Romei, & Murray, 2009). In particular, I would expect the newborns to look longer at the AC visual stimulus, but not at the R one, when paired with an increasing sound vs. when presented unimodally; conversely, I would expect them to attend for longer periods of time the R visual stimulus, but not the AC one, when paired with a decreasing sound vs. when presented unimodally.

4.4.4 Data Analysis

After the experimental session, I analysed offline the video recordings the newborns' eye movements. While doing so, I was blind to sessions and trials order, so unable to determine the ongoing trial. I coded how long each newborn looked at each side of the screen during both sessions and, in this way, I obtained a measure of the time that the newborns spent looking at each audio-visual stimulus in both sessions.

4.4.5 Results

4.4.5.1 Bimodal Audio-visual Paradigm Analysis

Recording how long each newborn looked at each side of the screen I obtained a measure of the time that the newborns spent looking at AC and R stimuli when paired with either the increasing or the decreasing sounds.

For each newborn I calculated the proportions of looking time (P(LT)) dividing the LT to each stimulus by the total exposure time of that stimulus. The results are summarised in Table 4.4.1 and Fig 4.4.2.

		Condition			
		Increasing sound		Decreasing sound	
		P(LT)	SE	P(LT)	SE
Movie	AC	.3070	.0196	.2631	.0181
	R	.2242	.0132	.2451	.0154

Table 4.4.1 Looking time results. The table shows the average proportions of looking time P(LT) to each stimulus in both sessions and their Standard Error (SE).

Figure 4.4.2 Proportions of looking time. Distribution of the proportions of looking time (P(LT)) directed to AC and R visual stimuli when paired with either increasing or decreasing sounds. The P(LT) were calculated dividing the LT to each stimulus by the total exposure time of that stimulus.

I ran a two-way repeated measures ANOVA, with Congruency and Sound condition as factors. It revealed a significant effect of the Interaction [$F(1, 19) = 6.652$, $p = .018$, $\eta^2 = .133$], whereas the main effects of Congruency and Sound condition were both non-significant [respectively, $F(1, 19) = 3.916$, $p = .063$, $\eta^2 = .055$; $F(1, 19) = .809$, $p = .380$, $\eta^2 = .008$]. All other control analyses (i.e. order of presentation of the session and of trials within each session) were non-significant. I followed this up with two paired planned comparisons, after verifying that the difference between the P(LT) to each pair of stimuli did not deviate from normality using the Kolmogorov-Smirnov test [Increasing sound condition, $D = .158$, $p = .200$;

Decreasing sound condition, D = .114, p = .200]. The paired comparisons showed a significantly different looking time to the two visual stimuli only in the Increasing sound condition: only in this condition the newborns looked significantly longer to the congruent (AC) visual stimulus, whereas in the Decreasing sound condition they attended both stimuli for similar amounts of time [Increasing sound condition: $t(19)$ = 3.562, p = .002, d_z = .797; Decreasing sound condition: $t(19)$ = .653, p = .521, d_z = .146] (Fig. 4.4.3).
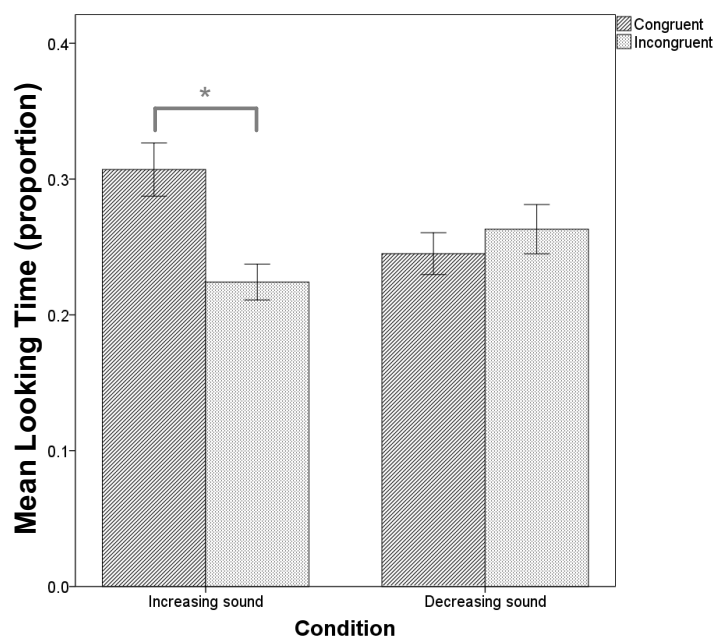
Figure 4.4.3 Means of the proportions of looking time. Means and S.E. of the P(LT) to congruent and incongruent stimuli in the Increasing sound condition (visual stimuli paired with an increasing sound, congruent with AC) and B (visual stimuli paired with a decreasing sound, congruent with R).

I also ran two additional paired one tailed t-tests, comparing the looking time to the same visual stimulus under the two different sound conditions, expecting the AC stimulus to be attended for longer periods of time when paired with the increasing vs. decreasing sound and, conversely, the R stimulus to be looked for longer periods of time when paired with the decreasing vs. increasing sound. The planned comparisons revealed that my hypothesis was true for the AC stimulus only [AC: one tailed $t(19)$ = 1.839, p = .041, d_z = .411; R: one tailed $t(19)$ = -1.225, p = .118, d_z = 0.274].

These results showed that the newborns manifested a visual preference for congruent audio-visual stimuli, but only when the sound was increasing (i.e. Increasing sound-AC pairing). When the sound was decreasing, instead, they seemed to direct their attention to the congruent and incongruent stimuli for a similar amount of time. The absence of a visual preference in the Decreasing sound condition ruled out the possibility that a sound (irrespective of its direction) could act as a general attention trigger and, instead, was suggestive of an interaction between multisensory integration principles and the ethological meaning of the stimuli.

4.4.5.2 Uni – Bimodal Comparison Analysis

In order to understand the role of multimodal stimulation in the processing of movement trajectories, I compared the results of this study with those of Study 1, where only unimodal visual stimuli were presented. In fact, a preference for congruent audio-visual stimuli does not – on its own – account for facilitated processing of multimodal vs. unimodal ethologically relevant stimuli such as impending collision ones (Cappe, Romei, Thut and Murray, 2009). The relevant P(LT) results from the previous study are summarised in Table 4.3.1, session A.

I ran two separated mixed ANOVAs, with Movie as a within participants factor and Modality (unimodal vs. multimodal) as a between participants one. The first ANOVA compared the results of the unimodal study (No sound condition) with those from the Increasing sound condition of the multimodal study and the second compared the results from the unimodal study (No sound condition) with those from the Decreasing sound condition of the multimodal study.

The first ANOVA (Fig. 4.4.4) showed a significant main effect of Movie [within participants, $F(1, 38) = 21.884$, $p < .001$, $\eta^2 = .364$], a tendency towards significance of the main effect of Modality [between participants, $F(1, 38) = 3.351$, $p = .075$, $\eta^2 = .083$] and no significant effect of the Interaction [$F(1, 38) = .120$, $p = .731$, $\eta^2 = .003$]. The main effect of

Movie highlighted that both groups of newborns looked longer at the AC stimulus than at the R one. The tendency towards significance of the main effect of Modality, instead, may suggest that the amount of time spent looking at the screen might have been slightly longer for the group of newborns presented with the multimodal stimuli.
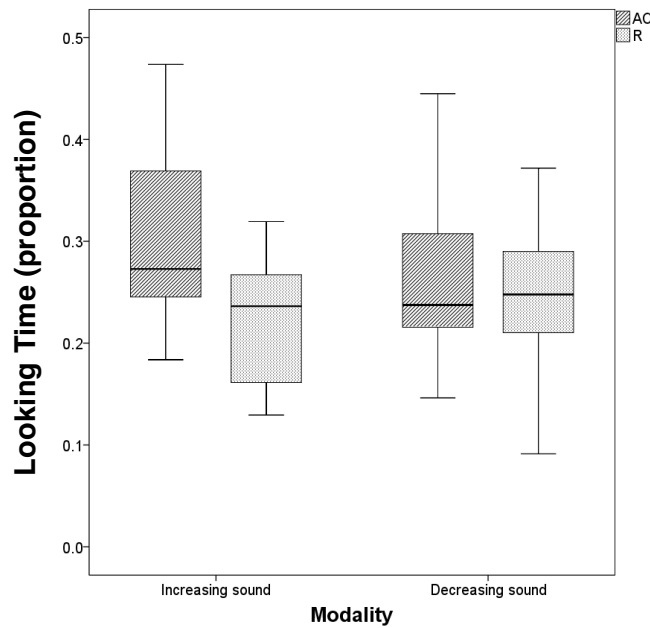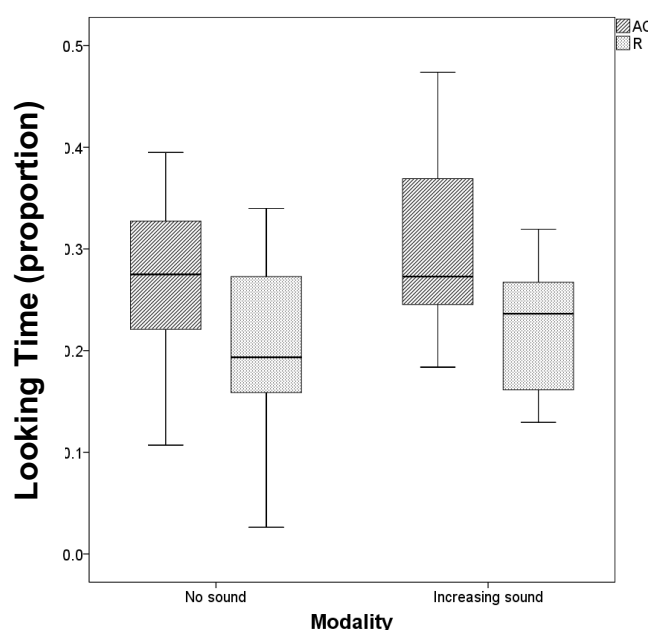

Figure 4.4.4 Proportions of looking time. Distribution of the proportions of looking time (P(LT)) directed to AC and R visual stimuli when paired with either no sound (Study 1) or an increasing sound (Study 2). The P(LT) were calculated dividing the LT to each stimulus by the total exposure time of that stimulus.

I ran a further independent sample, one-tailed t-test in order to test whether the looking time to the AC movie was enhanced by the perception of a simultaneous sound depicting motion in a congruent direction. The analysis highlighted that the newborns showed a tendency to look longer to the AC visual stimulus when paired with an increasing (congruent) sound rather than when presented alone [one tailed $t(38) = 1.408$, $p = .0875$, $d_z = .315$]. Conversely, the looking times to the R movie were not significantly different if it was paired with an incongruent sound or presented alone [two tailed $t(38) = 1.295$, $p = .211$, $d_z = .290$]. The differences of the P(LT) were normally distributed in both pairings of stimuli: Kolmogorov-Smirnov test, all $p > .05$. These results further supported my hypothesis that the presence of a sound combined with the visual stimuli is not a general "attention trigger", that enhances the

looking times irrespectively of its content: conversely, it seems to enhance only the amount of attention directed to those visual stimuli depicting a directionally congruent trajectory.

The second ANOVA (Fig. 4.4.5) showed a significant main effect of the Movie [within participants, $F(1, 38) = 6.122$, $p = .018$, $\eta^2 = .132$; whereas both the Modality of presentation [between participants, $F(1, 38) = 1.596$, $p = .241$, $\eta^2 = .039$] and the Interaction [$F(1, 38) = 2.183$, $p = .148$, $\eta^2 = .046$] did not yield to significant effects. However, the previously reported paired planned comparison (Par 4.4.5.1) revealed that the two visual stimuli were attended for a similar period of time when they were paired with the decreasing sound: when the stimuli were paired with a decreasing sound, in fact, no significant difference in the P(LT) to the AC vs. R stimuli was found [paired $t(19) = .653$, $p = .521$, $d_z = .146$].
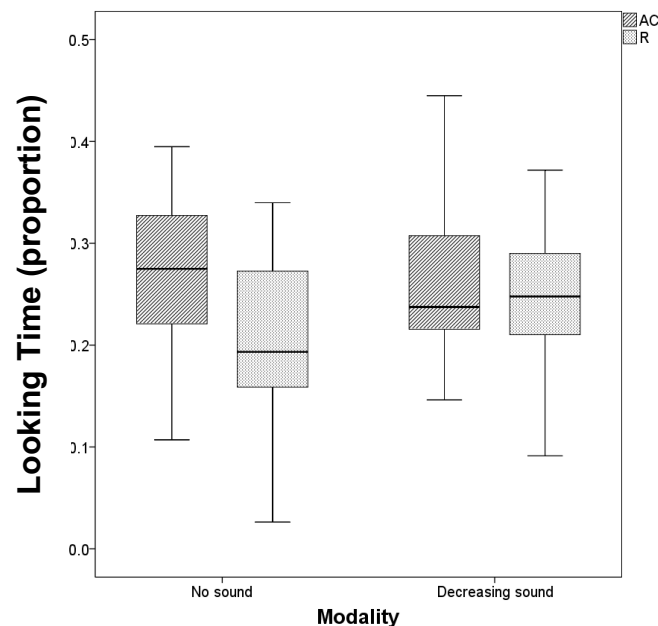
Figure 4.4.5 Proportions of looking time. Distribution of the proportions of looking time (P(LT)) directed to AC and R visual stimuli when paired with either no sound (Study 1) or a decreasing sound (Study 2). The P(LT) were calculated dividing the LT to each stimulus by the total exposure time of that stimulus.

An additional, independent sample, one tailed t-test was run to test whether a simultaneous and directionally congruent sound would increase the looking time to the R visual stimulus in comparison to when the same stimulus was presented alone. This analysis confirmed

that the R movie was looked significantly longer when paired with a decreasing sound than when presented alone [one tailed $t(38) = 2.249$, $p = .019$, $d_z = .503$]. On the contrary, the looking times to the AC movie were not significantly different if paired with the decreasing sound or presented unimodally [two tailed $t(38) = .358$, $p = .724$, $d_z = .080$]. The differences of the P(LT) were normally distributed in both pairings of stimuli: Kolmogorov-Smirnov test, all $p > .05$. Once again, these results highlighted that auditory stimuli did not enhance visual attention generally, increasing the total amount of time spent looking at the screen. Presenting a sound, instead, seemed to enhance newborns' attention only to the visual stimulus moving in the same direction of the auditory one.

4.4.6 Discussion

I previously demonstrated that newborns show a visual preference for approaching trajectories when presented in the visual modality (Study 1). This could be attributed to the adaptive importance of approaching objects, which could signal either an impending danger or an incoming occasion of social contact and communication (Cappe, Thut, Romei, & Murray, 2009; Kandula, Hofman, & Dijkerman, 2015; Maier & Ghazanfar, 2007; Van der Stoep, Nijboer, Van der Stigchel, & Spence, 2015). In any ecological situation, though, it is unlikely to detect the approach of a stimulus with the sole vision. In fact, stimuli could approach from outside the visual field or while eyes are closed, making vision inefficient in detecting them and enhancing the identifying role of audition (Ferri, Tajadura-Jiménez, Väljamäe, Vastano, & Costantini, 2015; Ghazanfar, Neuhoff, & Logothetis, 2002). Also, most of the times approaching stimuli are perceived thanks to the combination of visual and auditory signals: previous research identified a perceptual bias for multisensory looming stimuli in primates and selective integration of multimodal looming stimuli in human adults (Cappe et al., 2009; Maier, Neuhoff, Logothetis, & Ghazanfar, 2004).

This preferential processing of multisensory looming stimuli might be related to the already mentioned adaptive importance of looming trajectories and – if this were the case – it would be reasonable to expect multimodal looming stimuli to be preferentially processed right after birth. In order to investigate this hypothesis, I measured the looking behaviour of newborns presented with simultaneous auditory and visual information related to adaptively relevant trajectories. Specifically, I showed them two simultaneous visual stimuli, moving along an approaching and a receding trajectory, paired with a simultaneous sound, simulating either the approach or the recess of a sound source.

The results showed that newborns attended the approaching visual stimulus longer than the receding one when they were presented together with a simultaneous increasing sound,

whereas they looked at the two stimuli for a comparable amount of time when they were presented paired with a decreasing sound. The looking behaviour of the newborns' who participated in this study resembled that shown by rhesus monkeys participating in a similar study by Maier and colleagues (2004). Furthermore, when presented with a sound simulating the approach of a sound source, the newborns showed a tendency to look at the approaching visual stimulus (but not at the receding one) for a longer amount of time than when it was presented unimodally. Conversely, when presented with a sound simulating the recess of a sound source, the receding visual stimulus (but not the approaching one) was attended for a longer amount of time than when presented unimodally. In both situations, then, the looking time to the visual stimulus depicting a direction congruent to the direction of the sound was enhanced compared to when the same visual stimulus was presented unimodally.

I think that the overall pattern of these results suggests that humans could be able to integrate multimodal stimulation depicting information about moving trajectories already in first hours of life. Taken alone, the results from the Increasing sound condition cannot prove the ability of integrating together stimuli presented in the two different modalities. In fact, the pattern of looking times displayed in the Increasing sound condition was the same as that displayed when unimodal stimuli were presented (Study 1) and, overall, the time spent looking to the visual stimuli was only marginally longer than the time spent attending them when presented unimodally. Looking at this condition alone, then, it could be argued that the presence of a sound may have only slightly enhanced the time the newborns spent attending the screen. However, if this were the case, the same pattern of looking times would be expected also in the Decreasing sound condition. Conversely, the absence of a visual preference in the Decreasing sound condition supports the claim about newborns' ability of integrating congruent audio-visual stimuli in this context and is suggestive of an interaction between multisensory integration principles and ethological meaning of the stimuli. Specifically, I think that when

presented with a sound of decreasing intensity, simulating the recess of a sound source, newborns may be equally attracted by the receding and the approaching visual stimulus because while the former depicts a trajectory congruent with the direction of the sound, the latter is extremely salient from a behavioural point of view and, consequently, worth looking at per se. Also, the absence of a visual preference in the Decreasing sound condition might be related to a mechanism resembling the exclusive facilitation for looming multisensory stimuli (compared to receding ones) found in human adults (Cappe et al., 2009).

My claim about multisensory integration abilities in newborns can also supported by the fact that the looking time directed to both visual stimuli was longer (in particular for the receding visual stimulus) when they were paired with a sound moving in a congruent direction than when presented unimodally. The opposite was instead true for the stimulus travelling along a trajectory incongruent to that covered by the sound: in both sound conditions, in fact, the looking time to the incongruent video display did not significantly differ from that directed to the same visual stimulus during unimodal presentation. This latter result, along with the absence of a visual preference in the Decreasing sound condition, reinforces the idea that the presence of a sound did not generally augment the time that the newborns' spent looking at the screen, independently from its content, but increased visual attention only to the visual stimulus moving along the same trajectory of the auditory stimulus.

Concluding, these results suggest for the first time that at birth human infants seem to be already able to integrate stimuli coming from different senses if their motion in space follows the same trajectory. They also highlight how the presence of a sound moving in space could selectively enhance visual attention only to the stimulus moving along a spatially congruent pathway. Finally, they suggest that the processing of multimodal looming stimuli, compared to receding ones, could be selectively facilitated due to their high adaptive value (Cappe et al., 2009).

In light of these results, I decided to investigate how multimodal integration within this specific context evolves during the first year of life, in order to test whether the looking behaviour pattern identified in newborns and − particularly − their enhanced processing of audio-visual approaching stimuli should be attributed to an adaptive mechanism similar to adults' one (Cappe et al., 2009) or more generally to young infants' spontaneous preference for congruent, i.e. intersensory redundant, stimuli (Bahrick & Lickliter, 2000, 2012; Bahrick, Lickliter, & Flom, 2004; Filippetti, Lloyd-Fox, Dragovic, Johnson, & Farroni, 2014; Filippetti, Orioli, Johnson, & Farroni, 2015; Lewkowicz & Ghazanfar, 2006, 2009; Lewkowicz, Leo, & Simion, 2010; Lewkowicz, 2014).

5. DISCRIMINATION OF UNIMODAL AND MULTIMODAL TRAJECTORIES IN INFANTS (STUDY 3)

5.1 RATIONALE

After having studied newborns' ability to discriminate the different trajectories of stimuli moving within the near space and their preference for those approaching their body, I wanted to track the development of this ability during the first year of life, investigating also if and how it might correlate with infants' motor development.

For this reason, I decided to test infants when they reach two milestones in their motor development, i.e. when they learn to reach and grasp. I hypothesised that there might be a relationship between achieving reaching and grasping abilities and the perception of events happening in the space immediately surrounding the body as well as its representation, as the peripersonal space is also the space where reaching and grasping can take place. This hypothesis was also supported by findings showing neural activation in sensorimotor areas corresponding to reaching and grasping networks during tasks requiring to determine the expected time-to-contact (TTC) of a looming stimulus (Field & Wann, 2005; Billington & Wilkie, 2011). Field and Wann investigated the link between TTC judgements and coordinated action using fMRI. The authors identified selective activation of somatosensory areas, which they describe as targeted by information coming from the dorsal visual system, among which some are normally involved in the production of reaching-to-grasp responses (Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002). Using two different control tasks (inflation judgment and gap-closure) they ensured that this activation could not be related to the processing of image expansion or relative motion, nor to the movements that the participants performed in order to complete the task, but should be attributed to the preparation of a timed motor response to the looming stimulus, specifying motion towards the observer. More recently Billington and Wilkie (2011) compared,

as well using fMRI, neural responses to looming stimuli vs. to receding and motion-controlled static stimuli. Their results confirmed that the cortical regions associated with motor preparation showed activation in response to looming stimuli only.

Several studies investigated the emergence of reaching and grasping abilities in infancy. Von Hofsten (1991) described the onset of functional reaching as one of the "most remarkable and dramatic transitions in early motor development" (p. 280) and reported that this transition happens around 4 months of age. He highlighted that the onset of functional reaching, as all new forms of action, relies on multiple previous developmental achievements, including control of the arms and hands, improved postural control, precise perception of depth, perception of motion and control of smooth eye tracking, development of muscle strength and motivation to reach (von Hofsten, 2004). He reported that the first reaching movements are generally inaccurate and their hand trajectories are poorly controlled (von Hofsten, 1991), showing "characteristic jerky and zig-zag movements" (Thelen, Corbetta, & Spencer, 1996, p. 1059). The first successful reaches (15-18 weeks) include several acceleration and deceleration movement units, whereas as infants grow up their reaches become straighter and more precisely directed to the target, and include fewer movement units (Thelen et al.; von Hofsten, 1979). Von Hofsten (1979) also showed that the successful reaching for stationary and moving objects is mastered by infants at the same time, i.e. from about 18 weeks of age, and that young infants are able to reach fast-moving objects, predicting the meeting point between the reaching hand and the object (von Hofsten, 1980). Thelen and Spencer (1998), in a study investigating the interplay between postural control, coordination and intentional reaching, reported that their participants performed their first functional reaches between 12 and 20 weeks of life.

Von Hofsten and Rönnqvist (1988) investigated the emergence of early integrated reaching and grasping movements, where the grasping of the target is prepared already during the approach phase. They showed that some preparation for grasping the target during

reaching is present already at 5-6 months, but only at 9 months the opening of the hand is adjusted to the size of the target and only from 13 months of age also the timing and precision of the grasp shows adult-like properties. Rochat and Goubet (1995) studied the development of the relationship between reaching and sitting and showed a significantly increased frequency of grasping within their "sitters" group, aged between 22 and 37 weeks (5.5 to 9 months), compared to younger infants ("nonsitters" and "nearsitters"). Konczak and Dichgans (1997) reported reliable grasping between 3 and 4 months after the emergence of reaching, i.e. around 7 to 9 months of life. Fagard and colleagues investigated reaching and grasping of a moving object at 6, 8 and 10 months of life and showed a significant improvement of grasps in the 10-month-old infants compared with the two groups of younger infants (Fagard, Spekle, & von Hofsten, 2009).

In light of these findings, I decided to study the perception of uni and multimodal trajectories in two groups of infants, aged respectively 5 and 9 months on average. One study (Walker-Andrews, 1985) had already investigated 5-month-old infants' ability to match audio-visual information specifying movement direction, showing their preference for congruent audio-visual stimuli, irrespective of the direction of their movement. Nevertheless, I decided to run this study with infants aged 5 months in order to be able to compare the looking behaviour of infants of different ages (newborns, 5- and 9-month-old infants) presented with the same stimuli. I took this decision also in light of the possible adaptive value of the chosen stimuli, which could contribute to the investigation of the interplay between multisensory integration principles and the behavioural value of the stimuli. Furthermore, Walker-Andrews' (1985) study emphasised the attentional or perceptual benefits of multimodal congruent stimuli, but did not specifically show the presence of multisensory integration, which would be demonstrated by the selective facilitation of the perception of multimodal stimuli compared to their unimodal components (Cappe, Thut, Romei, & Murray, 2009).

This study involved two groups of 20 infants each. The infants were aged on average 5 months in one group and 9 months in the other one. Five-month-old infants (10 female) were aged on average 21.20 weeks at time of testing (SD = 1.42). Fifteen additional 5-month-old infants participated, but were excluded from further analyses due to fussiness (n = 6), experimental error (n = 1), side bias (n = 5) or lack of sufficient experimental data (n = 3). Nine-month-old infants (10 female) were aged on average 38.24 weeks at time of testing (SD = 1.84). Eleven additional 9-month-olds participated, but were excluded from further analyses due to fussiness (n = 3), experimental error (n = 3), side bias (n = 4) or lack of sufficient experimental data (n = 1).

The parents brought the infants to the Lab located within the Paediatric Unit of the Hospital of Monfalcone (GO) at a previously agreed time that suited their schedule. They were informed about the procedure and provided written informed consent to their child's participation. The local Ethical Committee of Psychology Research (University of Padua) approved the study protocol.

I decided to use two instruments in order to assess the motor abilities of the infants who participated in the study and in particular to verify their ability to reach for (at 5 months) and grasp (at 9 months) an object. On one side, I asked the parents to fill in a questionnaire measuring early motor skills (Early Motor Questionnaire, Libertus & Landa, 2013, described in the following paragraph); on the other side, I presented the infants with a simple "reaching assessment task" (Libertus & Needham, 2010, described in Ch. 5.3.2). In this way, I was able to make sure that both samples included infants with a similar level of motor development and that the infants in the two samples showed reaching and grasping abilities, respectively at 5 and 9 months of life.

5.3.1 Early Motor Questionnaire (EMQ)

The EMQ is a newly introduced, research-focused, parent-report measure of infants' early motor skills (Libertus & Landa, 2013). The necessity of creating this new instrument derived from two main reasons. On one side, classical examiner-administered assessments on motor skills are time consuming, expensive and at risk of underestimating the true abilities of the infant. On the other side, although parent-report measures could be more effective and precise, their validity cannot be clearly stated, as there are only a few questionnaires focusing specifically on this topic and even less cover the first two years of life (Libertus & Landa, 2013).

5.3.1.1 The questionnaire: creation and validation

The EMQ focuses particularly on early motor skills, which develop during the first two years of life, as in the early stages of life they play a particularly critical role for overall development (Libertus & Landa, 2013). This is true particularly because developing motor skills provide infants with the instruments for learning about the physical and social world around them, possibly leading to subsequent important effects on cognitive, social and linguistic

development (Bushnell & Boudreau, 1993; Gibson, 1988; Libertus & Needham, 2011). Due to this reason, together with the absence of a reliable and effective tool for extensively measuring early motor development, the authors created a new parent-report questionnaire for assessing motor skills in infancy (0-24 months).

The EMQ is a research (non-standardised) questionnaire, organised into 3 different sections investigating, respectively, Gross Motor (GM), Fine Motor (FM) and Perception-Action integration (PA) skills. The EMQ items are organised around the typical context that an infant of the interested age encounters in everyday situations and describe motor behaviours typically emerging within the first 2 years of life, similar to those commonly assessed by other motor assessments. Parents or caregivers are asked to rate each item on a 5-point scale, ranging between -2 and +2, which quantifies their certainty about the child's ability to perform every behaviour listed. Examples of prototypic items for each Scale are listed in Fig. 5.3.1 (Libertus & Landa, 2013).

Gross Motor Scale	
When placed into a sitting position on the floor, your child is able to...	
A	... *sit independently without support (hands lifted up).*
B	... *use hands and legs to scoot forward on his/her bottom?*
C	... *maintain a stable sitting position while turning head and torso to look around?*
Fine Motor Scale	
When sitting on your lap or in a high chair while playing with toys, you notice your child is able to...	
A	... *successfully hold on to a small object such as a ring or stick?*
B	... *reach for a toy with one hand by extending the arm and fingers?*
C	... *successfully grasp a toy with one hand following a reach?*
Perception-Action Scale	
While lying on his/her back in a crib, baby gym, or on the floor, your child sometimes will...	
A	... *turn the head all the way to one side (90°) to follow your face?*
B	... *notice his/her own hands and look at them for some time?*
C	... *swat at toys hanging from a baby gym or car seat?*

Notes: Parents respond to each item on a 5-point scale, ranging from −2 (parent is sure child does not show behavior) to +2 (parent is sure child shows behavior and remembers particular instance).

Figure 5.3.1 Sample EMQ items (from Libertus & Landa, 2013).

Concurrent and predictive validity of the questionnaire have been examined comparing the results of the parent report with those of two classical and standardised examiner-administered measures (Mullen Scales of Early Learning – MSEL and Peabody Developmental Motor Scales – PDMS-2) in 94 children aged between 3 and 24 months, using correlation

analyses. In order to increase the generalizability of the findings, additional partial correlations were used in order to control for those factors that may influence parents' reports (i.e. age, gap between the assessments, socio economic status, person completing EMQ, having vs. not having a sibling with ASD and time of completion; Libertus & Landa, 2013).

The results highlighted that the caregivers' responses on the EMQ are sensitive to developmental changes in motor development over time: both raw and partial correlation coefficients between EMQ scores and age were significant in all three domains (Fig. 5.3.2, from Libertus & Landa, 2013). Furthermore, concurrent validity of the questionnaire was shown. The results, in fact, suggested that parent reports on the EMQ were predictive of MSEL scores: both raw and partial correlation coefficients between corresponding EMQ and MSEL sections were significant (GM: r = .97, rPartial = .67, both p < .01; FM: r = .91, p < .01, rPartial = .22, p = .04; PA/VR: r = .91, p < .01, rPartial = .27, p = .02) (Fig. 5.3.3, from Libertus & Landa). Finally, a second visit, occurring roughly 4 months and a half after the first one, permitted to evaluate the predictive validity of the EMQ, which was shown to be effective as well: raw and partial correlation coefficients between the EMQ at time 1 and MSEL at time 2 resulted significant on all corresponding scales (Libertus & Landa, 2013).

These analyses showed that the EMQ is a reliable tool for measuring early motor development and provided evidence for the validity and accuracy of parental reports in this area. The EMQ high concurrent and predictive validity with one examiner-administered measure (MSEL) and the fact that its scores linearly increased with time confirmed its usefulness and appropriateness for research on infants' motor skills.
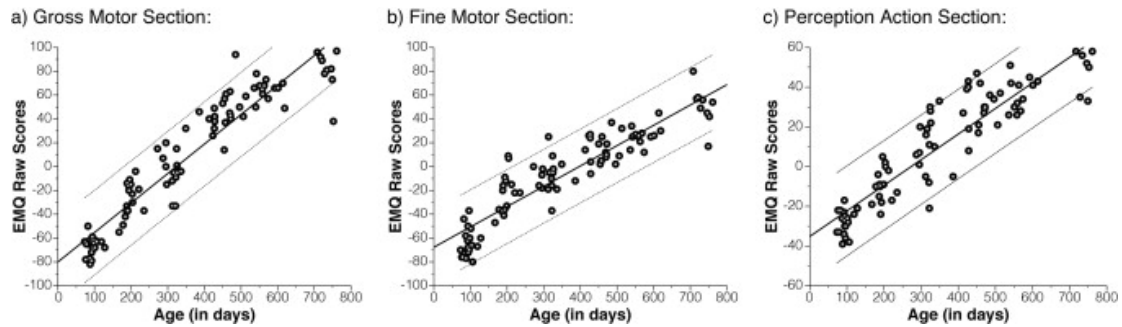
Figure 5.3.2 Correlations between EMQ and age (from Libertus & Landa, 2013). All three EMQ sections correlate strongly with age. Solid and dashed lines show linear fit with 95% confidence intervals.
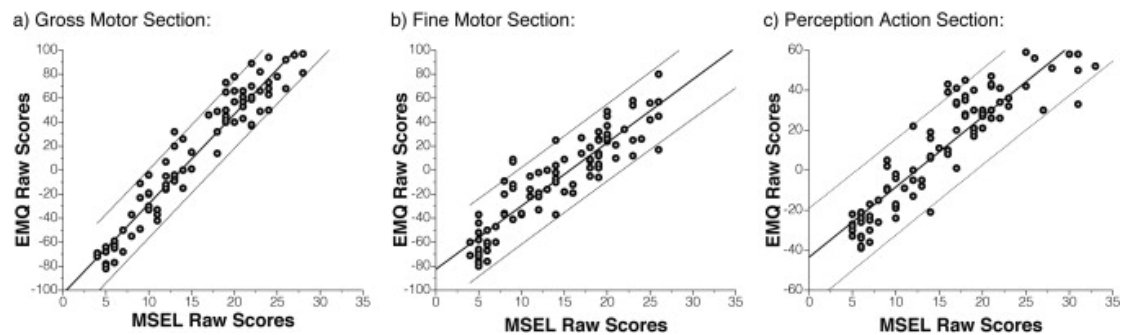
Figure 5.3.3 Concurrent validity of EMQ with MSEL (from Libertus & Landa, 2013). The EMQ and MSEL correlate strongly with each other on corresponding sections (Perception Action section corresponds to Visual Reception scale on MSEL). Correlations remain strong after controlling for influences of age and other factors. Solid and dashed lines show linear fit with 95% confidence intervals.

5.3.1.2 Translation

In order to use the questionnaire with Italian speaking parents, I translated each item of all three subscales in Italian, after having received the approval of the author. In order to assess the validity of the translation, I had it translated back in English and I compared the original and the new English versions, in order to check that there were no substantial differences between the two. Example items – matching those in Fig. 5.3.1 – can be found in Table 5.3.1.

Motricità Grossolana	
Quando seduto sul pavimento, il bambino/a...	
A	…siede autonomamente senza supporto (mani alzate)?
B	…si trascina con l'aiuto di mani e gambe, tenendo il sederino appoggiato a terra?
C	…mantiene una posizione stabile mentre gira la testa e il busto per guardarsi attorno?

Motricità Fine	
Quando seduto in braccio o sul seggiolone mentre gioca con dei giocattoli, notate che il bambino/a è capace	
A	…tenere in mano un piccolo oggetto, come un anello o un bastoncino?
B	…raggiungere un oggetto con una mano allungando il braccio e le dita?
C	…afferrare con successo un giocattolo con una mano dopo averlo raggiunto?

Mentre è disteso sulla schiena nella culla, in una palestrina per bambini o sul pavimento, il bambino/a	
A	…gira la testa di 90° per seguire il suo volto?
B	…nota le sue mani (del b.no/a) e le fissa per un certo periodo di tempo?
C	…colpisce i giocattoli che dondolano nella palestrina o nel seggiolino per l'auto?

Table 5.3.1 Example items of the Italian translation of the EMQ.

5.3.1.3 Analyses and results

I introduced the EMQ questionnaire to assess the motor skills of the infants who took part in the studies, because I aimed for a comparable level of motor development across the infants being part of each of the two experimental groups. To address this, I checked that all the infants included in the final samples (for both age groups) did not score lower that 2 standard deviations below the group mean on each of the three subscales (GM, FM and PA).

I also computed an additional subscale, including all those items referring specifically to reaching and grasping abilities (RG) (e.g.: "when placed into a crawling position […] your child will shift weight to one arm and extend the other to reach?"; "while […] lying […] in a crib, […] you notice your child pulling on a string to obtain an object beyond reach?"; "while […] lying […] in a crib, […] you notice your child successfully grasp a toy with one hand following a reach?" etc..).

In order to check for the homogeneity of the motor skills within each of the age groups, I ran correlation analyses between the values of each subscale and the age (in days) of the participants, following the method used in the validation process (Libertus & Landa, 2013). For 7 infants (17.5%) the data were incomplete because the parents skipped one or more responses, leading to missing values. As in Libertus and Landa (2013), missing singleton values were replaced with scores of 0 (5-month-olds: 3 infants, 9-month-olds, 2 infants), whereas if multiple values were missing in a row, the affected subscale was removed from analyses (5-month-olds: 1 infant, 9-month-olds: 1 infant). All the analyses were performed using raw scores. The values of Gross Motor and Perception Action subscales were not normally distributed in the 5-month-

olds group [GM: $D = .196$, $p = .043$; PA: $D = .262$, $p = .001$], so I performed non-parametric correlations, computing Kendall's tau rank coefficient as the sample sizes were small.

Within each group, I did not find any significant correlation between the scores in every subscale of the EMQ and the age in days of the participants, as can be seen in Table 5.3.2 and Fig 5.3.4. The same was true also for the scores in the items related to reaching and grasping abilities.

		GM	FM	PA	RG
Age in days	**5-month-olds**				
	τ_b	.082	.155	.056	.204
	p	.624	.361	.742	.224
	9-month-olds				
	τ_b	.140	.207	.074	.240
	p	.557	.395	.757	.308

Table 5.3.2 Correlations between EMQ and age. Within each group, there were no significant correlations between the age in days and the scores in the three sections of the EMQ, nor in the reaching-and-grasping-related items.
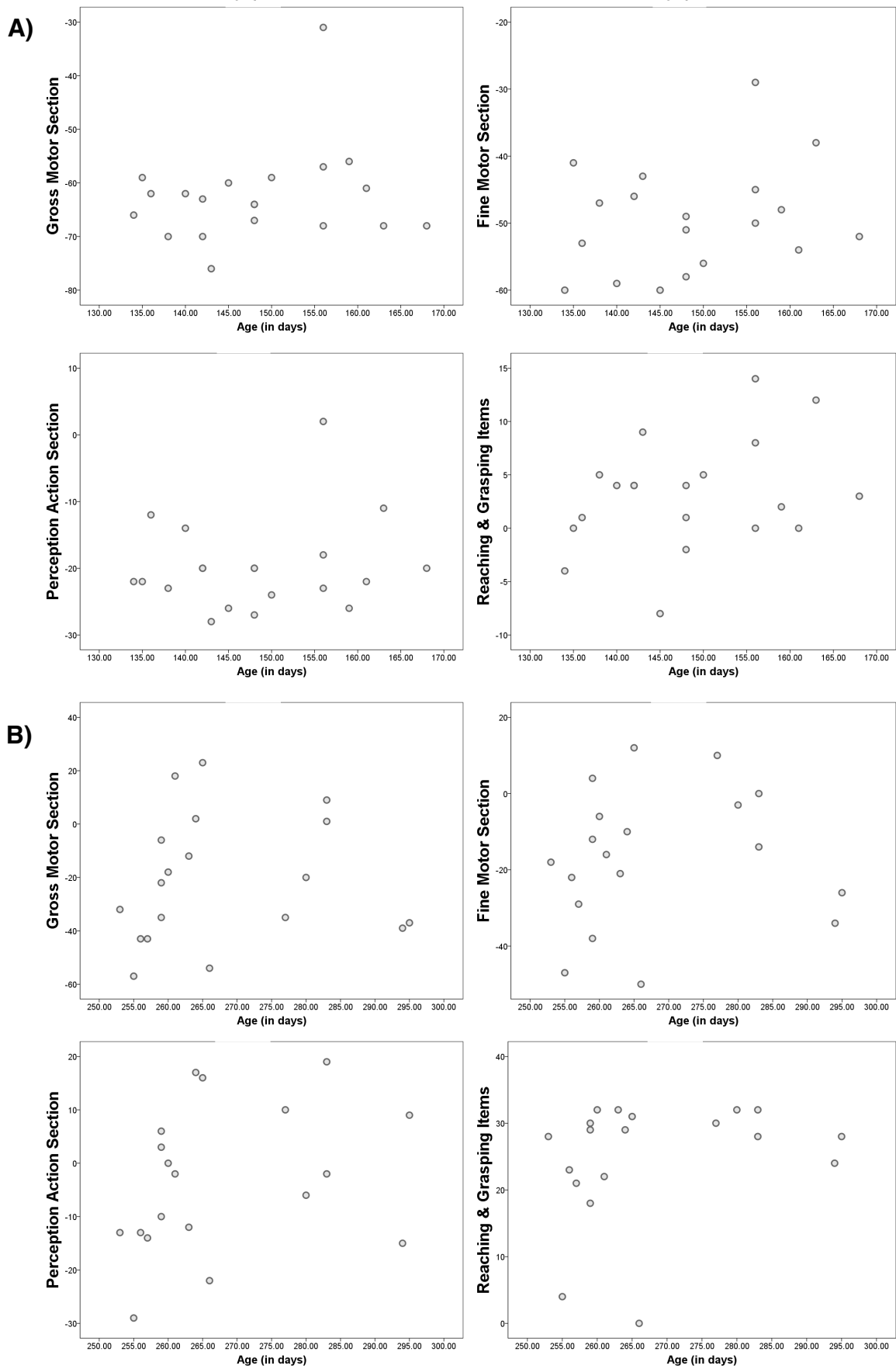
Figure 5.3.4 Correlations between EMQ and age. A) 5-month-olds group; B) 9-month-olds group. Within each group, there were no significant correlations between the age in days and the scores in the three sections of the EMQ, nor in the reaching-and-grasping-related items.

5.3.2 Reaching and grasping task

The task that I decided to use to assess the reaching and grasping abilities of the participants was first introduced by Libertus and Needham (2010) in a study investigating the effect of reaching training on visual exploration of agents and objects in a live and televised context. It is a four-step assessment where a toy (a rattle) is placed in four different positions and the infants' attempts to reach it and grasp it are recorded. The positions are respectively beyond reach, far but within reach, next to the hand and in the infants' hand (Fig. 5.3.5). The order of the steps is fixed and each step lasts approximately 30 s.
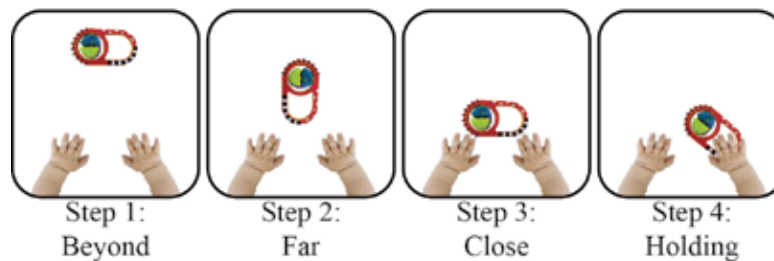
Figure 5.3.5 Example of the four-step reaching assessment (from Libertus & Needham, 2014). A small toy was sequentially placed I) beyond reach, II) far but within reach, III) close to hands at midline, and IV) placed into the infant's hands. Each step lasted about 30 sec.

During every step, several behaviours are assessed: looking at the toy or at the experimenter, reaching for the toy, touching the toy, grasping the toy, bi-manually exploring the toy, swatting at it and mouthing it (Libertus & Needham, 2010). Libertus and Needham focused their attention on looking behaviour (looking to the toy or the experimenter) during the first and last steps (toy beyond reach and infant holding the toy) and on reaching and grasping behaviour during the second and third steps (toy far and close).

The same authors used the above task also in other studies, including one experiment (Libertus & Needham, 2014) investigating the aspects of active reaching training that facilitate reaching and face preference. In this study they analysed infants' behaviours during steps 2 and 3 and defined successful reaching as "an arm movement toward the toy that results in contact

with the object and a partial or complete lift of the object off the table" (Libertus & Needham, 2014, p. 20). In this analysis they combined reaching and grasping, as both behaviours were functional at the exploration of the toy. The duration of a successful reaching unit was quantified from when the infants moved their hands towards they toy to when they released it on the table or floor.

I analysed the behaviour of the infants following Libertus and Needham (2014), but keeping reaching and grasping behaviours separated from each other. Hence, I considered as a successful reaching unit the period of time from when the infants moved their hands towards the toy to when they touched it and a successful grasping unit the period of time from when they touched and grasped it until when they released it. Reaching included also touching behaviours, if the toy was not lifted. Grasping included every period of time when the infants engaged with the toy (lifting, shaking, mouthing…) as long as the contact between the hand and the toy was maintained.

For the 5-month-olds group, 15/20 recordings of the reaching and grasping task were available. Step 4 was never performed because all infants reached the toy already during steps 2 or 3. Each step lasted on average 20 s. The infants in this group spent on average 44% of the time in step 1 and 82% of the time in step 2 looking either at the toy or at the observer. Most infants attempted to reach the toy during step 3, spending on average 39% of the time reaching for it or touching it. Five infants attempted to reach the object already during steps 1 and 2 and spent a good amount of time (33%) during step 3 grasping or mouthing the object and exploring it with both hands. Overall, all the 15 infants showed effective reaching when the toy was close enough to their body (step 3). Averaged percentages of time spent performing each of the 7 assessed behaviours during every step are represented in Fig. 5.3.6.

Figure 5.3.6 Reaching and grasping task (5-month-olds). The graphs represent the averaged percentages of time spent by the group of 5-month-old infants performing each of the 7 assessed behaviours during every step of the task.

For the 9-month-olds group, 15/20 recordings of the reaching and grasping task were available. Steps 3 and 4 were never performed because all infants successfully grasped the toy already during step 2. In 3 cases only step 1 was performed because the infants successfully grasped the toy already when it was beyond reach. Each step lasted on average 27 s. The infants in this group spent on average 32% of the time during step 1 and 10% of the time during step 2 looking either at the toy or at the observer. They spent 19% of the time during step 1 and 23% of the time during step 2 reaching for the object and touching it. Finally, they spent 21% of the time during step 1 and 62% of the time during step 2 grasping the object and exploring it with both hands. Overall, all the 15 infants showed successful grasping when the toy was far from the body but within reach and some of them also grasped it when it was still beyond reach. Averaged percentages of time spent performing each of the 6 behaviours assessed during each step are represented in Fig. 5.3.7.
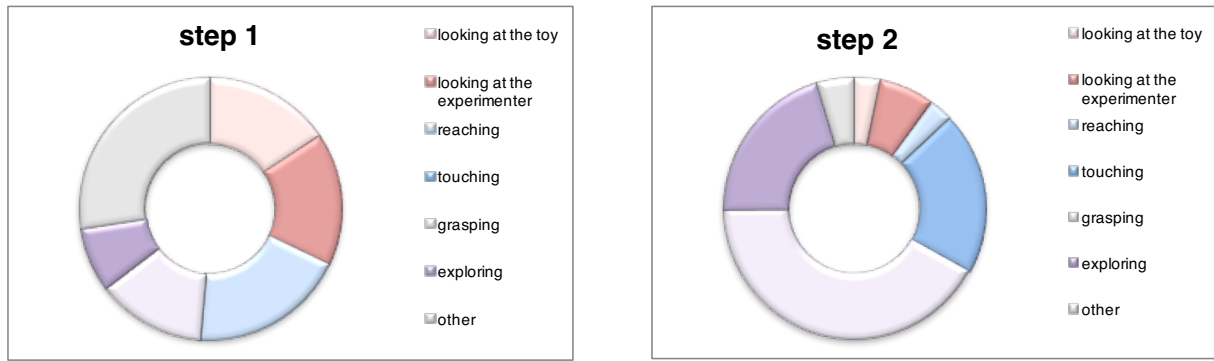
Figure 5.3.7 Reaching and grasping task (9-month-olds). The graphs represent the averaged percentages of time spent by the group of 9-month-old infants performing each of the 7 assessed behaviours during every step of the task.

5.4 METHOD, PROCEDURE AND STIMULI

The study was conducted with a preferential looking paradigm, as described in Chapter 3, using the visual stimuli described in Ch. 4.2.1 and the auditory stimuli described in Ch. 4.2.2.

The paradigm included three sessions, each corresponding to a different condition and each comprising two trials. Each infant took part in all three sessions.

During the No sound condition, the infants were presented with unimodal stimuli, constituted by two simultaneous movies. The two movies were displayed one on the left- and one on the right-hand side of the screen: they were located in the peripheral area of the screen to ensure that the infants' attention was engaged. During the Increasing sound condition and the Decreasing sound condition, the infants were presented with multimodal stimuli, constituted by two simultaneous movies and a simultaneous sound, which was different between the two conditions. The sound was conveyed by two loudspeakers positioned under the monitor, one under the left and one under the right halves of the screen. The order of presentation of the sessions and the trials within each session was counterbalanced across infants, with the No sound condition being presented only as the first or last one.

The experiment began as soon as the infants were seated and attending to the centre of the screen. During all the three conditions, they were presented with two different movies on the two sides of the screen: on one side they could see an approaching and colliding visual stimulus (AC), whereas on the other side they could see a receding visual stimulus (R). The side of presentation of each movie was counterbalanced between the two trials. In the No sound condition, the visual stimuli were presented unimodally; in the Increasing sound condition they were accompanied by an increasing sound, depicting a trajectory congruent with the approaching visual stimulus (AC); in the Decreasing sound condition they were paired with a decreasing sound, congruent with the receding visual stimulus (R) (Fig. 5.4.1) Stimuli were presented using E-Prime 2.0.10.
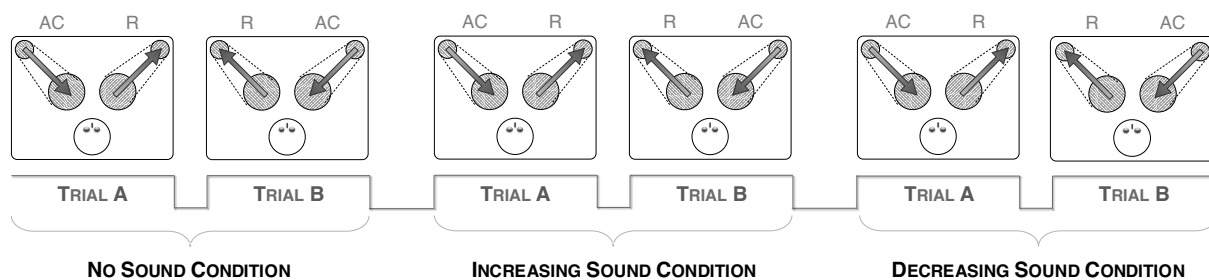
Figure 5.4.1 Description of the experimental procedure. The experiment consisted of three sessions, each representing a different condition and each including two trials. The three sessions and the two trials within each session were presented in counterbalanced order across participants, with the No sound condition being either the first or the last one. In each trial of each session I compared AC and R movies (8 repetitions); the positions of the two movies were counterbalanced across trials. In the No sound condition, stimuli were presented unimodally (only visually), in the Increasing sound condition they were paired with an increasing sound, congruent with the AC visual stimulus, whereas in the Decreasing sound condition they were paired with a decreasing sound, congruent with the R visual stimulus.

5.5 HYPOTHESES

In light of the results obtained in the first two studies run with newborns (Ch. 4), I expected the older infants to be able to discriminate between different trajectories when presented only through visual cues. Specifically, I expected both groups of infants to attend for longer periods of time the visual stimuli approaching them and targeting their body, due to their high adaptive relevance and ethological meaning.

Nonetheless, I was greatly interested in the looking behaviour that infants would show when presented with multimodal stimuli depicting different trajectories happening within the portion of space immediately around their bodies. I thought about four possible different outcomes. If infants were not able to integrate information coming from different sensory modalities and if the presence of a simultaneous sound would only enhance their attention, without having an impact on their visual preference, I would expect them to always look longer to the approaching movie, irrespective of the paired sound, possibly for longer periods of time in the multimodal conditions than in the unimodal one. However, a previous study (Study 2, Ch. 4.4) showed that newborns could integrate multimodal stimuli conveying information about motion trajectories and that the presence of a sound did not simply trigger newborns' attention irrespective of the information conveyed by the sound. In light of these findings, this first

outcome seemed unlikely. Hypothesising that infants would be able to integrate multimodal information, three different outcomes were possible: they could show a spontaneous preference for congruent audio-visual stimuli (i.e. visual and auditory stimuli moving along the same trajectory), for incongruent audio-visual stimuli, or for either congruent or incongruent audio-visual stimuli depending on their age. I thought that the last foreseen outcome would be the most likely and, in particular, I expected the younger infants to prefer multimodal stimuli depicting congruent trajectories and the older infants to be more interested in looking at incongruent (and then unexpected) multimodal trajectories.

I believe that this outcome would be the most likely in light of previous findings on multisensory integration in infancy and adulthood. It has been suggested that in the earliest stages of development, when infants are overwhelmed with stimulation coming from multiple events and multiple senses concurrently, their attention would be captured by amodal information redundantly presented across two sensory modalities at the same time and in the same space (Bahrick & Lickliter, 2000, 2012; Bahrick, Lickliter, & Flom, 2004, Lewkowicz, 2008). According to this theoretic framework, amodal information is to be considered not specific to a particular sense modality, possibly conveyed redundantly by multiple senses and including information about fundamental aspects of stimulation, like time, space and intensity (Bahrick & Lickliter, 2000; 2012; Bahrick et al., 2004). Focusing the attention on redundant sensory information could be fundamental for perceptual development, as it would allow infants to perceive the critical aspects of the stimulation that constitute unitary events, ignoring simultaneous stimulation deriving from unrelated events that happen at the same time and space (Bahrick et al., 2004). The Intersensory Redundancy Hypothesis (IRH) suggests that during early infancy intersensory redundancy biases selective attention towards the detection of amodal information from multimodal events. In this way, it promotes the processing of the redundantly specified properties of the stimuli and, thus, guides the perceptual processing to

focus on meaningful and unitary events (Bahrick et al., 2004). The IRH predicts that in the earliest stages of development the processing and learning of amodal properties would be facilitated when they are multimodal and redundant (vs. unimodal), whereas the processing of modality-specific properties would be easier in unimodal presentation. It does also hypothesise that, across development, perceptual processing becomes increasingly flexible and, as a consequence, both amodal and modality-specific properties can be detected both in uni and multisensory contexts (Bahrick et al., 2004). In light of this theoretical hypothesis, I expected that younger infants would direct their attention towards congruent stimuli, which depict intersensory redundant information on the trajectory direction. Conversely, I expected that 9-month-old infants would have mastered a more flexible perceptual processing and would direct their attention in a more "adult-like" fashion, i.e. showing an enhanced and facilitated processing of audio-visual looming (Cappe, Thut, Romei, & Murray, 2009; Ch. 2.1).

5.6 DATA ANALYSIS

After the experimental session, I coded offline the video recordings of the eye movements of the infants' in both groups. Two other independent observers also coded the infants' eye movements, one judging the 5- and one the 9-month-olds groups. For both groups, the second coder was unaware of the hypotheses, while all the three judges were always blind to the order of presentation of the sessions and of the trials. The observers coded how long each infant looked at each side of the screen during each session. In this way, I obtained relative measures of the time that the infants spent looking at AC and R movies in each session.

For both groups, two interrater reliability analyses were performed: the Pearson's r correlation analysis and the Interclass Correlation Coefficient (ICC). For the 5-month-olds group, the Pearson's r correlation was performed on the data from 13 infants (65% of the sample), and revealed a score of $r = .947$; the ICC was instead performed on the 20% of the sample (n = 4), and showed an agreement between coders = .966. Similarly, for the 9-month-olds group, the Pearson's r correlation was performed on the data from 13 infants (65% of the sample), and revealed a score of $r = .986$; the ICC was performed on the 20% of the sample (n = 4), and showed an agreement between coders = .974.

5.7.1 Looking paradigm

I calculated the proportion of looking time (P(LT)) that each infant directed to each stimulus dividing the LT to each stimulus by the total exposure time of that stimulus. Data are summarised in Table 5.7.1 and Fig. 5.7.1 and 5.7.2.

			No sound		Increasing sound		Decreasing sound	
			Condition					
			P(LT)	SE	P(LT)	SE	P(LT)	SE
5 MONTH OLDS	Movie	**AC**	.2781	.0254	.2644	.0192	.2319	.0206
		R	.2335	.0236	.2378	.0218	.2994	.0276
9 MONTH OLDS	Movie	**AC**	.3138	.0265	.3193	.0277	.3139	.0177
		R	.2411	.0179	.3027	.0215	.2663	.0212

Table 5.7.1 Looking time results. The table shows the average proportions of looking time P(LT) to each movie in all three sessions and their Standard Error (SE), for both age groups.
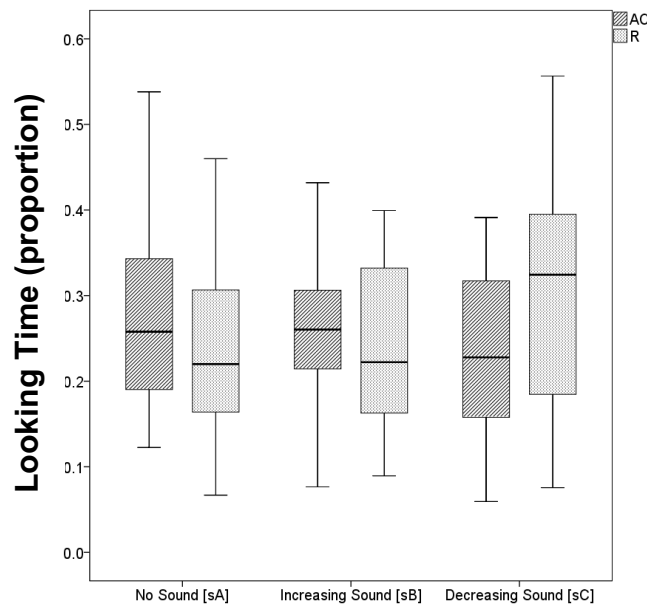
Figure 5.7.1 Proportions of looking time in the group of 5-month-old infants. Distribution of the proportions of looking time (P(LT)) directed to Approaching and Colliding (AC) and Receding (R) stimuli when presented paired with no sound, increasing sound or decreasing sound. The P(LT) were calculated dividing the LT to each stimulus by the total exposure time of that stimulus.
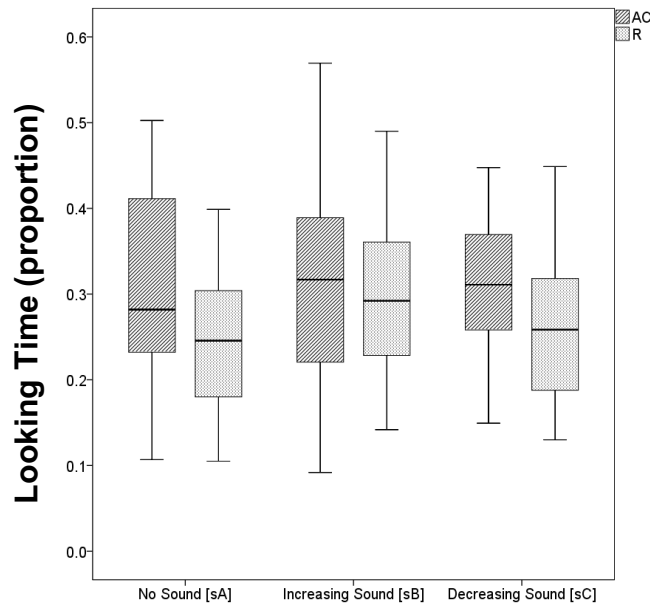
Figure 5.7.2 Proportions of looking time in the group of 9-month-old infants. Distribution of the proportions of looking time (P(LT)) directed to Approaching and Colliding (AC) and Receding (R) stimuli when presented paired with no sound, increasing sound or decreasing sound. The P(LT) were calculated dividing the LT to each stimulus by the total exposure time of that stimulus.

Data from the three sessions were analysed separately, with two different ANOVAs, one investigating the looking behaviour in the unimodal condition, the other in the two multimodal conditions. Both analyses compared the looking behaviour between the two groups of infants.

The looking behaviour in the unimodal condition was analysed using a two-way mixed ANOVA, with Movie as a within subject factor and Group as a between subject factor. It revealed a significant main effect of the Movie [within participants, $F(1, 38) = 19.672$, $p < .001$, $\eta^2 = .335$], whereas both the main effect of Group [between participants, $F(1, 38) = .499$, $p = .484$, $\eta^2 = .012$] and the Interaction effect were not significant [$F(1, 38) = 1.133$, $p = .294$, $\eta^2 = .019$]. The main effect of the Movie highlighted that both groups of infants, irrespective of their age, looked longer at AC stimuli in the unimodal condition (Fig. 5.7.3).
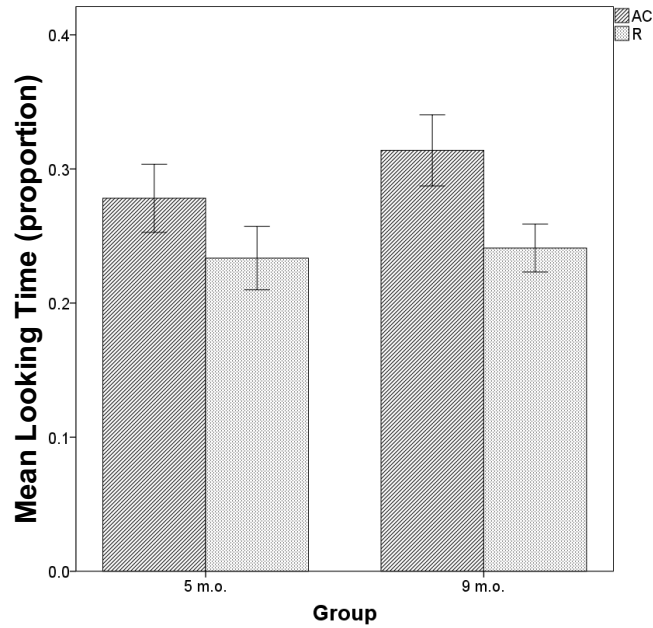
Figure 5.7.3 Means of the proportions of looking time in the No sound condition. Mean and S.E. of the P(LT) to AC and R stimuli when presented unimodally in the two groups.

The looking behaviour in the two multimodal sessions was investigated through a three-way mixed ANOVA, with Congruency and Sound condition as within subject factors and Group as a between subject factor. The analysis revealed a significant interaction between Congruency and Group [$F(1, 38) = 9.354$, $p = .004$, $\eta^2 = .047$]. The interaction between Congruency, Sound condition and Group approached significance [$F(1, 38) = 3.534$, $p = .068$, $\eta^2 = .034$], whereas none of the other main effects nor interactions were significant [Congruency, $F(1, 38) = 2.382$, $p = .131$, $\eta^2 = .012$; Sound condition, $F(1, 38) = .056$, $p = .814$, $\eta^2 < .001$; Group, $F(1, 38) = 3.400$, $p = .073$, $\eta^2 = .082$; Sound condition*Group, $F(1, 38) = 1.741$, $p = .195$, $\eta^2 = .016$; Congruency*Sound condition, $F(1, 38) = .175$, $p = .678$, $\eta^2 = .001$]. All other control analyses (i.e. order of presentation of the sessions and the trials within each session) were also non-significant. The significant interaction between Congruency and Group revealed that infants of different ages showed a different looking behaviour when presented with congruent vs. incongruent audio-visual stimuli.

In order to further investigate this interaction, I ran two additional two-way repeated measures ANOVAs, one for each group of infants, both with Congruency and Sound condition as factors. In the 5-month-olds group, the analysis yielded to a significant main effect of Congruency [$F(1, 19) = 12.195$, $p = .002$, $\eta^2 = .112$]: in both session, infants looked longer to the congruent audio-visual display (AC in the Increasing sound condition and R in the Decreasing sound condition; Fig. 5.7.4); the main effect of Sound condition and the interaction were both non-significant [respectively, $F(1, 19) = .819$, $p = .377$, $\eta^2 = .010$ and $F(1, 19) = .940$, $p = .344$, $\eta^2 = .020$].
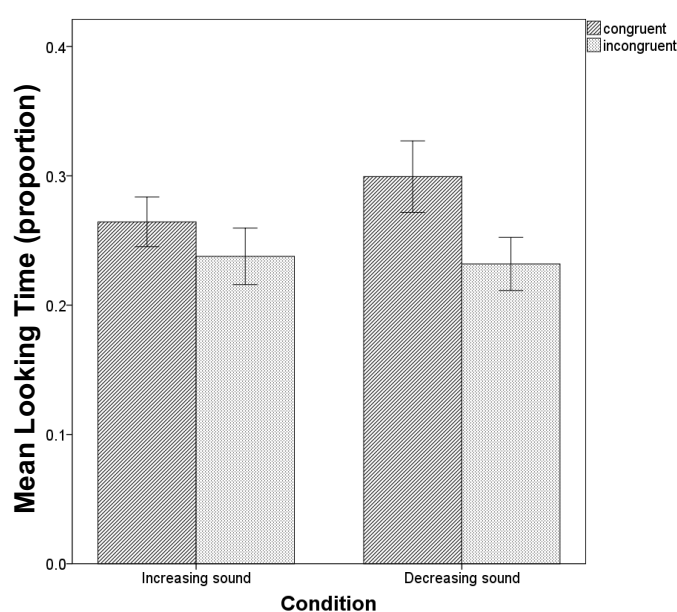
Figure 5.7.4 Means of the proportions of looking time in the Increasing and Decreasing sound conditions, 5-month-old infants group. Means and S.E. of the P(LT) to congruent and incongruent stimuli when presented paired with and increasing or decreasing sound, in the group of 5-month-old infants.

In the 9-month-olds group, instead, the analysis revealed that neither of the main effects were significant [Congruency, $F(1, 19) = 1.014$, $p = .327$, $\eta^2 = .013$; Sound condition, $F(1, 19) = .944$, $p = .344$, $\eta^2 = .023$]. However, the interaction between Congruency and Sound condition showed a tendency towards significance [$F(1, 19) = 3.059$, $p = .096$, $\eta^2 = .053$]. When the sound was decreasing, the P(LT) were longer to the incongruent audio-visual display (AC − incongruent = .314 > R − congruent = .266); when the sound was increasing, instead, the P(LT)

to the congruent and incongruent audio-visual display were comparable (AC − congruent = .319 ≈ R − incongruent = .303) (Fig. 5.7.5).
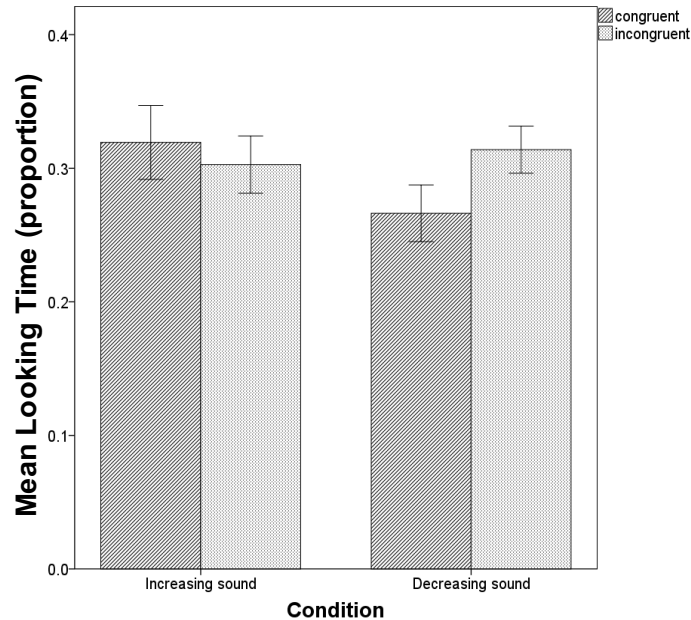
Figure 5.7.5 Means of the proportions of looking time in the Increasing and Decreasing sound conditions, 9-month-old infants group. Means and S.E. of the P(LT) to congruent and incongruent stimuli when presented paired with and increasing or decreasing sound, in the group of 9-month-old infants.

I was also interested in investigating the effect of multimodal vs. unimodal stimulation on the looking behaviour within each of the two different groups, as well as the existence of any facilitative effects related to the multimodal stimulation. To address this, I ran two further separated ANOVAs, each one comparing the P(LT) in the unimodal condition with those in each of the two multimodal conditions (Increasing sound or Decreasing sound).

The first ANOVA compared the P(LT) to AC and R visual stimuli when presented unimodally vs. when paired with an increasing sound, congruent with AC. It revealed a significant main effect of Movie [$F(1, 38) = 10.618$, $p = .002$, $\eta^2 = .082$]. The effect of the interactions between Movie and Modality was approaching significance [$F(1, 38) = 3.578$, $p = .066$, $\eta^2 = .018$], whereas all the other main effects and interactions were non-significant [Modality: $F(1, 38) = 1.030$, $p = .317$, $\eta^2 = .010$; Group: $F(1, 38) = 2.664$, $p = .111$, $\eta^2 = .066$;

Movie*Group: $F(1, 38) = .135$, $p = .715$, $\eta^2 = .001$; Modality*Group: $F(1, 38) = 1.816$, $p = .186$, $\eta^2 = .019$; Movie*Modality*Group: $F(1, 38) = .952$, $p = .335$, $\eta^2 = .005$]. This showed that the AC movie was attended for longer periods of time compared to the R movie both when presented unimodally and when paired with a congruent sound. Furthermore, it showed that both groups of infants showed the same pattern of looking times, although the previous analyses showed that the amount of looking time that older infants directed to AC and R movies when they were paired with an increasing sound was not significantly different. Furthermore, both groups of infants tended to increase their looking time to the screen when the stimuli where presented multimodally.

The second ANOVA compared the P(LT) to AC and R visual stimuli when presented unimodally vs. when paired with a decreasing sound, congruent with R. It yielded to a significant main effect of Movie [$F(1, 38) = 4.558$, $p = .039$, $\eta^2 = .029$] and to significant interactions between Movie and Group, Movie and Modality and Movie, Modality and Group [respectively, $F(1, 38) = 9.858$, $p = .003$, $\eta^2 = .062$, $F(1, 38) = 12.129$, $p = .001$, $\eta^2 = .057$, $F(1, 38) = 4.869$, $p = .033$, $\eta^2 = .023$]. The main effects of Modality and Group and the interaction between Modality and Group were instead non-significant [respectively, $F(1, 38) = .525$, $p = .473$, $\eta^2 = .006$; $F(1, 38) = .922$, $p = .343$, $\eta^2 = .023$; $F(1, 38) = .008$, $p = .928$, $\eta^2 < .001$]. I followed up on this with two further ANOVAs, one for each group, each one with Movie and Modality as within participants factors. In the 9-month-old infants group, the analysis showed a significant main effect of Movie [$F(1, 19) = 23.137$, $p < .001$, $\eta^2 = .181$], whereas both Modality and the interaction between the two factors did not show any significant effects [respectively, $F(1, 19) = .300$, $p = .590$ $\eta^2 = .008$; $F(1, 19) = 1.029$, $p = .323$, $\eta^2 = .008$]. It seemed, then, that older infants attended the AC movie longer both when presented unimodally and when paired with an incongruent (increasing) sound. In the 5-month-old infants group, instead, the interaction between Movie and Modality yielded to a significant effect [$F(1, 19) =$

13.385, $p = .002$, $\eta^2 = .137$], whereas neither of the main effects did [Movie: $F(1, 19) = .361$, $p = .555$, $\eta^2 = .007$; Modality: $F(1, 19) = .224$, $p = .641$, $\eta^2 = .004$]. I further investigated this result with two paired planned comparisons, comparing the P(LT) to each movie when presented alone or together with a decreasing sound. Both comparisons yielded to significant results, but in different directions [No sound condition: $t(19) = 2.196$, $p = .041$, $d_z = .455$; Decreasing sound condition: $t(19) = -2.409$, $p = .026$, $d_z = .539$]: this showed that younger infants looked longer at the AC movie when presented alone, but at the R movie when paired with a congruent (decreasing) sound.

5.7.2 Relationship between looking behaviour and motor development

I also wanted to investigate the existence of a possible link between the looking behaviour shown by the infants and their motor skills. To address this, I ran correlation analyses between the P(LT) in all trials of the experiment and the EMQ scores in each of the three subscales as well as in the reaching and grasping items. Before doing this, I had to exclude a few participants for each EMQ subscale, as they were identified as outliers. In the 5-month-olds group, I excluded one infant from all subscales, plus two additional ones in the Perception-Action subscale and one from the reaching and grasping items subscale; in the 9-month-olds group, instead, I only had to exclude two infants from the reaching and grasping items subscale (missing data were pairwise excluded from the correlations).

When considering the two groups separately, none of the correlations performed showed a significant effect, in any of the two groups. However, when I analysed together the data from the two groups, a few correlations reached, or approached, significance level. In particular, the scores on the Gross Motor Scale were positively related to the looking time directed to the AC visual stimuli when paired with both increasing and decreasing sounds [respectively, $\tau_b = .247$, $p = .028$; $\tau_b = .295$, $p = .009$] (Fig. 5.7.6). The scores on the Fine Motor

and Perception-Action Scales as well were positively related to the looking time to the AC visual stimulus, but only when paired with the increasing sound [respectively, $\tau_b = .279$, $p = .004$; $\tau_b = .263$, $p = .020$] (Fig. 5.7.7).
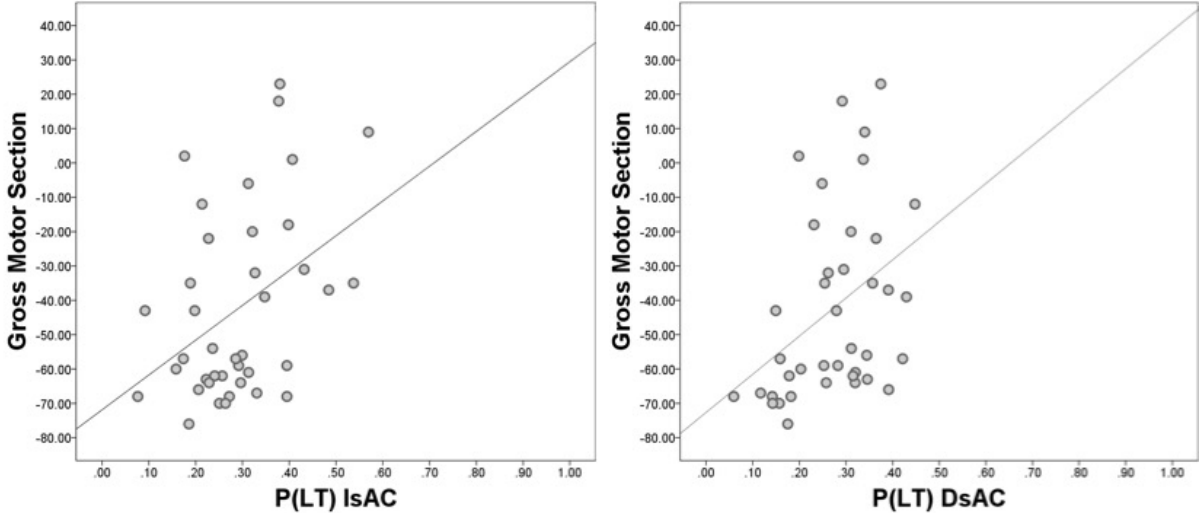
Figure 5.7.6 Correlation between looking behaviour and motor development: relationship – across age groups – between the scores on the Gross Motor Scale and the P(LT) to the AC visual stimulus when paired with an increasing (right) or a decreasing (left) sound.
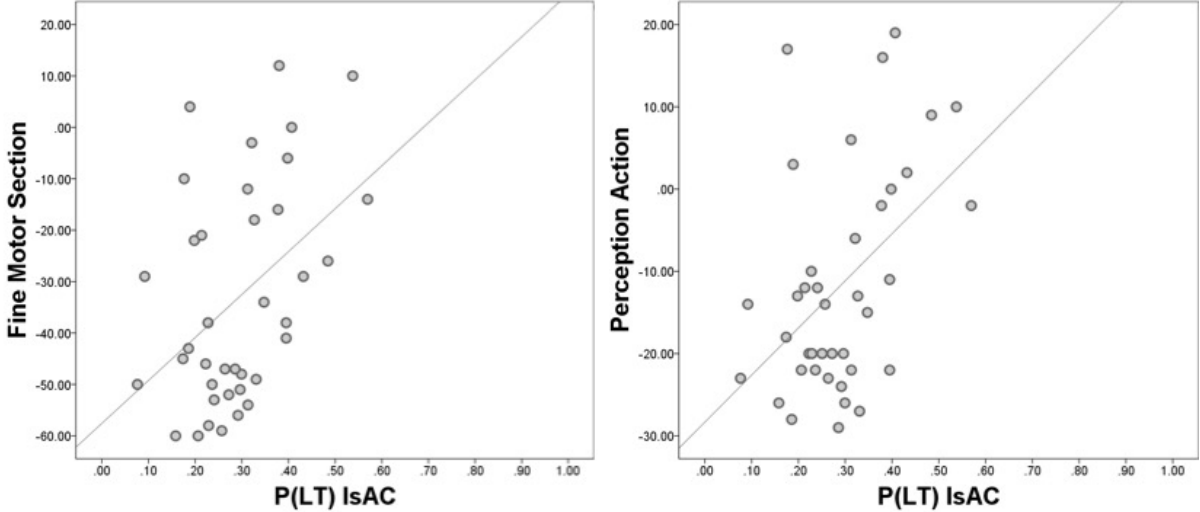
Figure 5.7.7 Correlation between looking behaviour and motor development: relationship – across age groups – between the scores on the Fine Motor (right) or Perception-Action Scales (left) and the P(LT) to the AC visual stimulus paired with an increasing sound.

I then computed the average P(LT) to the AC visual stimulus under each sound condition (No sound, Increasing sound or Decreasing sound) and the average P(LT) in the Increasing sound condition and performed additional correlations involving these averaged

P(LT) values. These new analyses showed a significant positive relationship between the scores on the Gross Motor Scale and the P(LT) to the AC visual stimulus across sound conditions [τ_b = .320, p = .004] and a tendency towards a significant positive correlation between values on the Perception-Action Scale and the P(LT) to the AC visual stimulus across sound conditions [τ_b = .218, p = .054] (Fig. 5.6.8). Moreover, a significant positive correlation was found between the values on each motor scale and the P(LT) when the increasing sound was played [GM: τ_b = .284, p = .011; FM: τ_b = .252, p = .027; PA: τ_b = .263, p = .020]. The proportions of looking time when the increasing sound was played correlated positively also with the RG items [τ_b = .238, p = .036] (Tab. 5.7.9).
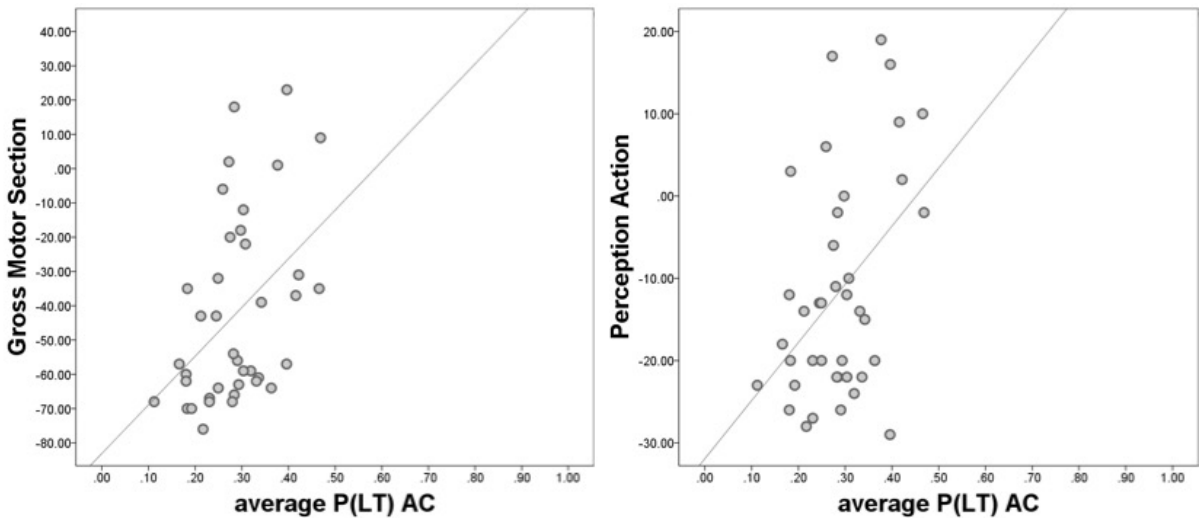
Figure 5.7.8 Correlation between looking behaviour and motor development: relationship – across age groups – between Gross Motor Skills (right) or Perception-Action Skills (left) and the average P(LT) to the AC stimulus across sessions
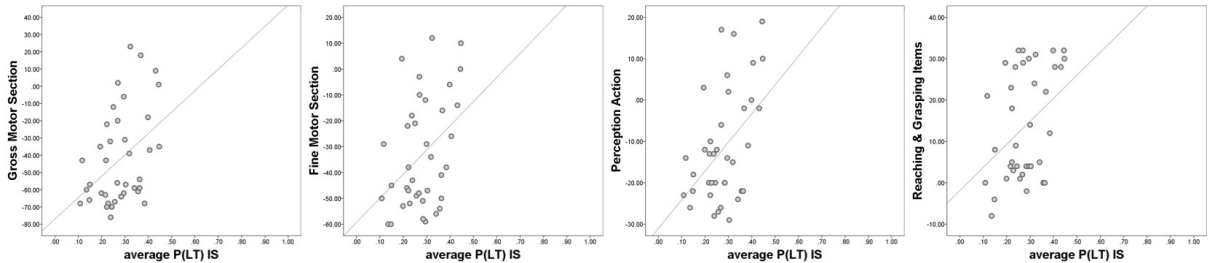
Figure 5.7.9 Correlation between looking behaviour and motor development: relationship – across age groups – between the average P(LT) to the visual stimuli when paired with an increasing sound and the scores on each of the motor scales of the EMQ.

These correlations seemed to suggest a positive relationship between the time that infants spent looking at the AC visual stimulus – irrespective of the presence and direction of a simultaneous sound – and their gross motor and perception-action abilities, with longer looking times when motor abilities were better developed. They also suggested a positive relationship between the looking time to the screen (irrespective of the visual stimulus shown) when an Increasing sound was played and motor abilities in any domain, once again highlighting a link between longer periods of looking time and more evolved motor skills. However, as no correlation reached significance when the two age groups were analysed separately, possibly due to the small sample size, these results can be considered only exploratory.

5.8 DISCUSSION

This study allowed to track, throughout the first year of life, the development of infants' ability to discriminate between different trajectories and to combine multimodal signals depicting the motion of stimuli in the space around the body. The study focused in particular on two important stages of infants' motor development, namely the acquisition of reaching and grasping abilities, taking place respectively around 5 and 9 months of age.

I presented 2 groups of 20 infants each with visual stimuli depicting a ball either approaching their body or receding towards the background. The videos could be presented either unimodally or paired with a sound, which could be either increasing or decreasing in intensity, simulating respectively the approach or recess of a sound source. Measuring the infants' looking behaviour gave me the opportunity of investigating their visual preference for different visual trajectories, both when presented alone and when paired with a sound moving in either a congruent or incongruent direction.

When the visual stimuli were presented alone, both groups of infants showed a significant visual preference for the one approaching their body. Furthermore, the time spent looking at the preferred visual stimulus did not seem to change significantly with age, as the two groups attended it for a comparable amount of time. This preference for stimuli moving towards one's own body seems to appear immediately after birth (Study 1) and to remain stable at least until 9 months of life. I think that this stable visual preference might be due to the fact that stimuli approaching the infants along a colliding pathway may be invested of a major adaptive salience and have a higher ethological value, as they could possibly come into direct contact with them. As already highlighted (Ch. 4.3.6), preferential looking paradigms do not provide any information about the reasons why a stimulus is visually preferred over another one (Banks & Ginsberg, 1985). As a consequence, it is not possible to infer if the infants participating in

these studies visually preferred the approaching visual stimulus because it represented a possible danger or a cue to an upcoming interesting interaction.

When multimodal stimuli were presented, an interesting interaction between congruency and age was found: the infants in the two different age groups showed a different looking behaviour to audio-visual stimuli depicting trajectories with congruent or incongruent direction. The younger infants showed a visual preference for congruent audio-visual stimuli, irrespective of their motion direction: they looked longer to the approaching movie when it was presented together with an increasing sound and to the receding movie when it was paired with a decreasing sound. The older infants, instead, showed a more complex visual behaviour: although no significant effects were revealed from the analysis, they showed a trending interaction between congruency and sound. Specifically, 9-month-old infants seemed to spend more time looking to the incongruent (AC) audio-visual display when a decreasing sound was presented and, instead, to direct a similar amount of looking time to both visual stimuli an increasing sound was played.

The results of the analyses of infants' looking behaviour in the multimodal conditions are particularly interesting, because they might help to outline the developmental path of multimodal integration of adaptively relevant stimuli in infancy. Newborns showed a visual preference for the approaching visual stimulus when it was paired with an increasing sound, simulating motion in a congruent direction, and no preference for either of the visual stimuli when they were paired with a decreasing sound, simulating the movement of a receding sound source (Study 2). As a previous study (Study 1) showed that human infants can discriminate the trajectories of moving visual stimuli right after birth, the absence of a visual preference for either of the stimuli when paired with a decreasing sound cannot be related to a lack of discrimination. Conversely, I think that newborns' spontaneous preference for congruent multimodal stimuli, shown in the increasing sound condition, was challenged by the strong ethological and

behavioural importance of stimuli moving towards their own body, resulting in similar looking times to both the approaching and the receding video when they were paired with a decreasing sound. The looking behaviour of five-month-old infants, instead, did not seem to be affected by the adaptive value of the stimuli, but appeared to be driven by a spontaneous preference for multimodal stimuli depicting movement in a congruent direction. Finally, 9-month-olds seemed to prefer looking at the incongruent visual stimulus when paired with a decreasing sound and to attend both visual stimuli for a comparable amount of time when paired with an increasing sound. Overall, their looking behaviour pattern seemed to be the opposite of that presented by newborns: where the latter were attracted by congruent stimuli as well as adaptively relevant ones, the former revealed a spontaneous preference for incongruent stimuli, which was in turn challenged by adaptively salient ones, resulting – in both instances – in comparable looking times to the two categories of stimuli when they were simultaneously available. As for newborns, it could be argued that 9-month-old infants lacked the ability to integrate multimodal stimuli and that, therefore, they directed their attention only based on the visual stimuli presented. However, this explanation is unlikely as younger infants and even newborns showed multisensory integration abilities in this specific context. I speculate, instead, that older infants might generally be more attracted by incongruent multimodal stimuli (e.g. approaching movie paired with decreasing sound) as they contrast their expectations. However, at the same time, their preference could be weakened when both modalities provide them with behaviourally relevant information. As a consequence, when the visual stimuli were paired with an increasing sound, older infants directed their attention for a similar amount of time to the approaching movie, adaptively important per se, and the receding movie, depicting a trajectory incongruent to the one depicted by the sound.

Young infants' preference for congruent audio-visual stimulation fits into the multisensory processing framework suggested by the Intersensory Redundancy Hypothesis

(IRH, Bahrick & Lickliter, 2000, 2012; Bahrick, Lickliter, & Flom, 2004). The IRH hypothesises that in the earliest stages of development infants' attention is captured by intersensory redundancy, which is the "spatially and temporally congruent presentation of the same amodal information across two or more senses" (Flom & Bahrick, 2007, p. 246). The IRH suggests that processing amodal, redundant information is fundamental for perceptual development, allowing young infants to selectively attend those aspects of the stimulation that constitute unitary events (Bahrick & Lickliter, 2000, 2012; Bahrick, Lickliter, & Flom, 2004). Accordingly, the attention of the 5-month-old participants could have been captured by auditory and visual stimuli specifying movement along the same spatial direction, which referred to a unitary event. As a consequence, the processing of these congruent events might have been prioritised in comparison to the processing of the simultaneously available, non-redundant motion information coming from incongruent audio-visual pairs. The IRH also suggests that, thanks to the increase of perceptual differentiation, processing efficiency and attentional flexibility occurring during development, infants will eventually master the ability of detecting both amodal and modality-specific properties of the events from both uni and multimodal stimulation (Bahrick & Lickliter, 2012; Bahrick, Lickliter, & Flom, 2004). This assumption could help understand the looking behaviour of 9-month-old infants, especially when presented with the sound increasing in intensity. In fact, it could be speculated that they were able to process separately the direction of the trajectory of the two separated visual stimuli even when presented in a multimodal context (i.e. paired with a moving sound). As a consequence, their attention could have been captured at the same time by the unexpected incongruent pairing depicted by the increasing sound and the receding movie and by the adaptively salient visual looming stimulus, invested of a special relevance as in adulthood (Ch. 2.1). These two coexisting and similarly interesting stimulations might have led to the absence of a visual preference for either of the visual stimuli when an increasing sound was presented.

Taking these results together, I speculate that right after birth humans might seemingly direct their attention to relevant as well as congruent stimuli; later on, the necessity of extracting regularities from their everyday experiences might bias them towards congruent stimulation coming from different sensory modalities; eventually, they might be puzzled by unexpected incongruent visual stimuli and direct their attention towards them, but not if one sensory modality conveys, at the same time, adaptively relevant information, in which case they seem to be equally interested in incongruent and salient stimuli.

6. ELECTROENCEPHALOGRAPHIC CORRELATES OF THE PERCEPTION OF UNIMODAL TRAJECTORIES IN 5-MONTH-OLD INFANTS (STUDY 4)

6.1 RATIONALE AND HYPOTHESES

In a previous study (Study 3), I investigated infants' visual discrimination of uni- and multimodal audio-visual trajectories at 5 and 9 months of life, when two important motor skills, i.e. respectively reaching and grasping, emerge. The results revealed that when presented with unimodal visual stimuli, both groups of infants showed a visual preference for those depicting an approaching trajectory, whereas when presented with multimodal, audio-visual stimuli, their visual preferences changed depending on their age. Infants aged 5 months showed a consistent visual preference for congruent audio-visual stimuli, irrespective of the motion direction depicted by either the visual or the auditory cues. The looking behaviour showed by 9-month-old infants, instead, seemed more complex: when presented with receding sounds, the infants in this group showed a visual preference for incongruent, approaching visual stimuli, whereas when presented with approaching sounds, they directed their attention to the approaching and receding visual stimuli for a similar amount of time. In light of these data, I speculated that younger infants might be generally more attracted by congruent information coming from different senses, which could help them to learn about their environment through the extraction of regularities from it, whereas older infants might be more interested in the unexpected incongruent stimuli, which contradict their notions about the same environment. However, at the same time, they seem to be also captured by adaptively salient approaching stimuli: the necessity of appropriately processing behaviourally relevant stimuli might challenge their spontaneous preference for incongruent multimodal stimulation, leading to equally distributed looking times across the two competing categories.

After having studied infants' visual preferences towards uni and multimodal congruent or incongruent stimuli depicting trajectories moving in the peripersonal space, I also wanted to investigate the neural correlates of their perception and processing during infancy.

A few studies previously investigated the neural responses to looming as well as optic flow stimuli in infancy. For example, Van der Meer and colleagues recorded EEG in 8-month-old infants and in adults in order to study the electrical brain responses to optic flow (radial motion of dots directed outwards from the centre of the display) vs. random visual motion (van der Meer, Fallet, & van der Weel, 2008). They analysed the visual evoked potentials (VEPs) and found a significant, stimulus-dependent modulation of the N2 component both within and between age groups. Specifically, the N2 latency was shorter for optic flow vs. random motion in both groups and, at the same time, infants showed larger amplitudes and longer latencies, particularly for the random motion stimuli, compared to adults. The authors also investigated the time-dependent changes in spectral power (TSE): in this analysis, infants showed a stimulus-induced desynchronization within the theta-band in response to any kind of motion stimuli compared to a static dot pattern, with the maximum desynchronization occurring later than 500 ms after stimulus onset. Adults, instead, showed an induced synchronization within the middle beta-band, for both optic flow and random motion compared to the static visual stimulus, with the maximum desynchronization occurring later than 650 ms after stimulus onset. However, there were no differences in the TSE for the two motion stimuli, in either of the two groups. The authors speculated, in light of their results, that for both infants and adults it is probably easier to detect the coherence in optic flow, which leads to shorter latencies of the N2 compared to random motion. They suggested that this might reflect the importance of optic flow as reliable information for effective motion within the environment, which is supposed to develop in parallel with self-produced locomotion. With regards to the TSE data, the authors speculated that the desynchronization observed in theta-bands in infants following both motion

stimuli might suggest that they both required a more complex processing compared to the static dot pattern (van der Meer et al., 2008).

Later on, Van der Weel and van der Meer (2009) investigated, using high-density EEG, the brain responses of 5- to 11-month-old infants to timing information for impending collision, presenting the infants with looming stimuli approaching them with three different accelerations. They were particularly interested in exploring the possibility that, in the infant brain, event-related theta-band activity could provide information about impending collision and time-to−contact of the approaching stimulus. They ran a time-frequency analysis on the grand average data across looming speeds and age groups and found theta-band event-related oscillations taking place in the left visual cortex dipole in response to the looming stimuli, consistent with the role of theta synchronization in attentional mechanisms responsible for the processing of perceptual information. Furthermore, they transformed the EEG scalp signal into a new voltage sequence of the summed activity over time in different dipoles. They then showed that in the left visual cortex dipole the source waveform shapes were similar across ages, whereas their duration decreased with age, probably thanks to the improvement of myelination as well as synaptic maturation. They also noticed that source waveforms per se did not allow discrimination of the speed of the looming stimuli, whereas the coupling between the source waveform rate of change and the rate of change of the loom indicated that older infants discriminated the different speeds of looming stimuli better than the younger ones, who seemed to process all the stimuli as if they were fast. According to the authors, these data suggested that 10- and 11-month-old infants showed a well-established neural network for processing impending collision, which did not seem to be developed in 5- to 7-month-olds. They also reported that this network seemed to be in the process of developing around 8- and 9-months of life, when, on average, infants start crawling, suggesting a link between self-produced locomotion and the ability to perceive looming stimuli (van der Weel & van der Meer).

More recently, the same group of authors investigated the visual evoked potentials in response to looming stimuli longitudinally, in infants aged 5/6 and 12/13 months (van der Meer, Svantesson, & van der Weel, 2012). They presented the infants with looming stimuli approaching them with three different speeds and investigated their electrical brain responses and whether they were modulated by the strategies used by infants to estimate the time-to-contact of the looming object. The duration and timing (with respect to the time remaining until the virtual collision) of each looming-related VEP peak were recorded. Moreover, the values of looming visual angle, speed and time-to-contact were computed in correspondence with every VEP peak, in order to correlate the electrical brain activity with the timing strategies adopted by the infants. Looming related VEP peaks were found to be more prominent in the electrodes corresponding to channels O1, Oz and O2 in the 10-20 system, extending to channels P3 and Pz in older infants (second testing session). The results showed that both the timing and the duration of the EEG responses changed with age: the VEP peaks occurred earlier in the looming sequence and had longer durations when infants were aged between 5 and 6 months of life compared to when they were aged between 12 and 13 months of life. Furthermore, they highlighted that the occipital area was maximally activated during the VEP peaks when infants were aged between 5 and 6 months and that its activation decreased with development, whereas the parietal area showed the opposite pattern, with its maximum activation happening when the infants were aged between 12 and 13 months. The authors suggested that shorter VEP peaks happening closer to the actual time-to-contact of the looming stimulus indicated a developmental shift in the processing of looming stimuli, further supported by the appearance of a more efficient timing strategy in some infants (4 out of 10) as well as by the propagation of the peak VEP activation towards higher processing areas in older infants (van der Meer et al., 2012).

However, I thought that the studies by van der Meer and colleagues contained some methodological weaknesses that should be improved. For example, the number of participants (6) and the minimum number of trials accepted per condition per participant (3) were small and the same infants contributed data to two different studies involving related processes (i.e. optic flow and looming perception). Moreover, some aspects of the analyses were controversial: the VEPs, which were analysed at the electrode level, varied across participants in terms of the electrode that was selected for the analyses (van der Meer et al., 2008), and the data were high-pass filtered at 1.6 Hz, whereas the majority of infant studies use a filter between 0.1 and 0.5 Hz. Less conservative filters might lead to significant artefactual effects in the ERP waveform, especially in special populations, like children, patients and elderly people (Luck, 2014).

Most importantly, the motivation behind my study was different from the one of the abovementioned studies. Van der Meer and colleagues were mainly interested in investigating the neural correlates of optic flow processing and of prospective responses to looming stimuli and their relationship with the development of self-locomotion abilities in infants. Conversely, I wanted to investigate the neural correlates of the processing of different trajectories (i.e. not only looming) when perceived from different sensory modalities, either presented on their own (in this study) or paired together (future directions). I was particularly interested in studying the processing of trajectories whose motion was depicted by stimuli conveyed in different modalities, as they can provide complementary information about the environment. For example, with regards to the perception of moving stimuli, audition provides a continuous flow of information, also when the eyes are closed, and provides information also about events occurring outside the visual field; furthermore, it's a powerful change detector, capable of quickly orient towards potential threats in the environment (Ferri, Tajadura-Jiménez, Väljamäe, Vastano, & Costantini, 2015). Moreover, studying the processing of motion signals conveyed by each single modality was the necessary preliminary step before investigating, in

the future, the processing of multimodal cues depicting moving stimuli. This would, in turn, provide the opportunity to further investigate multisensory integration during infancy and, in particular, the interplay of multisensory integration principles and behaviourally relevant information at the neural level. In fact, studying the development of multisensory integration is particularly relevant as efficiently integrating information coming from different modalities has important adaptive benefits, but, at the same time, it is a significant challenge with which humans are confronted during development (Bremner, Lewkowicz, & Spence, 2012) and that could become even more relevant when the stimuli presented are embedded of a special behavioural relevance.

In this first study, I specifically wanted to focus the attention on two aspects: i) the neural processing of trajectories that could have different behavioural relevance (i.e. approaching vs. receding trajectories); ii) the processing of trajectories depicted by auditory and visual cues in clusters of electrodes positioned over the brain areas considered to be responsible for the primary processing of vision and audition.

With regards to the first aspect, a recent study investigated the neural mechanisms of visual looming processing when the stimuli presented have different emotional valence (Vagnoni, Lourenco, & Longo, 2015, Ch. 2.1). The authors presented a group of adult participants with threatening and non-threatening looming stimuli and showed that the affective value of the presented stimulus modulated several event related potentials and oscillatory components (Vagnoni et al., 2015). They showed, in agreement with other findings (Carretié, Hinojosa, Martín-Loeches, Mercado, & Tapia, 2004; Smith, Cacioffo, Larsen, & Chartrand, 2003), that positive and negative stimuli are differentiated by the brain since the earliest stages of processing and immediately receive different amounts of attention. Specifically, they found that the P1 amplitude was smaller for negative vs. positive stimuli and that the occipital N1 was enhanced for negative vs. positive pictures. Furthermore, they showed a less

positive amplitude for threatening stimuli in the EPN (early posterior negativity), which is thought to index the greater attention paid to emotional stimuli (Dolcos & Cabeza, 2002; Lang, Bradley, & Cuthbert, 1997; Olofsson, Nordin, Sequeira, & Polich, 2008; Schupp, Junghöfer, Weike, & Hamm, 2004; Schupp et al., 2000, Vagnoni et al., 2015).

In light of these results, I expected the early visual evoked potentials in response to the visual stimuli to be modulated by their valence during infancy as well. According to previous results (Begleiter, Gross, & Kissin, 1967; Begleiter, Gross, Porjesz, & Kissin, 1969; Vagnoni et al., 2015), I hypothesised that, if young infants processed approaching (looming) stimuli as threatening, the amplitude of the P1 could be smaller for the approaching (negative) vs. receding (positive) stimuli, as they could signal imminent contact of the stimulus with the observer's body. However, also the opposite scenario could be possible, in accordance with other findings showing a larger amplitude of the P1 for negative vs. positive stimuli (Carretié et al., 2004; Smith et al., 2003).

The second aspect in which I was interested regarded the processing of trajectories depicted by auditory and visual cues in clusters of electrodes positioned over the brain areas considered to be responsible for the primary processing of vision and audition. With regards to this aspect, I specifically wanted to investigate the recently suggested possibility that the primary sensory cortices might play a role in multisensory integration: according to this suggestion, both the primary auditory and visual cortices may respond to both auditory and visual stimuli (Kayser, Petkov, & Logothetis, 2009; Murray et al., 2016). Murray and colleagues (2016) have reported that a new view of brain organisation and perception was recently proposed, wherein the "integration of information from different senses within low-level cortices is a rule rather than an exception" (Murray et al., p. 161). From an anatomical point of view, a growing number of studies are showing the presence of connectivity between primary visual and auditory cortices and demonstrating the presence of auditory inputs to the primary visual cortex (Beer, Plank, &

Greenlee, 2011; Beer, Plank, Meyer, & Greenlee, 2013). Also research with blind or visually impaired individuals is providing evidence in favour of the presence of auditory responses within the visual cortices (Ricciardi, Bonino, Pellegrini, & Pietrini, 2014). Taken together, these findings suggest the existence of anatomical underpinnings that would allow multisensory processes to take place within the visual cortices (Murray et al.). Murray and colleagues also review fMRI studies describing activation of the visual cortex in response to auditory stimuli, as in the so-called "flash-beep illusion", in which the participants often report the presence of two flashes when a single flash is presented close in time with two beeps (Shams, Kamitani, & Shimojo, 2000). Among functional studies, they also review recent evidence demonstrating that "it is possible to decode the category of natural sounds heard by the participants based on the patterns of activity within the primary visual cortex" (Murray et al., p. 164; Vetter, Smith, & Muckli, 2014). Overall, haemodynamic findings seem to provide strong evidence for a link between perception and crossmodal responses in the visual cortex (Murray et al.). With regards to event-related potential studies, they report their group's previous results (Cappe, Thut, Romei, & Murray, 2010; Cappe, Thelen, Romei, Thut, & Murray, 2012) showing nonlinear multisensory neural responses occurring around 60 ms post-stimulus onset in a network comprising the primary visual and auditory cortices other than the posterior superior temporal sulcus (an area typically associated with multisensory integration). More specifically, Cappe and colleagues (2010) investigated the latency at which nonlinear interactions begin and their likely underlying neurophysiology. They analysed the ERPs in response to static auditory, visual and audio-visual stimuli that required attention but not motor responses and showed subadditive nonlinear interactions for the multisensory condition, whose sources were localised within occipital, temporal and temporo-parietal areas. Later on, the same authors demonstrated that these early non-linear interactions could be enhanced when the stimuli are looming vs. static, showing the behavioural importance of early multisensory integration itself (Cappe et al., 2012,

Ch. 2.1). In order to do so, they contrasted the ERPs in response to the multisensory condition with the summed ERPs in response to the constituent auditory and visual conditions. Visual inspection of an exemplar occipital electrode (Oz) suggested that nonlinear interactions began earlier for the congruent looming conditions than for the congruent receding and the incongruent conditions, as confirmed by paired t-tests analyses. Finally, Murray and colleagues report that several independent studies demonstrated that auditory stimuli enhance the TMS induced excitability of low-level visual cortices within the occipital pole, supporting a direct role of visual cortices in behavioural responses to sounds. Furthermore, the latency at which the visual cortices excitability was enhanced changed depending on whether looming or stationary sounds were presented, suggesting that the visual cortex discriminated the nature of the sound before the participant was aware of it (Romei, Murray, Cappe, & Thut, 2009, Ch. 2.1).

According to these findings, I wanted to investigate whether during infancy the primary sensory cortices might process similarly stimuli coming from different modalities, especially if they convey behaviourally relevant information. In particular, I hypothesised that − if the primary sensory cortices had a role in the early integration of multisensory stimuli − the electrical brain responses to stimuli depicting the same trajectory through different modalities might be similar in the electrodes positioned in correspondence with the primary visual and auditory areas of the infant brain, especially during the earliest stages of processing.

To summarise, I was interested in investigating the EEG correlates of the processing of trajectories with a different behavioural relevance conveyed by auditory and visual cues, in clusters of electrodes positioned over the brain areas considered to be responsible for the primary processing of vision and audition. To address these points, I recorded, using a high-density electrode system, the electrical brain activity of a sample of 5-month-old infants while they were attending to unimodal (auditory or visual) approaching and receding trajectories.

The final sample of this study included nine 5-month-old infants (6 female). The 9 infants were aged on average 159 days at time of testing (SD = 6.62, range 150-167). Fifteen additional 5-months-old infants participated, but were excluded from further analyses due to fussiness (i.e. if the participant appeared to be upset or moved excessively, n = 4), sleepiness (n = 1), noisy or poor recordings or an insufficient number of valid trials (the participants were required to complete a minimum of 7 artefact free trials for each condition to be included in analyses; infants excluded for this reason, n = 10). The relatively high drop-out rate (67%) is likely to be related to the elevated number of conditions, which might have made it difficult for young infants to sit still and maintain their attention for long periods of time (Hoehl & Wahl, 2012). Hoehl and Wahl reported that in previous studies with three or four conditions the drop-out rates were comparable to that of this study (60-73%, Hoehl & Striano, 2008; Reid, Hoehl, Landt, & Striano, 2008). Another possible reason for the high drop-out might be intrinsically related to the paradigm. In infant studies, it is quite customary to have children-friendly attention getters between one trial and the next, like cartoons or clips from children's TV programs (Hoehl & Wahl, 2012). However, as the stimuli used in this study were possibly invested of an emotional value, I decided to opt for a less appealing attention getter, which would not convey any emotional information (Ch. 6.3 for more detail). In fact, I wanted to avoid the possibility that the attention getter could entrain activity in the theta frequency band, which has previously been related to the processing of both looming stimuli (van der Meer et al., 2008; van der Weel & van der Meer, 2009) and emotional stimuli (Orekhova, Stroganova, Posikera, & Elam, 2006). I think that, possibly, the use of a less attractive attention getter might as well have contributed to the high drop-out rate, by reducing the chances of effectively redirecting infants' attention towards the screen between one trial and the next one.

The parents brought their child to the InfantLab at a previously agreed time and testing took place only if and when the infants were awake and in an alert state. The parents were informed about the procedure and provided written informed consent to their child's participation. The Ethics Committee of the Department of Psychology of Goldsmiths, University of London approved the study protocol.

When the families arrived at the InfantLab, the infants' head circumference was measured and the appropriate EEG net was selected (Ch. 3.2.1). While the net was soaking in electrolyte solution, the researchers interacted with the parents and tried to make the infants feel comfortable in the lab environment. They also asked the parents to fill in the consent form. After about 10 minutes, the net was placed on the infants' head and the infants and their parent moved to the testing room.

The infants sat on their parent's lap on a chair positioned about 90 cm from a 24" screen. In order to attract infants' attention towards the screen, a music video designed for infants was played until the infants were attending to the screen, then the experiment began. The infants were presented with a black circle flickering on a white background at 10 Hz, which served as an attention getter and was maintained until the infants were attending to the centre of the screen. The frequency of the flickering rate of the attention getter was chosen in order to avoid entraining electrical brain activity within the theta-band (i.e. $3.6 - 5.6$ Hz in infants, Orekhova, Stroganova, Posikera, & Elam, 2006), which, according to previous findings (van der Meer et al., 2008; van der Weel & van der Meer, 2009), could be related to the processing of looming stimuli. As already mentioned, also the nature of the attention was chosen in order to avoid entraining activity in the theta frequency band: a more attractive attention getter might have served better its purpose but, at the same time, would have also been more likely to interfere with theta frequencies, seen as related to emotional processing in infancy (Orekhova et al., 2006). As soon as the infants were looking to the attention getter, the experimenter triggered the start of the trial. First, a black rectangle (subtending a visual angle of 38.35° x 19.45°) appeared in the middle of a grey background and stayed up for 100 ms, constituting the baseline for the EEG recordings. Then, the experimental stimulus appeared, lasting 2000 ms (Fig. 6.3.1). As soon as it disappeared, a new attention getter was presented, to redirect infants'

attention in case they were not focusing on the centre of the screen any longer. Four different experimental stimuli were presented, repeated in a random order as long as the infants' attention was sustained.
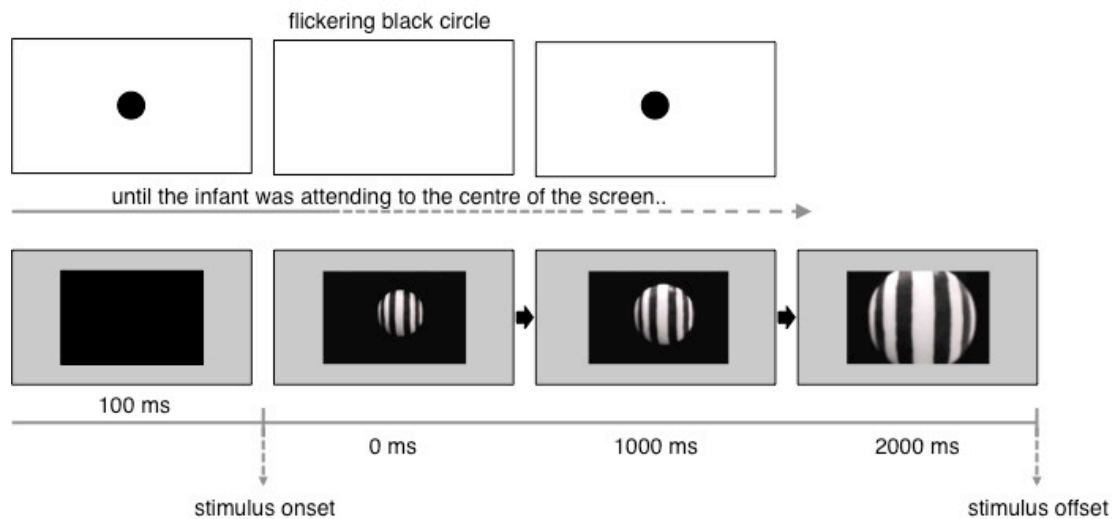
Figure 6.3.1 Example of an experimental trial. The infants were presented with a flickering black circle on a white background until they were attending to the centre of the screen. Then, when the experimenter triggered it, a black rectangle appeared on a grey background for 100 ms, serving as baseline for the EEG recordings. After that, the stimulus (visual approaching in this example) appeared and lasted for 2000 ms. Finally, the attention getter appeared again and a new trial (presenting a different stimulus) started.

The stimuli depicted either an approaching (looming) or a receding trajectory, either through visual or auditory cues. The visual stimuli were videos representing a black-and-white striped ball moving either towards the observer or towards the background, at a rate of 15 cm/s. The receding video was the approaching one played backwards, edited using the software "Final Cut Pro X". At the beginning of the approaching visual stimulus and at the end of the receding one, the ball had a diameter of 11.4 cm and subtended a visual angle of 14.26° x 10.68°; the stripes were 1.14 cm wide on average (1.43°). At the end of the approaching movie and at the beginning of the receding one, instead, the ball had a diameter of 26 cm and subtended a visual angle of 31.84° x 19.45°; the stripes were 2.6 cm wide on average (3.27°). The balls moved within a black background, surrounded by a grey frame, identical to that shown during the baseline period (100 ms) preceding their appearance. The auditory stimuli were two samples of a sinusoidal waveform with constant frequency (8000 Hz) and presenting

a variation in intensity of 15 dB SPL. Specifically, the approaching sound increased in intensity from 55 to 70 dB, whereas the receding sound decreased from 70 to 55 dB (Ch. 4.2.2). The auditory stimuli were delivered from two loudspeakers positioned underneath the monitor. When the auditory stimuli were presented, the black rectangle surrounded by the grey frame stayed on the screen, in order to minimize the visual change across the trials and to keep infants' attention towards the screen. Stimuli were presented using E-Prime 2.0.10.

The electrical brain activity was recorded continuously using a Hydrocel Geodesic Sensor Net (Electrical Geodesic Inc.), consisting of 128 silver-silver chloride electrodes evenly distributed across the scalp (124 electrodes were used). The vertex served as the reference. The electrical potential was amplified with 0.1 to 100 Hz band-pass, digitized at 500 Hz sampling rate and stored for off-line analyses (Hoehl & Wahl, 2012).

6.4 DATA ANALYSIS

The data were analysed off-line using NetStation 4.5.1 analysis software (Electrical Geodesic Inc.). Continuous EEG data were high-pass filtered at 0.3 Hz and low-pass filtered at 30 Hz using digital elliptical filtering (Hoehl & Wahl, 2012). They were then segmented in epochs from 100 ms before the stimulus onset until 1000 ms after it and baseline-corrected to the average amplitude of the 100 ms interval preceding the stimulus onset. Segments with movement artefacts were visually detected and rejected, as well as segments with more than 12 bad electrodes (10% of the number of channels recorded, Hoehl & Wahl, 2012). Bad electrodes (if less than 12) were interpolated on a trial-by-trial basis using spherical interpolation of neighbouring channel values. Artefact free data were then re-referenced to the average potential over the scalp. On average, the number of trials considered for the analyses was 11 (ranging from 8 to 17) for the visual approaching condition, 11 (ranging from 7 to 15) for the visual receding condition, 10 (ranging from 7 to 12) for the auditory approaching condition and 10 (ranging from 9 to 13) for the auditory receding condition. The relatively small number of trials available per condition could be related to the high number of different conditions in which the infants participated (N = 4) as well as to the duration of each trial (2000 ms). In fact, it is likely that infants will provide a smaller number of valid trials per condition when presented with a higher number of conditions, due to their limited ability to sit still and maintain their attention (Hoehl & Wahl, 2012). However, Hoehl and Wahl (2012, p. 196) reported that the "minimum number of artefact-free trials that is required from every infant in order to be included in the final sample of participants varies immensely between studies, ranging from 7 or 8 to 40 valid trials per condition" (Carver & Vaccaro, 2007; de Haan & Nelson, 1997). They also suggested that, generally, the number of valid trials required to include an infant in the final sample should depend on the noise of the data and on the ERP components measured and that in some situations it might be more sensible to include more infants even though each of them provided

only a small number of valid trials (Hoehl & Wahl). As already suggested, another possible reason for the high drop-out might be related to the attention getter that was presented to the infants between trials. In infant studies, it is quite customary to have a children-friendly attention getter between one trial and the next one (Hoehl & Wahl), but, as the stimuli used in this study were possibly invested of an emotional value, I decided to use a less appealing attention getter (i.e. a flickering black circle), which would not convey any emotional information. In fact, I wanted to avoid the possibility that the attention getter could entrain activity in the theta frequency band, which has previously been related to the processing of both looming stimuli (van der Meer et al., 2008; van der Weel & van der Meer, 2009) and emotional stimuli (Orekhova, Stroganova, Posikera, & Elam, 2006). Using a less attractive attention getter avoided this risk but, at the same time, it is likely to have reduced the chances of effectively redirecting infants' attention towards the screen between one trial and the next one, contributing to the high drop-out rate.

For ERP analyses, individual and grand averages were calculated. Driven by the intention of investigating the event-related brain activity in the primary sensory cortices, I identified two groups of electrodes for further analyses and I visually inspected the averaged waveforms (across participants) of the channels around the interested areas, in order to identify a representative sample of electrodes within each of them. Concerning the primary visual cortex, after visual inspection of the electrodes positioned over occipital sites (McCulloch, 2007), I identified a cluster of 7 electrodes surrounding the Oz channel (in the 10-20 system): 70, 71, 74, 75, 76, 82 and 83. Concerning the primary auditory cortex, the choice of the electrodes to be included in the analyses was based on the findings from a study that investigated the maturation of the auditory evoked potential during the first year of life (Kushnerenko et al., 2001). In this study, the authors examined the obligatory ERP components in response to three different tones at birth and then throughout the first year of life. They recorded the EEG at 8

scalp sites: F3 and F4, C3 and C4, P3 and P4 and T3 and T4 (according to the 10-20 system) and showed that the most reliable components of infant auditory evoked potential (AEP) reach their maximum amplitude in the central and frontal areas. In light of these findings, I visually inspected the electrodes positioned between channels F3, F4, C3 and C4 and I selected a cluster of 7 electrodes located between Fz and Cz (in the 10-20 system): 5, 6, 7, 12, 13, 106, 112 (Fig. 6.4.1).
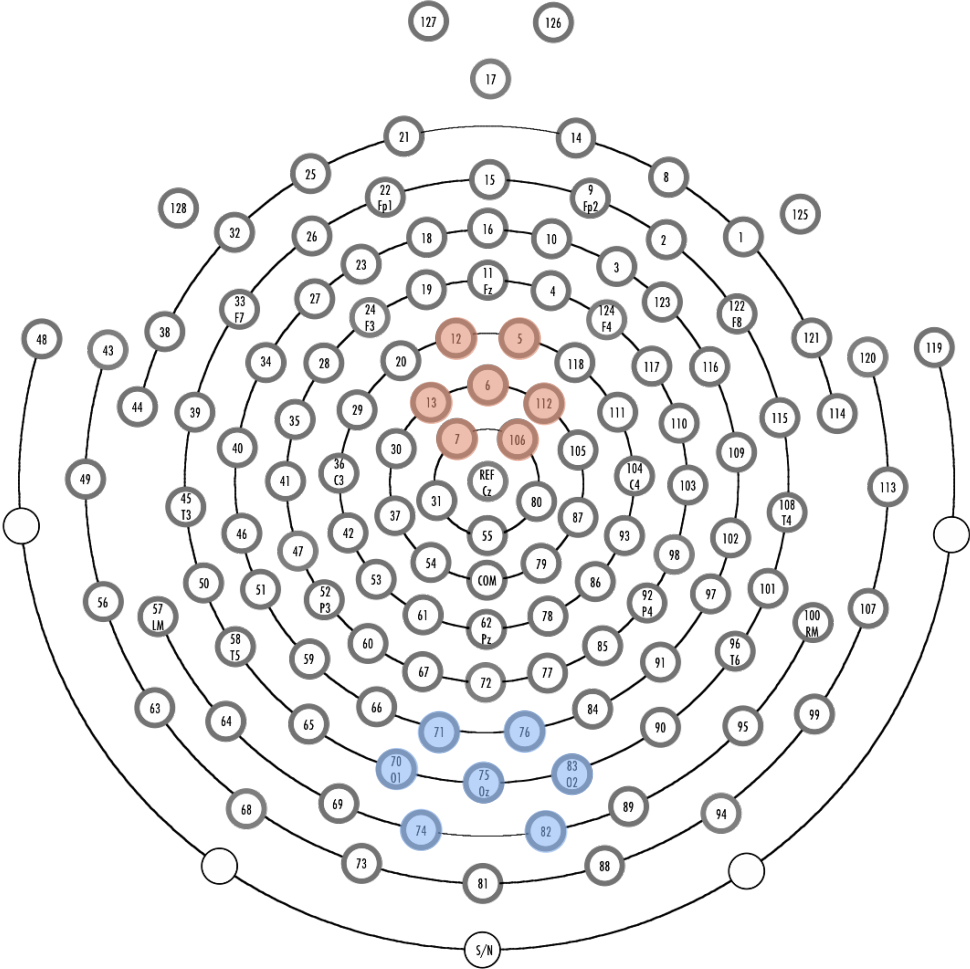
Figure 6.4.1 Hydrogel Geodesic Sensor Net 128 Channel Map with selected cluster of electrodes highlighted. The cluster of occipital electrodes is highlighted in blue and the cluster of fronto-parietal electrodes in red.

I analysed the ERP waveforms in each of the abovementioned clusters of electrodes using the Monte Carlo simulation method (custom MatLab script, MathWorks, Natick, MA, USA). This method allows identification of the time course of statistically reliable modulations of the ERPs, correcting for the autocorrelation of consecutive sample points (i.e. 2 ms intervals in this dataset). It also avoids the difficulties related to multiple comparisons and, at the same time, preserves the significance critical value at α = .05 (Rigato, Begum Ali, van Velzen, & Bremner, 2014). In fact, when computing several t-tests on the consecutive time points of an ERP waveform, it is necessary to correct for multiple comparisons, with the subsequent high risk of compromising the statistical power of the comparison itself, as "the underlying process generating the observed ERPs will have some degree of statistical continuity and thus when a t-value is below the limit, it is likely that adjacent t-values will also be significant" (Guthrie & Buchwald, 1991, p. 241). The Monte Carlo simulation calculates the shortest length of consecutive significant values which could be considered reliably significant with 95% probability, i.e. not generated by chance by the statistical dependence of the consecutive time points at which the EEG was recorder (autocorrelation of consecutive time points, Guthrie & Buchwald, 1991).

For each cluster of electrodes, the simulation estimated the first order autocorrelation present in the real difference waveforms across the specified time window (1000 ms following stimulus onset, i.e. 500 sample points). Then, it simulated 1000 datasets of randomly created waveforms, each having mean = 0 and variance = 1 at each time point, and the same level of autocorrelation as the average of the observed data, as well as the same number of participants and of sample points as the real data. Hence, it applied two-tailed one sample t-tests to every time point of the simulated data and recorded the significant vs. non-significant outcomes. For

each dataset, the simulation computed the longest sequence of consecutive significant outcomes of the t-test. Finally, it used the 95th percentile of this simulated "longest sequence length" to determine the minimum length that a sequence of significant t-tests in the difference waveforms of the real data must have in order to be reliably significantly different.

For each cluster of electrodes, I investigated the effect of the two factors subtended by the four stimuli presented to the infants during the experiment: Modality of presentation (auditory vs. visual) and Direction of the stimuli (approaching vs. receding), as well as the effect of their Interaction. For each comparison, the simulation ran a t-test on the difference between each couple of factors against chance. In this way, it could eliminate the mean activity common between the waveforms and evaluate the true differences in the responses to the different stimuli, reflected in the difference potential (Guthrie & Buchwald, 1991).

In the cluster of electrodes positioned over the scalp area corresponding to the occipital lobe, the simulation identified as reliably significant any sequence of consecutive significant t-tests longer than 164 ms for Modality, longer than 144 ms for Direction and longer than 176 ms for the Interaction between the two factors. The estimated autocorrelation at lag 1 was .997 for Modality, .995 for Direction and .996 for the Interaction, whereas at lag 5 was .970 for Modality, .944 for Direction and 965 for the Interaction. The analysis did not find any sequences of significant t-tests longer than the minimum reliable one for Direction, failing to identify an effect of the direction of the presented stimulus on the waveforms (Fig. 6.5.2). There was no Interaction between direction and modality. However, a significant effect of Modality was seen for 224 ms, from 466 to 690 ms after stimulus onset. The significant effect of Modality suggested that, after 466 ms of stimulus presentation, the infants' brain started to elaborate differently visual and auditory stimuli, showing a significantly greater amplitude of the ERPs for visual compared to auditory signals (Fig. 6.5.1).

Figure 6.5.1 Occipital cluster of electrodes: ERP waveforms in response to the different modalities of presentation of the stimuli. The plot represents the waveforms in response to the stimuli presented in the auditory and visual modalities (irrespective of the motion direction of the stimuli) and the difference waveform. The shaded area indicates the time course of statistically reliable effects of the modality of presentation on the waveform. The topographical maps represent the voltage distribution over the scalp during the period of reliable statistical difference. The small black disks indicate the locations of the electrodes chosen for the analyses.

Figure 6.5.2 Occipital cluster of electrodes: ERP waveforms in response to the different motion directions of the stimuli. The plot represents the waveforms in response to the approaching and receding stimuli (irrespective of the modality of presentation of the stimuli) and the difference waveform.

Within the cluster of electrodes positioned over the scalp area between Fz and Cz (fronto-central electrodes), the simulation identified as reliably significant any sequence of consecutive significant t-tests longer than 194 ms for Modality, longer than 144 ms for Direction and longer than 176 ms for the Interaction between the two factors. The estimated autocorrelation at lag 1 was .999 for Modality, .996 for Direction and .998 for the Interaction, whereas at lag 5 was .991 for Modality, .946 for Direction and 963 for the Interaction. The analysis did not find any sequences of significant t-tests longer than the minimum reliable one for Direction, failing in identifying an effect of the direction of the presented stimulus on the waveforms (Fig. 6.5.4). Conversely, it showed a significant effect of Modality for 426 ms, from 572 to 998 ms after stimulus onset and a significant effect of the Interaction for 192 ms, from 794 to 986 ms after stimulus onset. The significant effect of Modality suggested that, similarly to what happened in the occipital electrodes, after 572 ms of stimulus presentation, the infants' brain started to elaborate differently visual and auditory stimuli, showing a positive deflection for auditory stimuli and a negative deflection for visual ones (Fig. 6.5.3). It also showed that in the fronto-central electrodes, as well as in the occipital ones, during the earliest stages of processing visual and auditory stimuli did not seem to be processed differently. The significant effect of the Interaction was explained by a different modulation of the waveforms in response to the auditory and visual stimuli depicting approaching vs. receding trajectories. In particular, when the infants were presented with approaching stimuli, a reliably significant difference between the visual and auditory ERPs was found for 412 ms, between 586 and 998 ms after stimulus onset (minimum length of reliably significant differences = 176 ms; autocorrelation: lag 1 = .999 ; lag 5 = .988), whereas when they were presented with receding stimuli, the difference in the visual and auditory ERPs was reliably different for a shorter segment of time points, lasting only 238 ms, between 584 and 822 ms after stimulus onset (minimum length of reliably significant differences = 202 ms; autocorrelation: lag 1 = .999; lag 5 = .990). For both stimulus directions, the deflection showed by the ERP waveform was positive for the auditory stimuli and negative for the visual ones (Fig. 6.5.5).
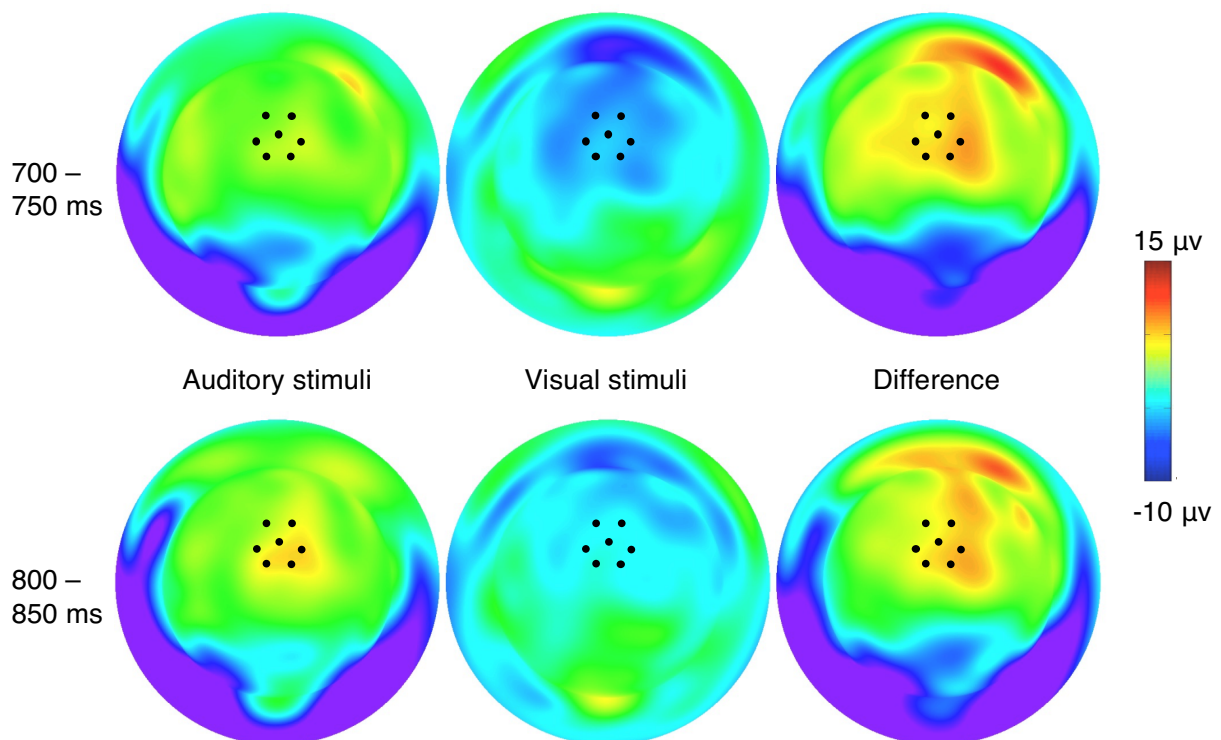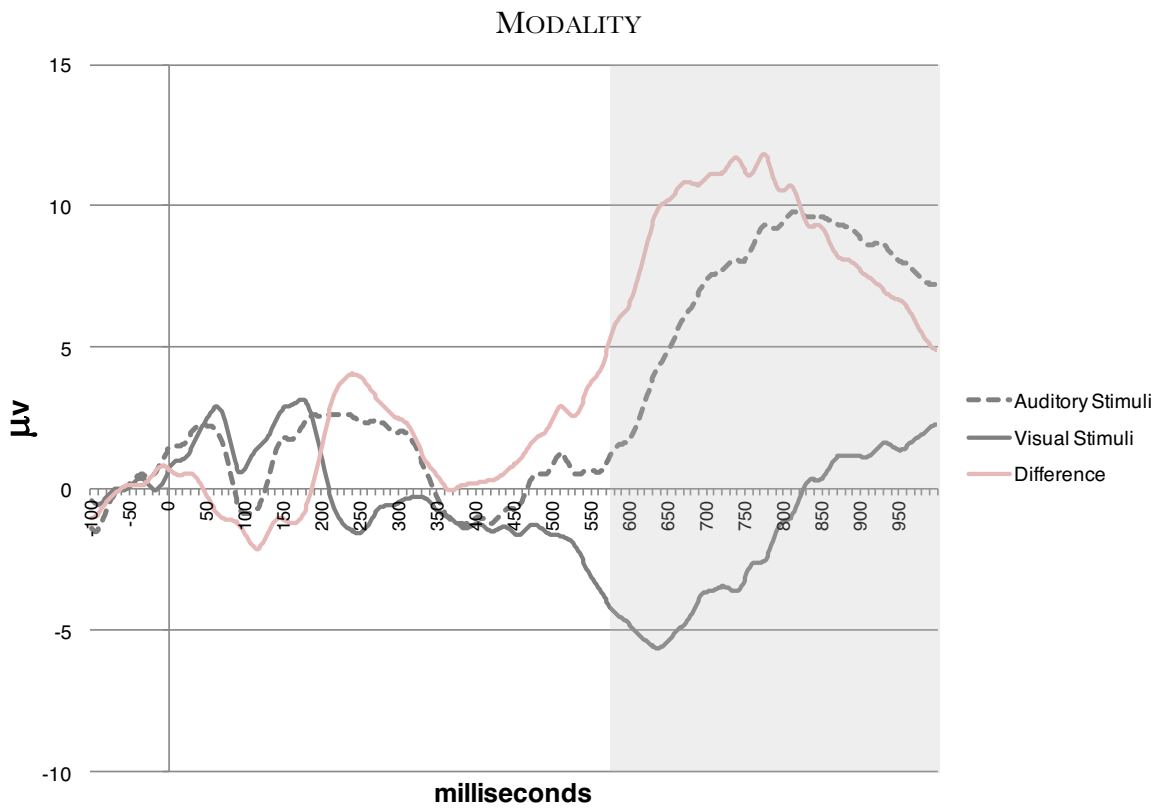
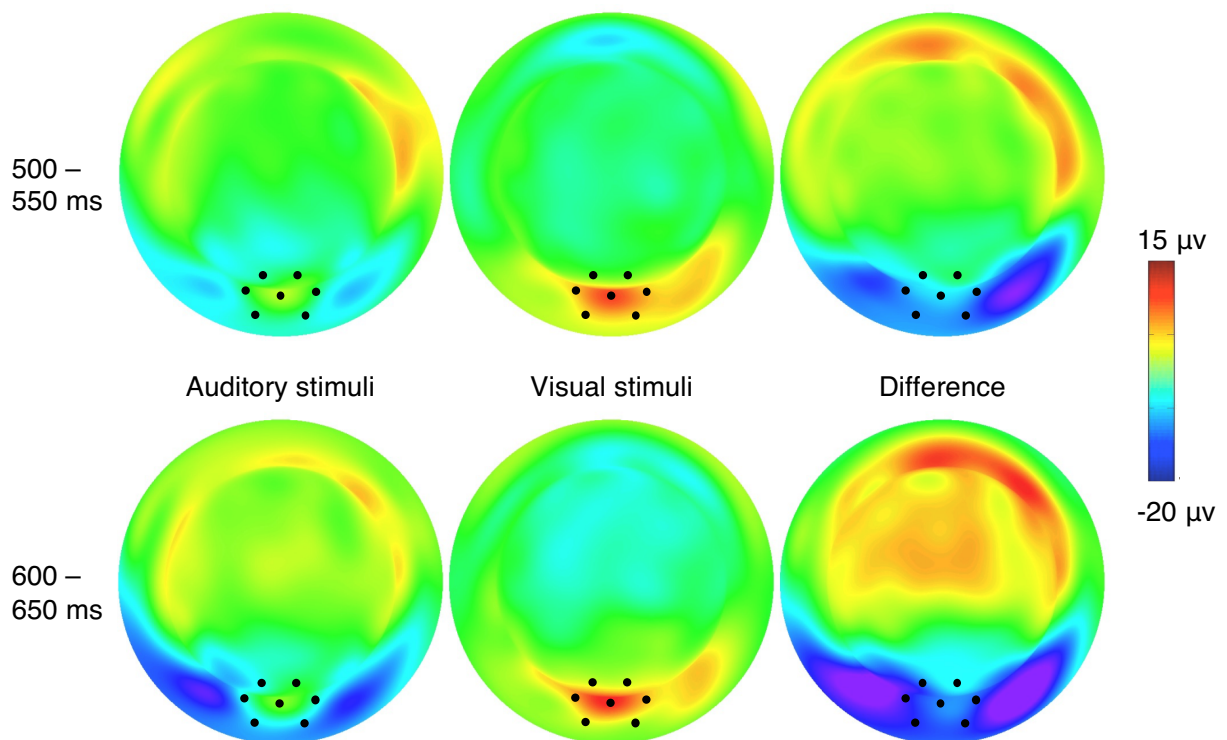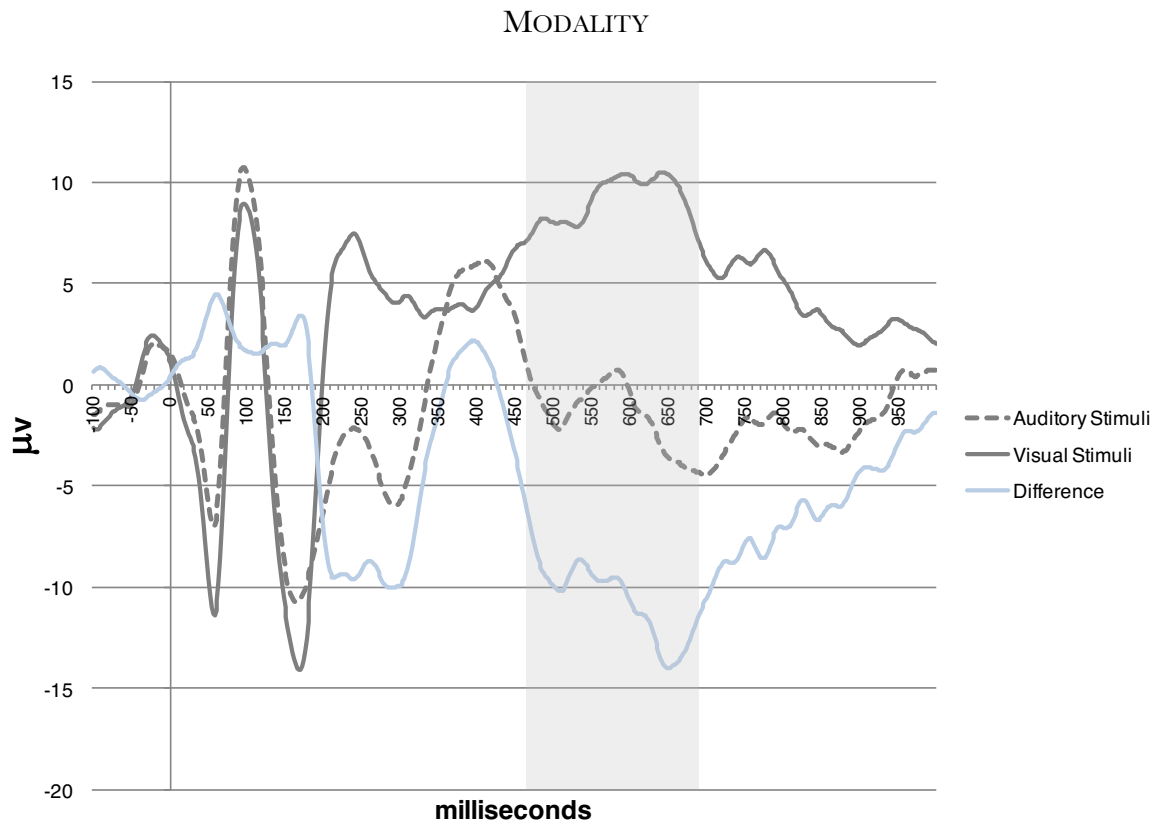**Figure 6.5.3 Fronto-central cluster of electrodes: ERP waveforms in response to the different modalities of presentation of the stimuli.** The plot represents the waveforms in response to the stimuli presented in the auditory and visual modalities (irrespective of the motion direction of the stimuli) and the difference waveform. The shaded area indicates the time course of statistically reliable effects of the modality of presentation on the waveform. The topographical maps represent the voltage distribution over the scalp during the period of reliable statistical difference. The small black disks indicate the locations of the electrodes chosen for the analyses.
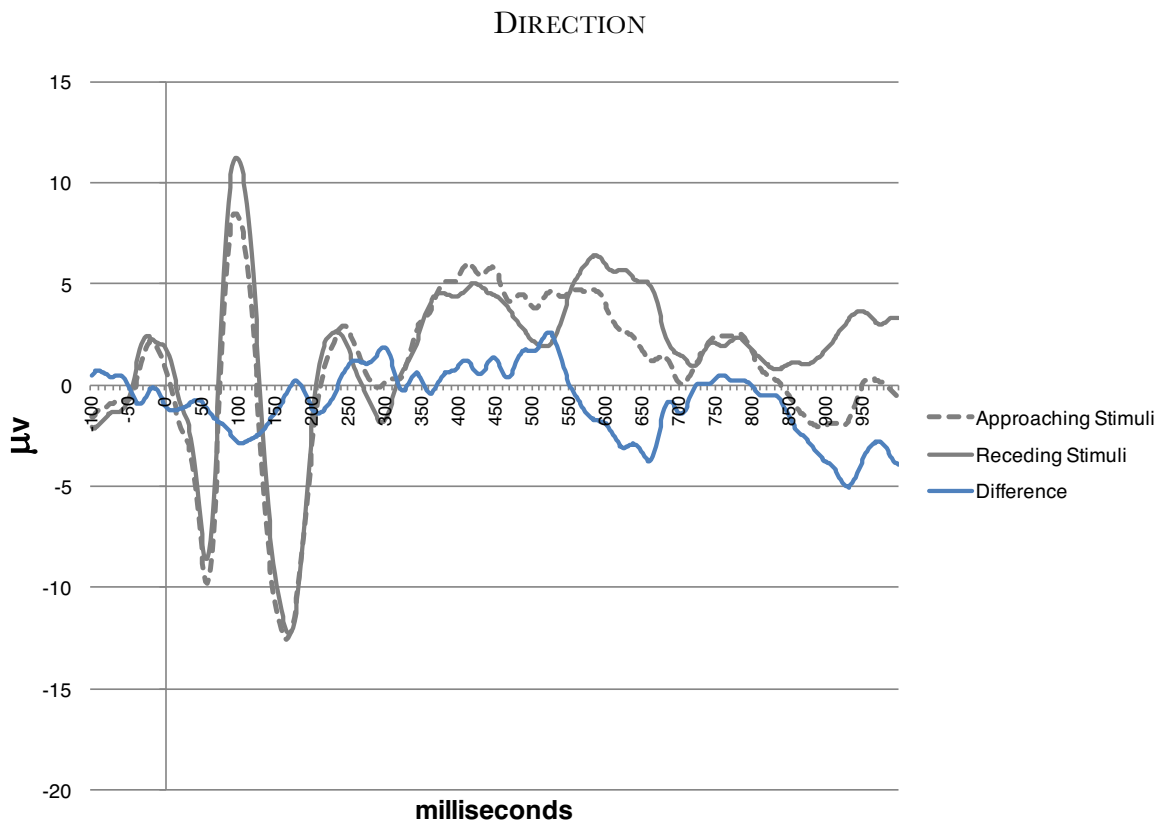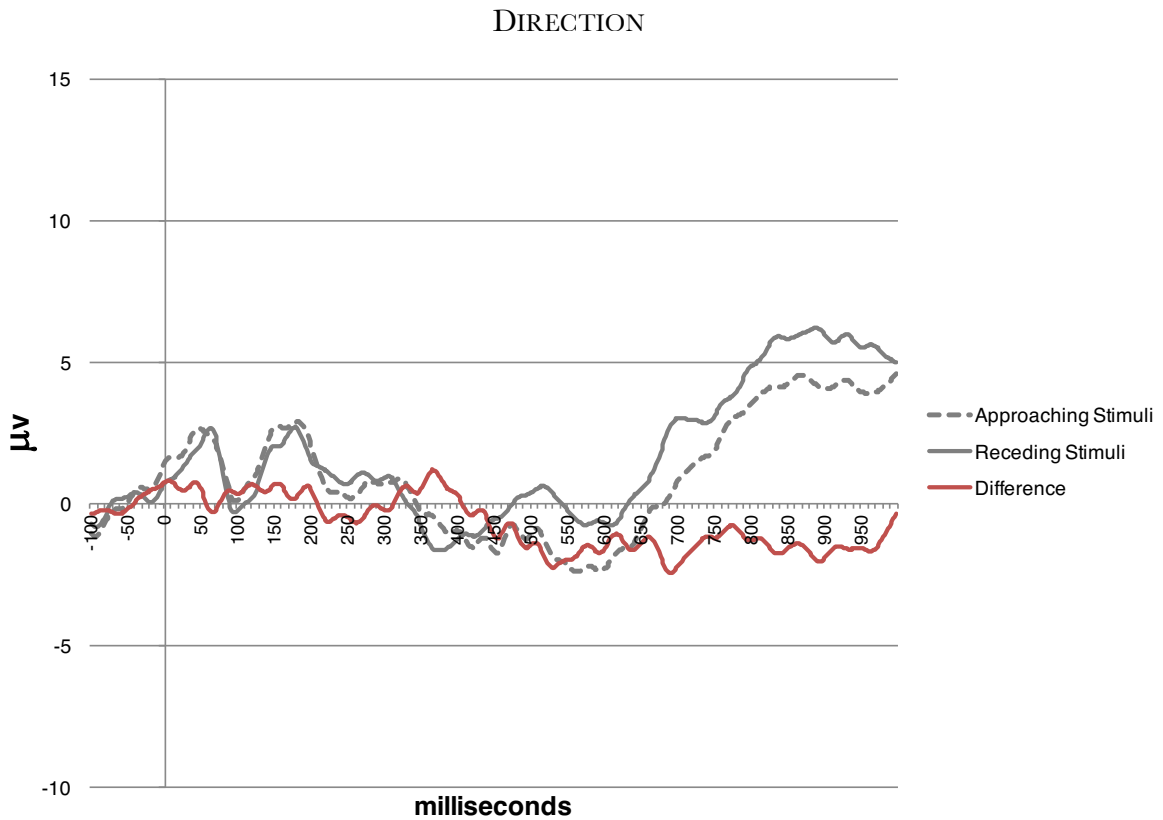
Figure 6.5.4 Fronto-central cluster of electrodes: ERP waveforms in response to the different motion directions of the stimuli. The plot represents the waveforms in response to the approaching and receding stimuli (irrespective of the modality of presentation of the stimuli) and the difference waveform.
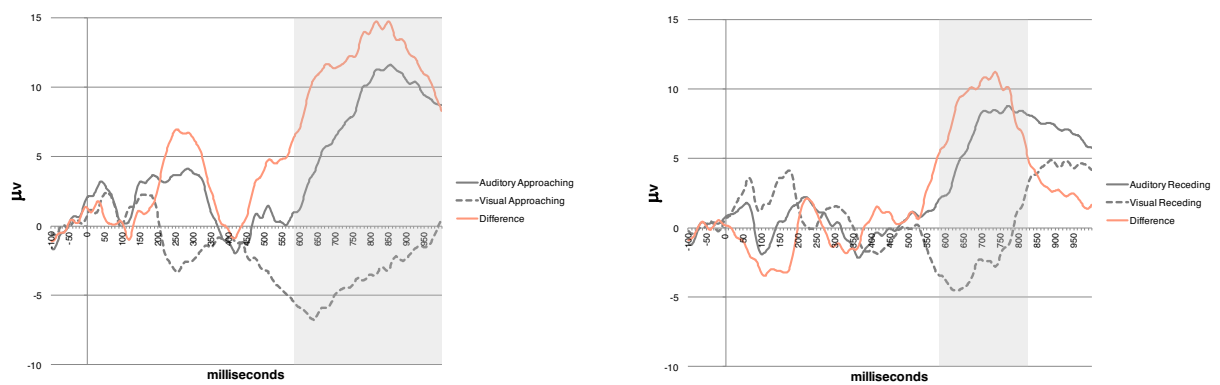
Figure 6.5.5 Grand averaged ERP waveforms for the approaching (Left - auditory vs. visual) and receding (Right - auditory vs. visual) stimuli in the fronto-central cluster of electrodes.

The Monte Caro simulation, despite its many advantages, is not sensitive to brief segments of significant differences in the potential activity and hence should not be used when the interest is focused on short sequences of time-points (Guthrie & Buchwald, 1991). Because of this and based on visual inspection of the data recorded over the occipital sites, I decided to use a more sensitive measure to investigate the existence of any differences in the earliest components (more confined in time) of the ERP waveforms recorded from the occipital cluster of electrodes. In particular, I wanted to investigate whether the event-related potentials reflecting the earliest stages of processing over the occipital sites were influenced by either the modality of presentation or the perceived direction of the stimuli. After visual inspection of the recorded waveforms, averaged across participants (Fig. 6.5.6), I decided to analyse the negative peaks occurring around 55 and 165 ms post stimulus onset and the positive peak occurring around 100 ms post stimulus onset (respectively N1, N2 and P1 from now onwards).
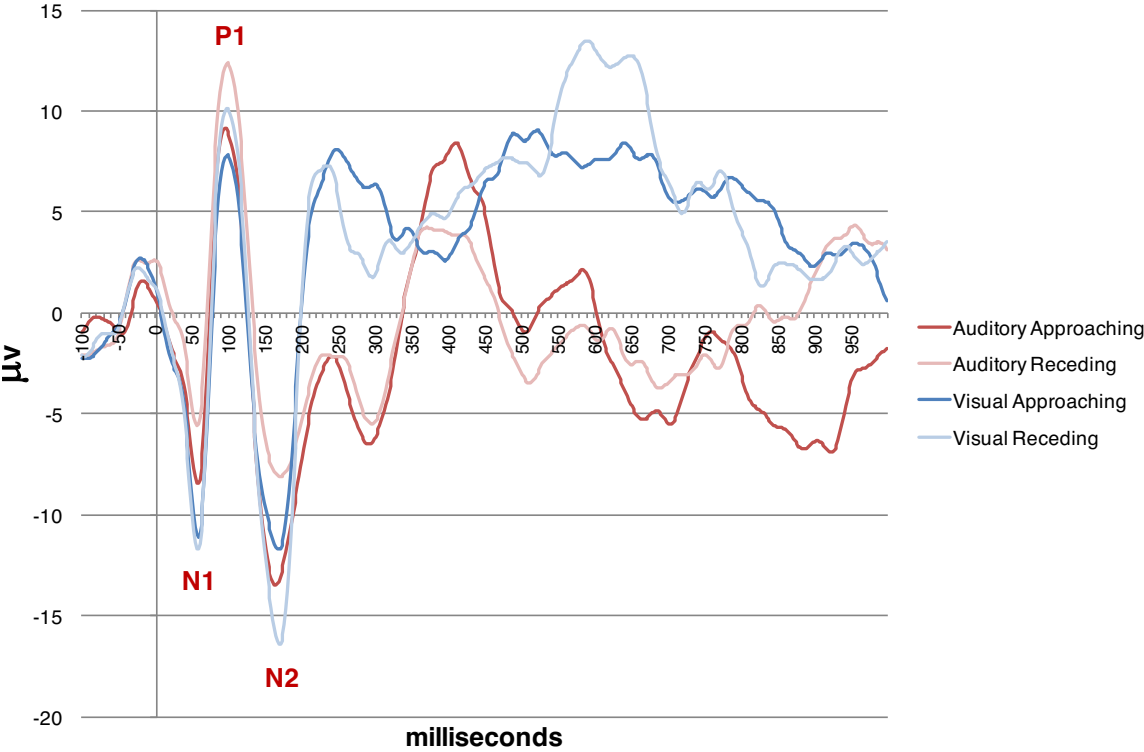
Figure 6.5.6 ERP waveforms recorded from the occipital electrodes in response to the four stimuli presented to the infants.

For the N1, I calculated the mean individual amplitude of the waveform between 40 and 70 ms post stimulus onset, for the P1 between 80 and 120 ms post stimulus onset and for the N2 between 140 and 190 ms post stimulus onset. Such time windows were chosen from visual inspection of the data in order to contain the point of maximum amplitude of each peak and, at the same time, to make sure that the slopes of the three peaks did not overlap with each other. I ran a two-way repeated measures ANOVA on each peak, with Modality and Direction as factors. For the N1, the analysis showed a tendency towards significance of the main effect of Modality [$F(1, 8) = 4.414$, $p = .069$, $\eta^2 = .226$], and no effect of Direction nor of the Interaction between the two factors [respectively, $F(1, 8) = 1.892$, $p = .206$, $\eta^2 = .020$; $F(1, 8) = 1.382$, $p = .274$, $\eta^2 = .039$]. Specifically, the deflection was more negative following visual vs. auditory stimuli (amplitude means: visual stimuli = -8.82 μv; auditory stimuli = -5.02 μv). For the P1, the analysis showed a tendency towards significance of the main effect of Direction [$F(1, 8) = 4.407$, $p = .069$, $\eta^2 = .084$], and no effect of Modality nor of the Interaction between the two factors [respectively, $F(1, 8) = .924$, $p = .365$, $\eta^2 = .042$; $F(1, 8) = .069$, $p = .779$, $\eta^2 = .003$]. For this component, the waveform amplitude was larger for receding vs. approaching stimuli (amplitude means: receding stimuli = 9.20 μv; approaching stimuli = 6.60 μv). Finally, for the N2, the ANOVA did not show any significant effects for any of the factors, nor their interaction [Modality: $F(1, 8) = .973$, $p = .353$, $\eta^2 = .042$; Direction: $F(1, 8) = 0.434$, $p = .528$, $\eta^2 = .004$; Interaction: $F(1, 8) = 3.581$, $p = .095$, $\eta^2 = .164$] (Fig. 6.5.7). Possibly, none of these effects reached significance level due to the small size of the final sample of participants. However, it is worth noticing that, overall, these preliminary data seem to suggest that the event-related potential recorded over the occipital sites was modulated by both the modality of presentation of the stimuli and their perceived direction already during the earliest stages of processing.
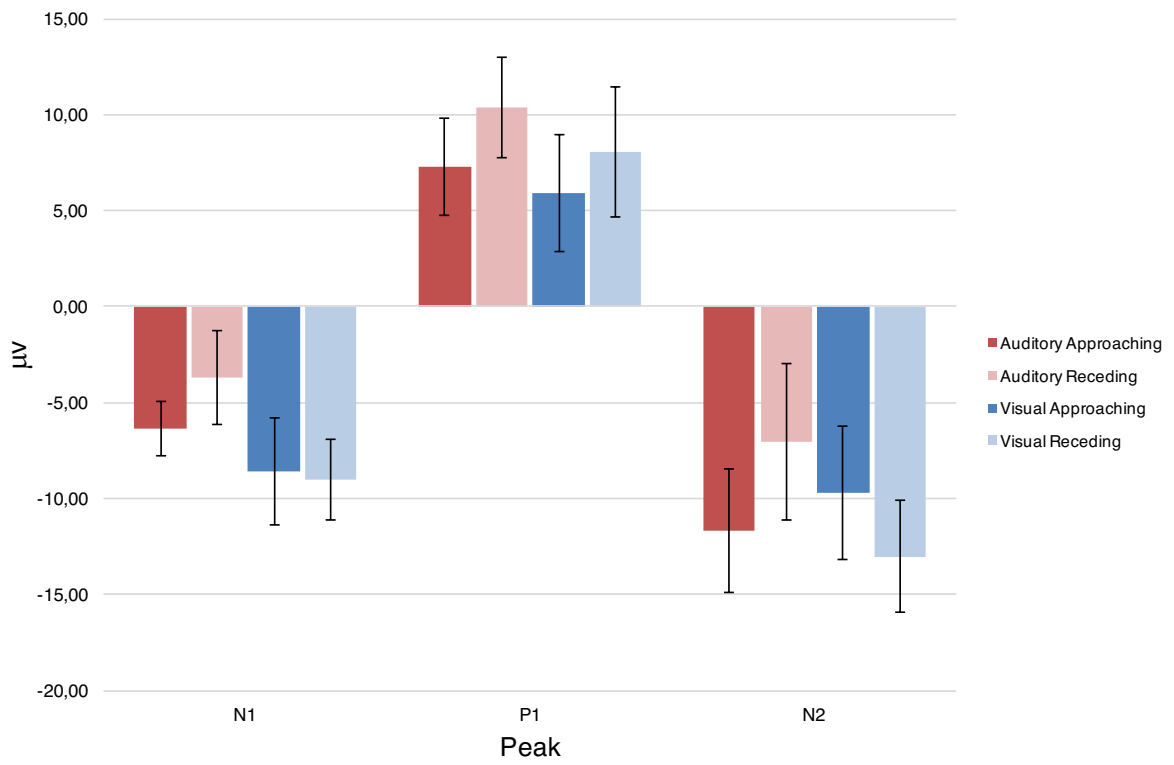
Figure 6.5.7 Averaged mean individual amplitude (and S.E.) of the N1, P1 and N2 peaks in response to each of the four presented stimuli, recorded from the occipital electrodes.

With this Study, I tried to begin to investigate the neural correlates of the perception of unimodal trajectories in 5-month-old infants. To address this, I presented a group of 9 5-month-olds with auditory and visual stimuli depicting a trajectory either approaching them or receding towards the background, while recording their spontaneous electrical activity.

I was particularly interested in studying whether the primary visual and auditory cortices could have a role in processing stimuli coming from the "other" modality and if the electrical activity during the earliest stages of processing (of the visual stimuli in particular) could be influenced by the trajectory of the moving stimulus. Regarding the first aspect, a new view of multisensory stimuli perception and brain organization has recently been suggested (Murray et al., 2016), according to which the primary sensory cortices should be considered multisensory in nature, rather than exclusively devoted to the processing of stimuli coming only from one modality. According to this view, I wanted to investigate if the visual and auditory stimuli presented to the infants were processed in similar ways in the primary visual and auditory cortices, suggesting a role of these cortices in crossmodal processing, or if, conversely, the signals coming from the two different senses were processed differently in the different areas of the infants' brain. With regards to the second aspect, instead, I hypothesised that if infants perceived either of the stimuli as more negative compared to the other one, the early stages of the stimulus processing could be influenced by the perceived valence of the stimulus itself. A recent study (Vagnoni, Lourenco, & Longo, 2015) investigated the neural mechanisms of the processing of visual looming stimuli with different emotional valence and showed that positive and negative stimuli are immediately differentiated by the brain and, hence, receive different amounts of attention since the earliest stages of processing. In particular, they found that the P1 amplitude was reduced, whereas the occipital N1 amplitude was enhanced for negative vs. positive stimuli.

In the study by Vagnoni and colleagues (2015) all the stimuli moved in the same direction (they were all approaching the participant) and their different valence was conveyed by semantic information on their identity (e.g. snakes vs. rabbits). Conversely, in this paradigm the stimuli were moving along different directions – i.e. approaching vs. receding – with the approaching ones being supposedly more negative than the receding ones. Therefore, the valence of the different stimuli was embedded in their motion direction itself. However, it is to date unclear whether young infants perceive looming stimuli as dangerous or threatening (hence negative) as opposed to interesting (hence positive).

Driven by the intention to investigate the event-related brain activity in the primary sensory cortices, I identified two clusters of electrodes for the analyses. On each cluster, I ran a Monte Carlo simulation (Guthrie & Buchwald, 1991) that investigated the effects on the ERPs modulation of the two factors subtended by the four stimuli (Modality and Direction), as well as their Interaction. This analysis identified sequences of reliably significant differences between the conditions, correcting for the autocorrelation that is likely to exist between successive time-points in the EEG recordings (Guthrie & Buchwald, 1991).

Concerning the primary visual cortex, I identified a cluster of 7 electrodes surrounding the Oz channel (in the 10-20 system). The Monte Carlo simulation highlighted a significant effect of the modality of presentation of the stimuli between 466 and 690 ms post stimulus onset showing, within this period, a reliable sequence of significant differences between the ERPs in response to visual and auditory stimuli. During this period of time, the amplitude of the waveform was significantly larger in response to the visual stimuli than to the auditory stimuli. Conversely, the simulation did not find any sequences of significant differences between approaching and receding stimuli longer than the minimum length considered reliable by the simulation itself (144 ms). These findings suggested on one side that the event related waveforms recorded in the occipital sites did not seem to differ depending on the direction of the presented

stimulus and, on the other side, that the modality of presentation of the stimuli had a clear impact on the modulation of the potential starting from the intermediate stages of processing.

The Monte Carlo simulation did not find any reliable sequences of significant differences in the ERP potentials during the earliest stages of processing. However, this might be because, despite its many advantages, this method is not sensitive to brief segments of significant differences in the waveforms and then should not be used when the interest is focused on short sequences of time-points (Guthrie & Buchwald, 1991). As a consequence, and after visual inspection of the waveforms recorded over the occipital electrodes, I decided to use a more sensitive measure to investigate more in detail the ERP components occurring in the first 200 ms after stimulus onset, which are more confined in time. Specifically, I wanted to consider the first three peaks highlighted by the visual inspection of the waveforms recorded over occipital sites, i.e. the negative peak occurring around 55 after stimulus onset, the positive peak occurring around 100 ms after stimulus onset and the negative peak occurring around 165 ms after stimulus onset (respectively N1, N2 and P1 from now onwards). In order to investigate the effects of the modality of presentation and of the direction of the stimuli on the waveforms, I compared the individual mean amplitude of the ERPs in response to the different stimuli during three latency windows, respectively 40-70 ms for N1, 80-120 ms for P1 and 140-190 ms for N2. The analyses showed that in the N1 peak the amplitude of the waveform was almost significantly modulated by the modality of presentation of the stimulus (irrespective of its direction), whereas in the P1 peak it was almost significantly modulated by direction of the stimulus (irrespective of the modality of presentation). Conversely, neither of the factors seemed to significantly influence the potential during the N2 peak. During the N1 peak, the deflection of the potential was more negative for the visual vs. auditory stimuli, whereas during the P1 peak the amplitude of the waveform was larger for the receding vs. approaching stimuli.

In the experimental procedure, the trials were separated from one another by an attention getter. When the infants were looking towards the screen, the experimenter triggered the next trial, interrupting the attention getter itself. As the attention getter itself was a visual stimulus (i.e. a flickering black circle), I wanted to avoid the possibility that the brain activity related to the visual processing of the attention getter interfered with the processing of the actual stimulus over occipital sites. For this reason, I decided to present a blank background (surrounded by a grey frame) during the event-related baseline, i.e. during the 100 ms preceding the appearance of the stimulus. Such background would then stay the same during the presentation of the stimulus, irrespective of the modality: visual stimuli would appear within that background, whereas auditory stimuli were presented while the infants could still see the background itself. As a consequence, I speculate that the ERPs identified over occipital sites for both visual and auditory stimuli could be considered as event-related responses to the onset of the background, taking place 100 ms prior to the appearance of the stimulus. Interestingly, though, the data suggested that the first of these potentials (N1) seemed to be modulated by the modality of presentation of the actual stimulus (being more negative for visual vs. auditory stimuli), whereas the amplitude of the second peak (P1) seemed to be influenced by the perceived direction of the stimulus, irrespective of the modality of presentation (being larger for approaching vs. receding stimuli). Therefore, I speculate that the visual ERP related to the onset of the visual background could have been modulated by the stimulus presented 100 ms later, and, more specifically, both by its modality and perceived direction.

Some additional speculations might be made with particular reference to the modulation of the P1 depending on the direction of the stimulus, irrespective of the modality of presentation. From the presented data it seemed that the amplitude of the waveform was larger in response to the receding vs. the approaching stimuli. This finding seems to suggest that already during infancy the brain might allocate different amounts of attention to stimuli with

different valence and seems to do so already during the earliest stages of processing (Vagnoni et al., 2015). In this specific context, the stimuli would be awarded a different value not by their semantic properties (as in Vagnoni et al.), but rather by the intrinsic behavioural information embedded in their trajectory. If the possible impending threat depicted by approaching stimuli would attribute them a negative value, the smaller amplitude of the P1 peak in response to approaching trajectories would support previous findings (Begleiter, Gross, & Kissin, 1967; Begleiter, Gross, Porjesz, & Kissin, 1969; Vagnoni et al., 2015), showing a smaller P1 amplitude for negative stimuli. However, it is now yet known if infants could discriminate the motion direction of the stimuli after being exposed to them for such a short time. Conversely, they might be responding to the initial size or loudness of the stimuli, being larger (and hence possibly more threatening) for receding stimuli during the first milliseconds of presentation. If this were the case, the data would support other findings suggesting larger amplitudes for negative vs. positive stimuli (Carretié, Hinojosa, Martín-Loeches, Mercado, & Tapia, 2004; Smith, Cacioffo, Larsen, & Chartrand, 2003). I am planning to run a control study in order to disentangle these two possible explanations. Irrespective of its direction, which is still controversial in adults as well (Vagnoni et al., 2015), the modulation of the P1 in response to the direction of the stimuli nevertheless suggests that infants' brain seems to allocate different amounts of attention to stimuli characterized by different valence already during the earliest stages of processing.

Concerning the primary auditory cortex, the grand averages of the waveforms recorded in the electrodes positioned between F3, F4, C3 and C4 were visually inspected and a cluster of 7 electrodes located between Fz and Cz (in the 10-20 system) was selected. Also within this cluster, the Monte Carlo simulation found a significant effect of the modality of presentation of the stimuli between 572 and 998 ms post stimulus onset, highlighting, within this time window, a reliable sequence of significant differences in the waveforms in response to visual and auditory

stimuli. During this period of time, the amplitude of the ERP waveform was significantly larger in response to the auditory stimuli than in response to the visual stimuli, with the former leading to a positive and the latter to a negative deflection of the electrical potential. As in the occipital cluster, also in this one the simulation could not find any sequences of significant differences longer than the minimum length considered reliable (144 ms) when comparing the stimuli depending on their direction. Similarly to the findings obtained from the occipital sites, these data suggested that the event related waveforms recorded over the fronto-central electrodes did not seem to differ depending on the direction of the presented stimulus and that the modality of presentation of the stimuli influenced the shape of the ERP waveforms from the intermediate stages of processing.

Given the small number of infants included so far in the final sample, these results should be considered only as preliminary and exploratory. In order to corroborate the results, I am working to increase the number of participants in the sample. I am also collecting data from a group of older infants (9-month-olds), to investigate the development of the neural processing of stimuli moving within the peripersonal space during the first year of life. Furthermore, I am planning to run some control conditions, to rule out possible factors that might confound the interpretation of the data, as for example the role of the size of the stimuli in the modulation of the P1 component. Nevertheless, the results obtained so far seem to support recent findings (for a review, see Kayser, Petkov, & Logothetis, 2009 for the auditory cortex and Murray et al., 2016 for the visual cortex) about the role of the primary sensory cortices in processing crossmodal stimuli, hence being intrinsically multisensory, and about the possibility that infants' brain could allocate different amounts of attention to different stimuli, based on their valence, from the earliest stages of processing (Vagnoni et al., 2015). At a later stage, I think that it would be extremely interesting to follow up on these first results investigating the neural correlates of the processing of multisensory congruent and incongruent stimuli. This would give the

opportunity to investigate the interplay between multisensory integration principles and behaviourally relevant information at the neural level, as well as to understand better the role of the primary sensory cortices in the perception of the motion of stimuli within the peripersonal space during infancy.

7. PERIPERSONAL SPACE BOUNDARIES IN NEWBORNS (STUDIES 5 AND 6)

7.1 RATIONALE

The peripersonal space (PPS) could be defined as "the space immediately surrounding the body", which "mediates every physical interaction between the body and the external world, because it is within its boundaries that we can reach and act upon objects, as well as avoid looming threats" (Canzoneri, Magosso, & Serino, 2012, p. 1) and is conceived as a "multisensory-motor interface between body and environment" (Teneggi, Canzoneri, di Pellegrino, & Serino, 2013, p. 1). Recent studies by Serino and colleagues investigated the PPS extension and identified its boundaries with an audio-tactile integration task (Canzoneri et al., 2012; Teneggi et al., 2013). Their results showed that auditory stimuli speeded up the processing of concurrent tactile stimuli when they were perceived within a certain distance from the body, which, as the authors suggested, should be considered the boundary of the PPS itself (Canzoneri et al., 2012, Ch. 1.2). They also demonstrated that this critical distance is subject to social modulation: when the far space is occupied by another person, the participants' PPS seems to shrink, whereas when a previous cooperative interaction between the participant and the other person has occurred, the PPS seems to expand, including the other person's PPS (Teneggi et al., 2013) (for more detail about these studies, Ch. 1.2).

The initial aim of my PhD research project was to investigate the existence and dimensions of this delimited portion of space in infants, as, to my knowledge, no studies tried to measure the boundaries of the PPS during development. My previous studies, Study 1 in particular (Ch. 4.3), provided the necessary ground for this investigation, demonstrating that humans show some rudimentary processing of the space surrounding their body right after birth. In fact, newborns seem to be equipped with an initial ability to differentiate the space surrounding them, showed by their efficient discrimination of different moving trajectories and

by their visual preference for those directed towards their own body. Furthermore, Study 2 (Ch. 4.4) showed that the integration of multimodal information about stimuli moving near the body works efficiently right after birth and that newborns' processing of congruent audio-visual trajectories seems facilitated. Taken together, these results suggest that the space immediately surrounding the body seems to be already processed and invested of a special salience in the earliest stages of postnatal development.

In order to measure the boundaries of the PPS in adults, Canzoneri and colleagues (2012) implemented a dynamic audio-tactile integration task. They presented their participants with a sample of pink noise simulating, through the dynamic change of its intensity, either the approach or the recess of a sound source. While the sound was playing, a tactile stimulus was delivered at the participants' right finger at different temporal delays from the onset of the auditory stimulus: in this way, the tactile stimulation occurred when the sound was perceived at different distances from the body (Canzoneri et al., Fig. 7.1.1). The participants were required to vocally respond to the tactile stimuli and their reaction times (RTs) were measured.
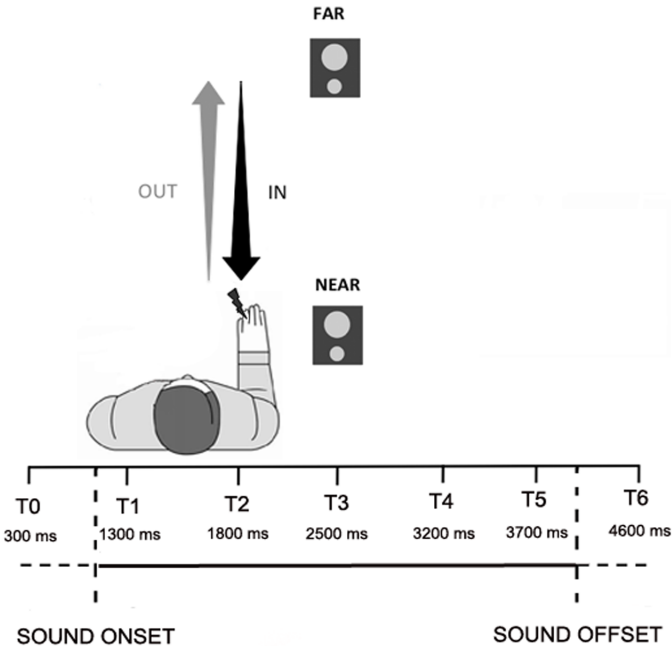
Figure 7.1.1 Procedure (from Canzoneri et al., 2012) Subjects received a tactile stimulus at their hand while task-irrelevant sounds either approached to or receded from the hand. Tactile stimuli were delivered at different temporal delays from sound onset (from T1 to T5), so that they were processed when sounds were perceived at a different distance from the hand.

I decided to adapt this task in order to use it with newborns with the aim of investigating the existence of the PPS as a delimited portion of space with identifiable boundaries right after birth. In the adapted version of the task, I decided to use static – rather than dynamic – auditory stimuli, to deliver the tactile stimulation touching the newborns' forehead with a paintbrush and to record the RTs measuring the saccadic latency to two visual targets appearing on the screen immediately after the audio-tactile stimulation. Clearly, deciding to measure the RTs to the visual targets would provide an indirect measure of the RTs to the audio-tactile stimuli. However, this choice was necessary as this was the most suitable way to obtain RT measures from a newborn population. Furthermore, despite this manipulation would probably lead to a small delay of the RTs, I could expect the delay to be consistent across the different Distance conditions, as the time between the audio-visual stimulation and the appearance of the visual targets was consistent across Distance conditions.

If the adapted paradigm was working and if the chosen sound intensities were perceived by the newborns around the boundaries of their PPS, I would expect their RTs to the visual display following the audio-tactile stimulation to be significantly speeded up when the auditory stimulus was perceived within the PPS itself. On the contrary, if the paradigm was not working, if newborns' PPS did not have clear boundaries or if the presented sounds were not perceived around these boundaries, I would expect the RTs to decrease constantly as the sound was perceived as closer to the body or, possibly, not to change at all.

In a first study (Study 5, Ch. 7.2) I implemented the adapted paradigm using 3 sounds, chosen accordingly to the positions used by Canzoneri and colleagues (Ch. 7.2.2). In light of the intriguing results of Study 5, I ran a further study (Study 6, Ch. 7.3) using 5 different sounds and including a control group that experienced only the auditory (and not the tactile) stimulation.

7.2 STUDY 5

7.2.1 Introduction and hypotheses

In order to measure the dimensions of newborns' PPS, I tried to adapt the dynamic audio-tactile interaction task used with adults by Canzoneri, Magosso and Serino (2012).

If the paradigm worked and if the presented sounds were perceived around the newborns' PPS boundaries, I would expect that the sounds perceived as closer to the body would speed up the processing of concurrent tactile stimulation, leading to faster saccadic RTs. In particular, I would expect to find a critical perceived distance (of the auditory stimulus) after which the RTs would be significantly speeded up. If found, this distance could be considered as the boundary of the PPS in newborns (Canzoneri et al., 2012).

However, if the paradigm did not work or if newborns' PPS was not delimited by clear boundaries (as well as if the presented sound were not perceived around its boundaries), I would expect the saccadic RTs to the audio-tactile stimuli to remain constant across Distance conditions or, possibly, to diminish gradually, but without significant changes between one sound position and another as the sound was perceived as closer to the body.

7.2.2 Participants

Eight newborns (5 female) aged from 16 to 75 hours of life at time of test took part in the study. Four additional newborns participated, but were excluded due to an experimental error (n = 1) or because they did not complete enough trials of each condition (n = 3). All the newborns that participated in the study met the screening criteria of normal delivery, birth weight > 2500 g, gestational age > 37 weeks and had an Apgar index score between 8 and 10 at the fifth minute of life. No abnormalities were present at birth. The 8 newborns included in the final sample had a mean age of 40.22 hours (SD = 20.16) at testing, a mean birth weight of 3436.25 g (SD = 432.27) and a mean gestational age of 39.48 weeks (SD = 1.01).

Testing took place when newborns were awake and alert, usually during the hour preceding feeding time. The parents were informed about the procedure and provided written informed consent to their child's participation. The local Ethical Committee of Psychology Research (University of Padua) approved the study protocol.

7.2.3 Stimuli and Procedure

In the adapted version of the audio-tactile integration task implemented by Canzoneri and colleagues (2012) I decided to use static auditory stimuli because I would have not been able to measure the newborns' RTs if they had been presented with dynamic sounds. Furthermore, I decided to use samples of a sinusoidal waveform (instead of pink noise) because, as already mentioned (Ch. 4.2.2), complex sounds seem to facilitate both multisensory integration and the processing of moving stimuli (Maier & Ghazanfar, 2004; Neuhoff, 1998; Romei, Murray, Cappe, & Thut, 2009).

In order to choose the intensity of the auditory stimuli, I calculated the intensity of the sound presented by Canzoneri and colleagues (2012) at each of the time points were the tactile stimulation was delivered. The sample of pink noise used in Canzoneri and colleagues' study changed from 55 to 70 dB and lasted 3000 ms, leading to an intensity change of 0.005 dB each ms. Table 7.2.1 shows the correspondence between each time point when the tactile stimulation was delivered in Canzoneri and colleagues' study and the intensity of the auditory stimulus at that time point.

	sound onset						sound offset	
T0		T1	T2	T3	T4	T5		T6
300 ms		1300 ms	1800 ms	2500 ms	3200 ms	3700 ms		4600 ms
	1000 ms						4000 ms	
	55 dB	56.5 dB	59 dB	62.5 dB	66 dB	68.5 dB	**70 dB**	

Table 7.2.1 Time points and intensity correspondence. Intensity of the sound at each of the time point where the tactile stimuli were delivered in Canzoneri and colleagues' (2012) audio-tactile interaction task.

After having calculated the intensity of the sound at each of the time points when Canzoneri and colleagues delivered the tactile stimuli, I decided to use 3 sounds (i.e. 3 Distance conditions). For two of them, the intensity was the same as, respectively, at the onset (55 dB – Distance 1) and the offset (70 dB – Distance 5) of the sound used in Canzoneri and colleagues' (2012) paradigm, For the third Distance, instead, I decided to use the intensity corresponding to the intensity of the sound at T3 in Canzoneri and colleagues' study (62.5 dB – Distance 3), i.e. the point in space where adults' PPS boundary seems to be positioned.

When the newborns were seated on the experimenter's lap (at about 35 cm apart from the screen) and were attending to the centre of the screen, the experiment began. The newborns were presented with a white circle flickering in the centre of a black background, with the purpose of keeping their attention focused on the centre of the screen. The flickering white circle was presented alone for 3000 ms, then an auditory stimulus was introduced, for further 2000 ms. While the auditory stimulus was presented, the white circle was still on the screen: I decided to keep it flickering during the sound presentation in order to keep the newborns' attention in the same position and avoid as many eye movements as possible. During the presentation of the auditory stimulus, the newborns' forehead was gently stroked with a paintbrush. I decided to stroke the forehead (instead of, for example, one cheek) in order not to bias the newborns' visual attention to any side of the screen. As soon as the sound terminated, two target visual stimuli appeared on the peripheral sides of the screen and were visible for 2000 ms. As soon as they disappeared, a new trial started, following the same sequence of events (Fig. 7.2.1). The newborns were presented with a maximum of 30 trials (10 per sound) in random order, as long as their attention lasted. The white circle flickered with a frequency of 2.5 Hz. The visual targets were two identical infant faces on a black background; the pupils were 1 in diameter, in order to make sure that the newborns could discriminate them (a generally accepted estimate of visual acuity at birth is 1 cycle per degree; Atkinson & Braddick, 1989). The sounds were a sample of

sinusoidal waveform of 2000 ms duration and constant frequency (8000 Hz); they were played at 3 different intensities, namely 55, 62.5 and 70 dB. The sound was conveyed by two loudspeakers positioned under the monitor, one under the left and one under the right halves of the screen. The intensity of the sounds was measured in the position where the newborns' head would have been during testing, at the average conditions of the room during testing (environmental noise, lighting and set up). The stimuli were presented on a 24" screen using E-Prime 2.0.10.
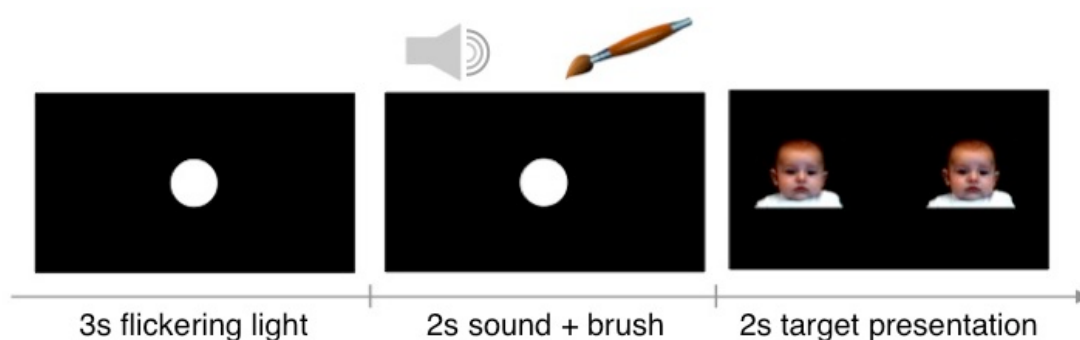
Figure 7.2.1 Experimental procedure. The newborns were presented with a flickering white circle on a black background for 3 s; then, one of the three possible sounds (55, 62.5 or 79 dB) was played for 2 s and at the same time their forehead was gently and slowly stroked (only once) with a paintbrush. In the meantime, the white circle kept flickering in order to keep the newborns' attention focused in the centre of the screen. Finally, two peripheral targets appeared and remained on the screen for another 2s.

7.2.4 Data Analysis

The newborns' eye movements were recorded throughout the experimental session in order to allow subsequent offline coding. After the experimental session, I coded the videos and I recorded the saccadic RTs, i.e. the "latency of the first eye movement away from the centre towards the peripheral target" (Farroni, Simion, Umiltà, & Dalla Barba, 1999, p. 176). While doing this, I was blind to the Distance condition of each trial.

The trials were considered valid only if the newborns were attending the centre of the screen immediately before the presentation of the peripheral targets. The infants were included in the final sample only if they completed at least two valid trials per each Distance condition.

7.2.5 Results

The newborns included in the final sample completed, on average, 49% of valid trials on the total number of trials that they attended (Table 7.2.2). The average RTs for each different Distance condition are summarised in Table 7.2.3.

	Distance 1	Distance 3	Distance 5	TOT
average no. of valid trials per newborn	4.00	4.75	4.50	13.25
SD	*1.60*	*1.58*	*1.20*	*2.92*
average total no. of trials per newborn	8.88	9.38	9.00	27.25
SD	*1.36*	*0.92*	*1.77*	*3.88*
average % of valid trials per newborn	45%	51%	50%	49%

Table 7.2.2 Valid trials results. Average number of valid trials completed by the newborns for each Distance condition (i.e. when each of the three sounds was presented) and overall, with Standard Deviations and percentage of valid trials relative to the total number of trials attended.

Distance	N	Minimum	Maximum	Mean	S.E.	SD
D1	8	560.00	1386.67	878.13	97.17	274.84
D3	8	240.00	780.00	518.14	71.06	200.10
D5	8	320.00	853.33	522.67	56.88	160.88

Table 7.2.3 Reaction times data. Descriptive statistics (minimum, maximum, mean, standard error and standard deviation) of newborns' reaction times to the visual target appearing immediately after the audio-tactile stimulation ceased, for each Distance condition.

In order to analyse the RTs to the peripheral visual target presented immediately after the audio-tactile stimulation finished, I ran a one-way repeated measures ANOVA, with perceived distance of the sound as factor. It revealed a significant main effect of Distance [$F_{(2, 14)}$ = 30.886, $p < .001$, η^2 = .815]. Then, after having verified that the differences between the RTs between all the three Distance conditions were normally distributed (Kolmogorov-Smirnov test, all $p > .05$), I ran two paired planned comparisons that revealed that the RTs differed significantly between Distance 1 and Distance 3 [$t_{(7)}$ = 7.546, $p < .001$, d_z = 2.668], but not between Distance 3 and Distance 5 [$t_{(7)}$ = -.088, $p = .932$, d_z = .031] (Fig. 7.2.2). In order to correct for multiple comparisons, the level of significance was $p = 0.025$.
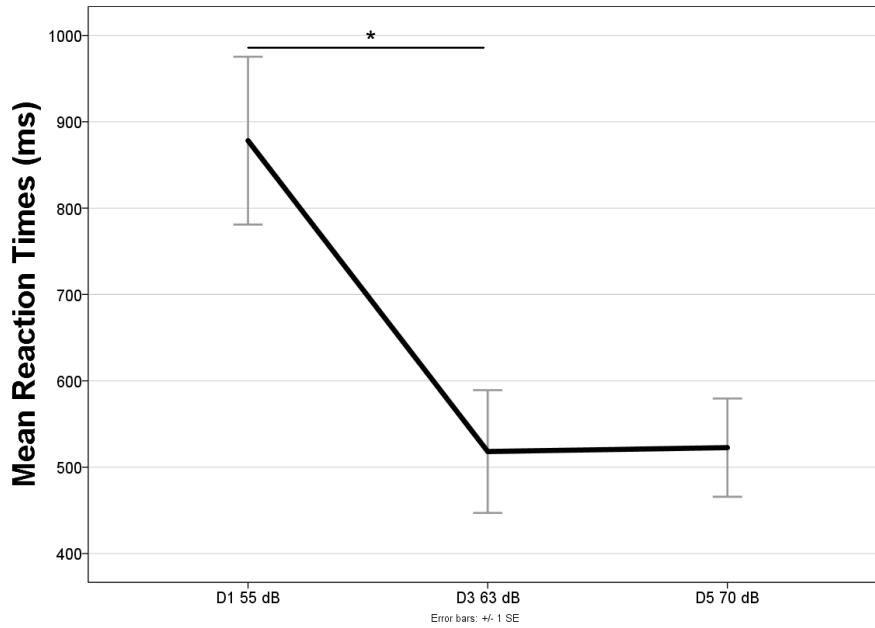
Figure 7.2.2 Effects of the perceived distance of the sound on newborns' reaction times. Mean visual RTs and S.E. in response to the visual targets immediately following the audio-tactile stimulation when the sound was perceived at different locations in space (from D1 to D5).
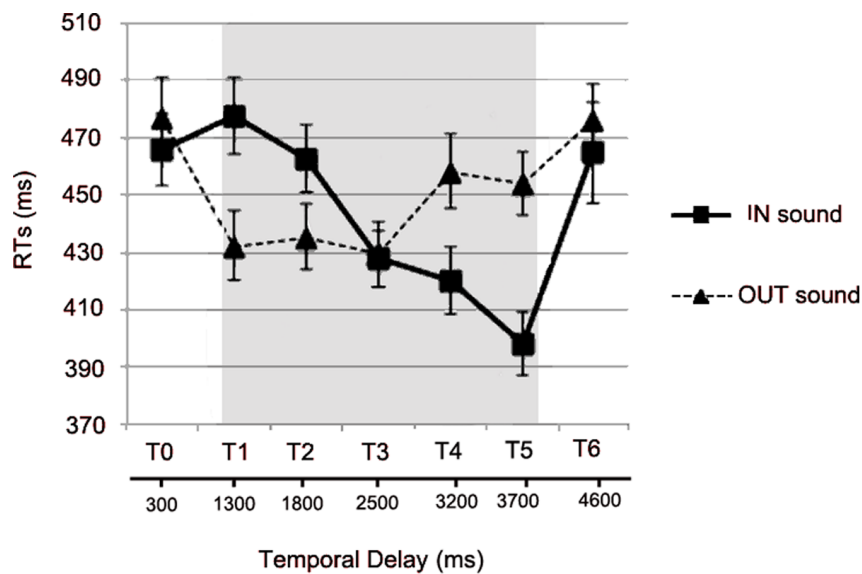
Figure 7.2.3 Effects of IN and OUT sounds on tactile processing (from Canzoneri et al., 2012). Mean RTs (and S.E.M.) to the tactile target at different temporal delays (from T0 to T6) for IN (filled line) and OUT (hatched line) sounds. The shaded region indicates the duration of the sounds.

7.2.6 Discussion

This first, exploratory study showed, despite the small number of participants, a clear modulation of the saccadic RTs following audio-tactile stimulation in newborns. The saccadic RTs were significantly speeded up when the sound was perceived at the intermediate distance from the body compared to when it was perceived farther away. The RTs between the intermediate distance and the one closest to the body, instead, were not significantly different (Fig. 7.2.2). This pattern of RTs closely resembled that showed by the adult participants of Canzoneri and colleagues' study (2012, Fig. 7.2.3) and suggested that adults and newborns show a similar modulation of the RTs to a tactile stimulus when a simultaneous auditory stimulus is perceived outside or inside the PPS. Deciding to measure the RTs to the visual targets immediately following the audio-tactile stimulation provided an indirect measure of the RTs to the audio-tactile stimuli, but at the same time it seemed the most suitable way to obtain RT measures from a newborn population. This manipulation would probably lead to a small delay of the RTs, but I could expect this delay to be consistent across the different perceived positions of the sound, because the time passing between the audio-visual stimulation and the appearance of the visual targets was consistent across Distance conditions. Furthermore, this delay would not constitute a confounding factor in the interpretation of the data, as I did not make any claim on the absolute value of the RTs, but rather on the perceived distance of the sound when a significant change in the RTs happened.

This first result looked particularly intriguing and, hence, I wanted to further study newborns' responses in this task, in particular investigating their RTs to audio-tactile stimulation when auditory cues were perceived as located in other positions in space. I was specifically interested in two additional positions: one intermediate between Distance 1 and Distance 3, i.e. where the significant drop of RTs happened in Study 5, and the second one perceived farther away than Distance 1. The reason for the latter position lies in the fact that

Canzoneri and colleagues found that adults' RTs did not significantly differ from each other at any of the time points before or after the critical one (i.e. T3, considered as the boundary of the PPS) and I wanted to verify whether the same was true also for newborns.

Furthermore, I wanted to investigate whether the effect shown in this study was specifically related to the simultaneous audio-tactile stimulation presented to the newborns and to rule out the possibility that it could be simply due to a progressive diminishment of the RTs as the sound was perceived closer to the body, i.e. it was due to the auditory stimulation on its own.

For these reasons, I ran an additional study in which I presented the auditory stimuli at five possible perceived locations to two different groups of newborns: one group was presented with multimodal audio-tactile stimulation, whereas the other one experienced only unimodal auditory stimulation.

7.3 Study 6

7.3.1 Introduction and hypotheses

The saccadic reaction times (RTs) of the newborns who participated in Study 5 showed a pattern that resembled quite closely the one shown by adults (Canzoneri, Magosso, & Serino, 2012). In particular, the newborns' RTs seemed to be speeded up when the sound was perceived at a certain critical distance from the body or closer to the body than that same distance. According to the interpretation given by Canzoneri and colleagues to their findings, this distance could be considered as the boundary of the PPS.

Following up on this intriguing result, I wanted to further investigate newborns' RTs when the sound was perceived at different locations in space and to verify that the effect found in Study 5 did specifically depend on the simultaneous audio-tactile stimulation and was not simply function of the perceived vicinity of the sound. For this reason, I run a further study (Study 6) using the same paradigm used in Study 5, but including two further perceived distances of the sound and a control group that experienced only the auditory – but not the tactile – stimulation.

I hypothesised that the RTs of the two groups – i.e. of the newborns who experienced multimodal vs. unimodal stimulation – would be different. In particular, I expected that the RTs of the newborns in Multimodal group would be similar until a certain, critical perceived distance of the sound, after which they would be significantly speeded up, remaining then similar to each other as the sound was perceived closer to the body. Conversely, I expected that the RTs of the newborns in the Unimodal group would not change significantly across the different Distance conditions, but that they would, possibly, progressively diminish as the sound was perceived closer to the body. However, a different outcome was also possible: if the newborns neglected the tactile stimulation and oriented to the visual targets more or less fast

only depending on the perceived distance of the sound, both groups could show the same pattern of RTs.

In Study 5, newborns' RTs were significantly speeded up when the sound was perceived at Distance 3 or closer to the body. In this study, I included two new perceived positions of the sound, depicted by two new sound intensities: one sound position was intermediate between Distance 1 and Distance 3, i.e. where the significant drop of the RTs happened in Study 5. With respect to this new sounds, I hypothesised two different outcomes: I predicted that the RTs to the audio-tactile stimuli could be speeded up either at the same point in space as in Study 5 (i.e. Distance 3) or earlier, at Distance 2. The second sound position, instead, was perceived as farther away than Distance 1. This position was introduced in order to investigate whether newborns' RTs did not significantly differ from each other at any of the time points before the critical one, as it happened in adults (Canzoneri et al., 2012).

7.3.2 Participants

Study 6 involved two groups of newborns: one group experienced multimodal audio-tactile stimulation (Multimodal group), whereas the other group experienced only unimodal auditory stimulation (Unimodal group). Overall, 31 newborns (17 female) aged from 12 to 94 hours of life at time of test took part in the study. Seventeen additional newborns participated in the study but were excluded due to experimental errors (n = 1), sleepiness (n = 4), because they did not complete enough trials of each condition (n = 11) or because of a suspect hearing problem (advised by the mother, n = 1). All the newborns that participated in the study met the screening criteria of normal delivery, birth weight > 2500 g, gestational age > 37 weeks and had an Apgar index score between 8 and 10 at the fifth minute of life. No abnormalities were present at birth.

The Multimodal group included 16 newborns (8 female), which had a mean age of 64.98 hours (SD = 15.65) at testing, a mean birth weight of 3435.63 g (SD = 328.17) and a mean gestational age of 40.14 weeks (SD = 1.34). The Unimodal group included 15 newborns (9 female), which had a mean age of 40.16 hours (SD = 20.10) at testing, a mean birth weight of 3397.33 g (SD = 384.88) and a mean gestational age of 40.21 weeks (SD = 1.36).

Testing took place when newborns were awake and alert, usually during the hour preceding feeding time. The parents were informed about the procedure and provided written informed consent to their child's participation. The local Ethical Committee of Psychology Research (University of Padua) approved the study protocol.

7.3.3 Stimuli and Procedure

The stimuli and the procedure were the same as in Study 5. Concerning the procedure, the only difference was that only one group of infants experienced the tactile stimulation on their forehead. Concerning the stimuli, the only difference was that the newborns who took part in Study 6 were presented with 5 different sound intensities. In addition to the three sounds used in the previous study (Distance 1: 55 dB; Distance 3: 62.5 dB; Distance 5: 70 dB) they were also presented with a 59 dB sound (Distance 2, corresponding to the intensity of the sound at Time 2 in Canzoneri et al., 2012, Table 7.2.1) and with a 47.5 dB sound (Distance 0), perceived as farther away than Distance 1 and being apart from it of the same distance existing between Distances 1 and 3.

The intensity of the sounds was measured in the position where the newborns' head would have been during testing, at the average conditions of the room during testing (environmental noise, lighting and set up).

Up to 31 trials were presented (to keep the total length of the experiment similar to that of the previous one), 7 each for Distances 1, 3 and 5 and 5 each for the newly introduced Distances 0 and 2.

7.3.4 Data Analysis

The data analysis was conducted as in Study 5. In the same way, trials were considered valid only if the newborns were attending the centre of the screen immediately before the presentation of the peripheral targets. In this study, though, the newborns were included in the final sample if they had completed at least two valid trials per at least 4 out of the 5 Distance condition. The missing values (n = 5) were replaced with the average RTs of the whole group of newborns in that specific Distance condition.

The newborns included in the final sample completed, on average, 58% of valid trials on the total number of trials that they attended (Table 7.3.1). The RTs for each different Distance condition are summarised in Table 7.3.2.

	Distance 0	Distance 1	Distance 2	Distance 3	Distance 5	TOT
average no. of valid trials per newborn	2.63	3.63	2.69	3.94	3.38	16.25
SD	*0.96*	*1.86*	*0.95*	*1.48*	*1.20*	*3.44*
average total no. of trials per newborn	6.19	6.44	6.13	4.69	4.69	28.13
SD	*0.83*	*1.03*	*0.89*	*0.79*	*0.60*	*2.68*
average % of valid trials per newborn	42%	56%	44%	84%	72%	58%

Table 7.3.1 Valid trials results. Average number of valid trials completed by the newborns for each Distance condition (i.e. when each of the five sounds was presented) and overall, with Standard Deviations and percentage of valid trials relative to the total number of trials attended.

Group	Distance	N	Minimum	Maximum	Mean	S.E.	SD
Multimodal	D0	16	520.00	1480.00	894.44	58.55	234.22
	D1	16	660.00	1140.00	892.48	30.82	123.29
	D2	16	333.33	946.67	607.64	51.84	207.37
	D3	16	224.00	1200.00	584.02	65.74	262.96
	D5	16	200.00	1213.33	540.00	58.27	233.07
Unimodal	D0	15	380.00	1260.00	823.08	63.36	245.41
	D1	15	456.00	1140.00	794.71	56.80	220.00
	D2	15	360.00	1200.00	762.67	63.61	246.35
	D3	15	380.00	1300.00	752.89	77.41	299.79
	D5	15	240.00	1213.33	761.38	75.45	292.22

Table 7.3.2 Reaction times data. Descriptive statistics (minimum, maximum, mean, standard error and standard deviation) of newborns' reaction times to the visual target appearing immediately after the audio-tactile stimulation ceased, for each distance condition.

In order to analyse the RTs of both the Multimodal and Unimodal groups in each of the perceived Distance conditions, I ran a two-ways mixed ANOVA, with Distance and Group as factors, respectively within and between participants. It revealed a significant main effect of Distance [$F(4, 116) = 8.351$, $p < .001$, $\eta^2 = .200$] and a significant interaction between Distance and Group [$F(4, 116) = 4.484$, $p = .002$, $\eta^2 = .107$], whereas the main effect of Group was not significant [$F(1, 29) = 1.600$, $p = .261$, $\eta^2 = .052$] (Fig. 7.3.1).
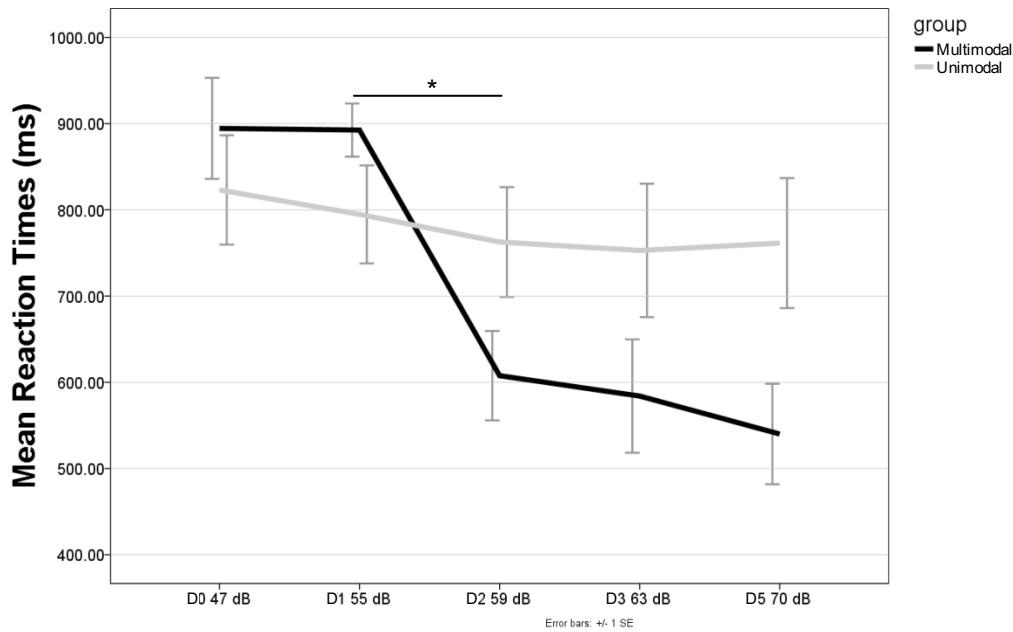
Figure 7.3.1 Effects of the perceived distance of the sound on newborns' reaction times.
Mean visual RTs and S.E. in response to the visual targets immediately following the auditory (Unimodal) or audio-tactile (Multimodal group) stimulation when the sound was perceived at different locations in space (from D0 to D5).

In order to further investigate the significant effect of the Interaction, I ran two separated one-way repeated measures ANOVAs, one per each group, both with Distance as a within participants factor. These analyses yielded to a significant main effect of Distance in the Multimodal group [$F(4, 60) = 14.295$, $p < .001$, $\eta^2 = .488$], but not in the Unimodal group [$F(4, 56) = .309$, $p = .871$, $\eta^2 = .022$]. As the differences between the RT scores in the pairings of perceived Distance conditions in the Multimodal group were not always normally distributed [Kolmogorov-Smirnov test, Δ D0-D1: $D(16) = .138$, $p = .200$; Δ D1-D2: $D(16) = .203$, $p = .077$; Δ D2-D3: $D(16) = .108$, $p = .200$; Δ D3-D5: $D(16) = .278$, $p = .002$], I followed up the significant effect of Distance in this group using non-parametric analyses. Wilcoxon Signed Ranks Test revealed a significant difference in the RTs between Distance 1 and Distance 2 [$Z = -3.237$, $p = .001$, $r = .362$], but not between any of the other couples of perceived distances [D0-D1: $Z = -.052$, $p = .959$, $r = .006$; D2-D3: $Z = -.052$, $p = .756$, $r = .006$; D3-D5: $Z = -.026$, $p = .979$, $r = .003$]. In order to correct for multiple comparisons (n = 4), the critical level of significance was $p = .0125$.

7.3.6 Discussion

The aim of Study 6 was to extend the preliminary findings of Study 5, investigating newborns' reaction times to a tactile stimulation simultaneous to an auditory stimulation whose source was perceived at different distances from the body. Another purpose of Study 6 was verifying whether newborns' RTs were modulated by the contemporary audio-tactile stimulation or whether their modulation depended solely on the perceived position of the sound in space, conveyed by auditory cues on their own.

The results of Study 6 showed an interesting modulation of newborns' RTs depending on the perceived distance of the auditory stimulus in space. Most importantly, only the group of newborns who experienced multimodal audio-tactile stimulation showed this modulation in their RTs: this demonstrated that the effect was clearly dependent on the presence of simultaneous auditory and tactile stimuli and was not simply function of the progressive decrease of the distance between the sound (i.e. its perceived position) and the newborns' body.

The RTs of the newborns in the Multimodal group did not change gradually as the sound was perceived closer to the body, but decreased following a peculiar pathway. The RTs to the audio-tactile stimulation were not significantly different from each other when the sound was perceived in the two farthest positions; in the same way, the RTs were not significantly different from each other when the sound was perceived at Distances 2, 3 and 5. Between Distance 1 and 2, instead, the RTs decreased significantly. As in Study 5, measuring the RTs to the visual targets that followed the audio-tactile stimulation provided an indirect measure of the RTs to the auditory or audio-tactile stimuli (depending on the group). However, as in Study 5, I would not expect that this manipulation could confound the interpretation of the data because i) even if it led to a small delay of the RTs, this would be consistent across the different perceived sound positions, and ii) I did not make any claim on the absolute value of the RTs,

but rather on the perceived distance of the sound when a significant change in the RTs happened.

The RT pattern shown by the newborns who participated in this study resembled quite closely the one found in adults by Canzoneri and colleagues' study (2012, Fig. 7.2.2). The authors used an audio-tactile integration task in order to measure the boundaries of adults' PPS: they asked their participants to vocally respond to a tactile stimulus delivered when a concomitant sound was perceived at 5 different locations in space. The RTs of their participants did not significantly change when the sound was perceived at the two farthest locations, then they significantly decreased at the third closest location to the body and then remained similar to each other as the sound moved closer to the body. The authors suggested that the speeding effect on the RTs that happened when the sound was perceived closer to the body may arise from the most efficient integration of multisensory inputs happening within the same portion of space, in this case the PPS around the hand. They showed that the sharp decrease of the RTs to the tactile stimulation happened when the sound crossed a specific spatial limit, which may be considered as the boundary of the PPS representation. Considering the similarity between their results and those obtained with newborns, I think that the results of my study could possibly suggest that already at birth the PPS may exist as a delimited portion of space where multisensory integration is more efficient and that it seems possible to determine its boundaries.

The newborns in the Multimodal group showed a sharp decrease in the RTs at Distance 2, when the sound intensity was 59 dB; the RTs of the adult participants of Canzoneri and colleagues (2012), instead, decreased significantly at T3, when the intensity of the sound was 62.5 dB (Fig. 7.3.2). In order to demonstrate that the sound source position was actually perceived at different locations in the space depending on the different timings of presentation of the tactile stimulus (T1 to T5), Canzoneri and colleagues ran a sound localization experiment on 7 naïve participants. The participants were presented with a sound changing in intensity as

in the main experiment (55 to 70 dB) and received a tactile stimulation on the forearm at each of the 5 different temporal delays used in the main experiment. They were asked to indicate the perceived position in space of the sound when the tactile stimulus happened, on a scale from 1 (very close) to 100 (very far). In this way, the authors could verify that the sound was perceived progressively closer to the body from T1 to T5. I could not find a way to adapt this experiment in order to run it with newborns, hence I cannot, at this stage, draw any conclusion on how far in space the sounds were perceived by newborns, nor on the similarity between the absolute positions in space where adults and newborns perceived the same sound. As a consequence, at this stage it is not possible to compare the absolute position of adults' and newborns' PPS boundary in space.

However, it may be possible to speculate that the distance of a sound source determined accordingly to the perceived intensity of the sound itself might be either absolute or might depend on the dimensions of the body. If either of these hypotheses were true, it may be inferred that newborns' PPS might be considered slightly bigger than adults' PPS. In fact, the intensity of the sound in correspondence with the drop of RTs that signalled the boundary of the PPS was softer in newborns than adults, meaning that the sound was perceived as farther away from the participants' body.

A previous study (Teneggi, Canzoneri, di Pellegrino, & Serino, 2013) demonstrated that the PPS boundaries are sensible to the presence of others in the far space and shaped by the quality of the interaction with them. They demonstrated that the critical perceived sound distance that determined a significant decrease of the RTs was closer to the body when another person was in the participants' extrapersonal space: in this situation, the PPS seemed to shrink, for defensive purposes. Conversely, the participants' PPS seemed to expand to include the other person and his/her PPS after a cooperative interaction: in this situation, the RTs decreased also for the farthest distances (i.e. the portion of space occupied by the other person) and the PPS

boundaries were not detectible anymore. Following the same line of reasoning and considering the different position of the PPS boundary in adults and in newborns, I might speculate that, as newborns need cooperative interactions with other humans (caregivers in particular), the PPS at birth might need to be bigger than in adulthood.

Recently, de Vignemont and Iannetti (2015) proposed a dual model of the PPS, distinguishing between its main two functions: body-protection and goal-directed action. They suggested that these two different functions, despite happening in the same portion of space, require different sensory and motor processes and follow different principles. I tried to link together this recent framework distinguishing between a protective and a working space, the findings about the sensitivity of the PPS boundaries to social modulation and the results of this study along with those of Study 1 (on newborns' ability of discriminate between different trajectories). Study 1 provided evidence that newborns did not show defensive reactions to looming stimuli that, particularly when entering the PPS, could signal the approach of a danger. Nevertheless, they showed their ability to discriminate between different trajectories of stimuli moving close to their body, demonstrating a rudimentary processing of the space surrounding them. Furthermore, Studies 5 and 6 demonstrated that newborns' RTs to an audio-tactile stimulation were noticeably speeded up when the sound was perceived within a certain distance from them. This suggested that already at birth the portion of space closer to the body is invested of a special salience and is characterised by a more efficient integration of multimodal stimuli, and may be already considered as a representation of the PPS. Finally, if the perceived distance of a sound might be considered either constant throughout the lifespan or proportional to the body dimensions of the observer, newborns' PPS might appear slightly bigger than the PPS of adults (Study 6). Taking all these aspects together, I speculate that newborns' PPS might be considered as a working space representation, predisposing them to the interaction with other humans within it and biasing their attention to stimuli moving towards them as they could

signal, rather than a threat, an approaching interesting object or person with whom they could interact.

Following up on the results of these studies, it would be interesting to investigate the dimensions and functions of the PPS also in older infants, considering all the important neural and behavioural changes that characterise infants' first year of life. Furthermore, it would be important to study the modulation of the RTs in response to tactile stimuli when paired with sounds perceived within or outside the PPS in both typically and atypically developing children (3- to 6-year-old), in particular children diagnosed with an Autistic Spectrum Disorder (ASD). In this respect, I hypothesise that the different features of multisensory integration in ASD (Iarocci & McDonald, 2006) might affect the PPS representation in this population, modulating in turn the dimensions of the PPS itself and, possibly, being responsible for some of the characteristic behavioural traits showed by children diagnosed with ASD.

CONCLUSIONS AND FUTURE DIRECTIONS

In my PhD research project, I wanted to investigate infants' representation of the peripersonal space, i.e. the portion of environment between the self and the others.

Research in the last three decades provided some evidence on infants' perception of their own bodies and of other individuals. With regards to the first aspect, recent findings showed newborns' and infants' visual preferences for temporally and spatially congruent visuo-tactile stimulation referred to their own bodies (Filippetti, Johnson, Lloyd-Fox, Dragovic, & Farroni, 2013; Filippetti, Orioli, Johnson, & Farroni, 2015; Zmyj, Jank, Schütz-Bosbach, & Daum, 2011). Regarding the latter aspect, instead, several findings showed newborns' predisposition to direct their attention to faces during the first days of life, supporting the hypothesis suggesting that they can discriminate face-like stimuli before significant postnatal experience (Farroni, Csibra, Simion, & Johnson, 2002; Farroni et al., 2005; Farroni, Menon, & Johnson, 2006; Johnson, Dziurawiec, Ellis, & Morton, 1991).

To my knowledge, however, not many studies investigated infants' representation of the portion of space where infants can interact with both objects and others, namely the peripersonal space. (PPS). The PPS is considered as a "multisensory-motor interface between body and environment" (Teneggi, Canzoneri, di Pellegrino, & Serino, 2013, p. 1), which "mediates every physical interaction between the body and the external world, because it is within its boundaries that we can reach and act upon objects, as well as avoid looming threats" (Canzoneri, Magosso, & Serino, 2012, p. 1). It is invested of a defensive as well as a goal-directed function (de Vignemont & Iannetti, 2015) and is defined by the quality of the multisensory interactions taking place within it (Van der Stoep, Nijboer, Van der Stigchel, & Spence, 2015). Considering the importance of the PPS, especially in light of both its functions, I thought that it could have been both interesting and important to investigate the development of its perception and representation during the first year of life. In fact, as the PPS is the space where

the earliest interactions can take place, I believed that it would have been worth investigating whether it existed prior to significant postnatal experience as a delimited portion of space, characterised by an enhanced processing of multisensory information, or whether its special salience emerged later, possibly in response to the interactions happening within it.

I decided to investigate the perception and the representation of the peripersonal space in infancy around two focuses of interest. On one side, I wanted to study how newborns and infants processed the space around them, and in particular if they differentiated between near and far space, possibly perceiving and integrating depth cues across sensory modalities, and when and how they started to respond to different movements occurring in the space surrounding their bodies. On the other side, I was interested in studying whether already at birth the PPS could be considered as a delimited portion of space with special characteristics and, relatedly, if its boundaries could be determined already in the first days of life.

In order to respond to my first question, I investigated newborns' behavioural responses to visual stimuli depicting trajectories moving towards different directions in the space immediately surrounding their body (Study 1, Ch. 4.3). Specifically, I measured the looking behaviour of a sample of 20 newborns in response to visual trajectories approaching them along a colliding or non-colliding path or receding towards the background. Previous research had investigated infants' discrimination of looming trajectories measuring their defensive reactions and, in particular, their eye blinks, which were considered the best indicator of awareness to impending collision in early infancy (Yonas, 1981). Within this line of research, Yonas and colleagues (1977) concluded that newborns are not sensitive to impending collision trajectories, as they do not show any appropriate defensive or avoiding behaviour in response to them. However, I thought that possibly focusing on defensive responses might have masked newborns' discrimination or adaptively relevant trajectories. Possibly, newborns might not have the necessary experience to attribute a threatening, negative valence to the objects approaching

them along a colliding trajectory and, instead, they might consider them as an interesting stimulus to interact with (as it would be, for example, their parent's face approaching them; de Vignemont & Iannetti, 2015; Kandula, Hofman, & Dijkerman 2015; Van der Stoep et al., 2015). As a consequence, I believed that a preferential looking paradigm might have informed better on newborns' discrimination of visual trajectories and on the existence of a visual preference for adaptively important ones. The results of this first study showed that newborns could discriminate between the trajectories of visual moving stimuli, showing a visual preference for those specifically directed towards their bodies. Most importantly, this preference was found not only when the stimuli moved in different directions (i.e. approaching the infant vs. receding towards the background), but also when they were both directed towards the PPS (i.e. approaching the infant along a colliding vs. non-colliding trajectory). This visual preference suggested that newborns seem to demonstrate, at birth, a rudimentary differentiation of the space surrounding them and to show a predisposition to perceive their presence in the environment and to adaptively focus their attention on their body and on the space around it. I speculate that newborns' visual preference for stimuli moving along a colliding trajectory with respect to their bodies could be ascribed to the adaptive salience of those stimuli that could come into direct contact with them. However, having used a preferential looking paradigm, based on these data it is not possible to draw a definite conclusion on whether newborns categorised the approaching stimuli as threatening or interesting.

In this first study, the motion direction was depicted using only visual cues. However, we know from our experience that in everyday life moving objects convey information about their trajectory through different sensory modalities at the same time, in particular vision and audition. Furthermore, the auditory system has several advantages over the visual system in terms of monitoring of the space around the body (Ferri, Tajadura-Jiménez, Väljamäe, Vastano, & Costantini, 2015). In fact, audition is a powerful change detector, capable of quickly

identifying potential threats within a continuous flow of information, which remains available also when the eyes are closed or when the events occur outside the visual field. Moreover, previous findings showed a perceptual bias towards multisensory looming stimuli and their selective integration, probably to be linked to their significant adaptive valence (Maier, Neuhoff, Logothetis, & Ghazanfar, 2004; Cappe, Thut, Romei, & Murray, 2009; Cappe, Thelen, Romei, Thut, & Murray, 2012).

In light of the importance of multisensory integration for the monitoring of the space immediately surrounding the body and of the events taking place within it, I wanted to investigate newborns' looking behaviour in response to congruent and incongruent audio-visual stimuli depicting approaching and receding trajectories taking place in the near space. Studying newborns' visual preferences towards this kind of multimodal events would have also given the opportunity of shedding further light on how newborns integrate multisensory stimuli. This topic is particularly relevant as the development of an efficient integration of the information coming from different senses has important adaptive benefits, but, at the same time, it is a significant challenge to be confronted during development (Bremner, Lewkowicz, & Spence, 2012). To address this, I measured the looking behaviour of a group of 20 newborns in response to approaching and receding visual trajectories paired with sounds simulating, through intensity changes, either the approach or the recess of a sound source (Study 2, Ch. 4.4). As in the previous one, also in this study I used a preferential looking paradigm: in this way, I could compare the looking times directed to the visual stimuli congruent and incongruent with the auditory stimuli, all of which provided the newborns with adaptive information about their environment. At the same time, the comparison between the looking behaviour in this study and in the previous one gave me the opportunity to investigate the existence of any facilitation of the processing of multisensory vs. unisensory stimuli within this context. The results showed that newborn infants looked longer to the approaching visual stimulus when it was paired with

a congruent, increasing, sound. Conversely, when the visual stimuli were paired with a decreasing sound (simulating a receding sound source), no visual preference was found. Furthermore, I compared the looking times directed to each visual stimulus when paired with a congruent sound vs. when presented unimodally (in Study 1). The results showed that the newborns looked longer to the visual stimuli in the multimodal vs. unimodal condition, but only when each visual stimulus was paired with a sound depicting motion along a congruent direction. I think that the overall pattern of the results suggests that human infants could be able to integrate multimodal stimulation depicting information about moving trajectories without significant postnatal experience, supporting previous findings on the existence of early multisensory integration abilities (Bahrick & Lickliter, 2000, 2012; Bahrick, Lickliter, & Flom, 2004; Filippetti, Lloyd- Fox, Dragovic, Johnson, & Farroni, 2013; Filippetti, Orioli, Johnson, & Farroni, 2015; Lewkowicz & Ghazanfar, 2006, 2009; Lewkowicz, Leo, & Simion, 2010; Lewkowicz, 2014). Specifically, I believe that the absence of a visual preference when the newborns were presented with a decreasing sound particularly supports my speculation. In fact, the direction of the visual preference when an increasing, approaching sound was presented was the same as that found in the previous, unimodal study and hence it could not, on its own, support a claim for early integration abilities. However, if newborns did not integrate the information coming from different senses, I would expect them to show the same pattern of looking times also when presented with a decreasing, receding sound. Instead, the absence of a visual preference together with the increase of the looking time only to the congruent, receding visual stimulus compared to when it was presented unimodally seemed to suggests that newborns' spontaneous preference for congruent multimodal stimulation was somewhat challenged by the great adaptive salience of visual approaching stimuli, leading to equally distributed periods of looking time across the behaviourally important (approaching) and the multisensory congruent (receding) stimuli.

In light of the findings obtained with newborns, I decided to investigate how the integration of multisensory stimuli moving in the near space develops during the first year of life. Specifically, I decided to study infants' looking behaviour in response to visual and audio-visual congruent or incongruent trajectories in correspondence with two important milestones in their motor development, i.e. the emergence of reaching and grasping abilities (Study 3, Ch. 5). In fact, I hypothesised that there might be a link between infants' ability to act voluntary and purposefully on the environment and their perception of the events taking place within the same environment. Moreover, recent studies showed that, in adults, the sensorimotor areas responsible for reaching and grasping actions were active during a task in which the participants were required to judge the expected time-to-contact of a looming stimulus (Field & Wann, 2005; Billington & Wilkie, 2011). These findings further supported the hypothesis of a possible link between reaching and grasping abilities and the perception of approaching and receding trajectories. Several studies investigated the development of reaching and grasping during infancy, showing the emergence of reaching abilities during the fifth month of life (von Hofsten, 1991) and the appearance of grasping abilities 3-4 months later (Konczak & Dichgans, 1997). Therefore, I decided to study two groups of infants, aged respectively 5 and 9 months of life. I measured their looking behaviour when presented with visual and audio-visual (congruent and incongruent) approaching and receding trajectories. I also assessed their motor development across three dimensions (Gross Motor skills, Fine Motor skills and Perception-Action), using a recently developed parent-report research questionnaire (Early Motor Questionnaire, Libertus & Landa, 2013). Furthermore, I measured their reaching and grasping abilities with an ad-hoc reaching assessment task (Libertus & Needham, 2010). The scoring of the questionnaires ensured that the infants within each group showed comparable motor skills; the scoring of the behaviours showed during the reaching assessment task, instead, confirmed that all the infants in the younger age group could successfully reach for an object and that all the older infants

could successfully grasp it. I also investigated the possible link between looking behaviour and motor skills. When analysing the data from the two groups of infants together, correlational results seemed to suggest the existence of a positive relationship between the time that infants spent attending the approaching visual stimuli (irrespective of the presence and direction of a simultaneous sound) and their gross motor skills. They also suggested the existence of a positive relationship between the looking time directed to the screen when an approaching sound was played and the level of motor development in any domain. With respect to the looking behaviour itself, the measures of the looking time to unimodal and multimodal stimuli were analysed separately. When presented with visual approaching and receding visual trajectories, both groups of infants looked significantly longer to the approaching visual stimulus. This demonstrated that throughout the first year of life infants showed a reliable preference for approaching unimodal (visual) stimuli, moving towards their bodies, over receding stimuli. I speculate that this preference could be related to the higher behavioural salience of the approaching stimuli, as they signal an impending interaction with the moving stimulus itself. The pattern of looking behaviour shown by infants when presented with multimodal stimuli, instead, was more complex and differed depending on their age. The younger infants showed a consistent visual preference for congruent audio-visual stimuli, irrespective of their motion direction, looking longer to the approaching movie when it was presented with an increasing sound and to the receding movie when paired with a decreasing sound. The older infants, instead, showed a visual preference for the incongruent visual display when the visual stimuli were presented together with a decreasing sound, whereas when the visual stimuli were paired with an increasing sound, the 9-month-old infants did not show any visual preference. The 9-month-olds' looking behaviour seemed the opposite of that showed by newborns, which looked longer at congruent stimuli when an approaching sound was presented, but directed a similar amount of attention to both visual displays when the presented sound was receding.

I speculate that, taken together, the findings of Studies 2 and 3 might help understand the development of the multisensory integration of stimuli with an adaptive valence during infancy. In particular, these studies provided evidence that right after birth infants showed a spontaneous visual preference for congruent audio-visual stimuli, which was challenged by a similarly strong visual preference for adaptively important visual stimuli moving towards their bodies. Therefore, when the two categories of preferred stimuli were presented together (i.e. an approaching video on one side and a receding video congruent with a simultaneous, decreasing sound on the other) they led to the absence of a visual preference for either category in newborns. The looking behaviour of the 5-month-old infants, instead, seemed to be driven only by a spontaneous preference for multimodal congruent stimuli, i.e. depicting motion along the same trajectory, irrespective of the adaptive value of the information conveyed by either of the two sensory components of the stimulus. I speculate that, during this stage of their life, infants might be particularly interested in congruent multisensory stimulation as it might help them to extract regularities from the environment and to bind together different stimulations that refer to a unitary event. The nine-month-old infants, instead, seemed to be similarly attracted by incongruent as well as behaviourally relevant stimuli. Similarly to what happened with newborns, presenting the 9-month-old infants with the two categories of preferred stimuli simultaneously led to the absence of a visual preference. In light of this, I speculate that the older infants might be spontaneously interested in incongruent stimuli, because they contrast the expectations that they built up attending congruent events during the first months of their life. However, their preference for incongruent multimodal stimulation could be, at the same time, weakened when both the visual and the auditory modalities convey information that is important for adaptive behaviour, like, in this case, approaching stimuli.

All the studies mentioned so far contributed to respond from a behavioural point of view to my first question on the representation of the peripersonal space during infancy, i.e. if and

how newborns and infants discriminate between different movements taking place in the space around them and how they integrate the audio-visual cues depicting those movements. However, I was also interested in the neural underpinnings of the processing of relevant trajectories occurring in the near space and conveyed by either visual or auditory cues. I was particularly interested in investigating the neural processing of trajectories invested of a different behavioural relevance (i.e. approaching vs. receding trajectories) and the processing of auditory and visual stimuli signalling motion in the brain areas considered responsible for the primary processing of vision and audition. To address this, I measured the electrical brain activity of a sample of 5-month-old infants while they were attending unimodal, auditory or visual, approaching and receding trajectories (Study 4, Ch. 6). For the analyses, two clusters of electrodes were selected, located over the occipital lobe for putative visual ERPs and immediately in front of the vertex for putative auditory ERPs. For each cluster of electrodes, I investigated, using a Monte Carlo simulation (Guthrie & Buchwald, 1991), the effect that the modality of presentation of the stimuli and the direction of the depicted trajectories had on the shape of the ERP waveforms. Over occipital sites as well as in the fronto-central electrodes, a reliably significant difference between the waveforms in response to auditory and visual stimuli was found after 450 ms of presentation, suggesting that the modality of presentation of the stimuli had a clear impact on the modulation of the ERPs starting from the intermediate stages of processing. The emergence at an intermediate stage of processing of a reliable modulation of the electrical responses dependent on the modality of presentation of the stimuli might support a new, recently proposed view of perception and of brain organization (Murray et al., 2016). According to this view, the primary sensory cortices should be considered as inherently multisensory and the integration of multisensory information within low-level sensory cortices should be considered the rule. Regarding the effect of the direction of the trajectories, the Monte Carlo simulation could not find a reliable difference in response to different trajectories in the

occipital nor in the fronto-central clusters of electrodes. However, the analysis of the mean individual amplitude of the potentials recorded over occipital sites during the earliest stages of processing seemed to show a modulation of the first positive peak, occurring around 100 ms after stimulus onset, depending on the direction of the perceived stimulus, irrespective of the modality of presentation. Such ERPs, recorded over occipital sites for both visual and auditory stimuli, should be considered as event-related responses to the change in the visual environment following the end of the inter-trial attention getter and the simultaneous beginning of stimulus presentation. Nevertheless, it is worth noticing that both visual and auditory stimuli modulated such responses in the same way, i.e. depending on the direction of the depicted trajectory. Specifically, the amplitude of the positive peak (P1) was larger in response to approaching vs. receding stimuli, suggesting that already in infancy − similarly to what recently demonstrated in adulthood (Vagnoni, Lourenco, & Longo, 2015) − the brain might allocate different amounts of attention to stimuli with a different valence since the earliest stages of processing. The valence attributed by the infants to each trajectory, though, has yet to be demonstrated: if infants' brain discriminated the motion trajectory of a stimulus in a few milliseconds of presentation, a more negative connotation of approaching stimuli could be hypothesised; if it did not, a more negative value of receding stimuli, louder or bigger in size at the beginning of their motion, could be suggested. These results should be considered − in light of the small sample size − only exploratory and preliminary but, overall, they so far seem to provide evidence in support of the role of the primary sensory cortices in the processing of crossmodal stimuli (Kayser, Petkov, & Logothetis, 2009; Murray et al., 2016) and about the possibility that infants' brain could allocate, already during the earliest stages of processing, different amounts of attention to stimuli with different valence (Vagnoni et al., 2015).

The last couple of studies (Studies 5 and 6, Ch. 7) wanted to address my second question, namely whether already at birth the PPS could be considered as a delimited portion of space

with special characteristics and, relatedly, if its boundaries could be determined. To address this, I measured newborns' saccadic reaction times (RTs) to tactile stimuli presented simultaneously to a sound perceived at different distances from their body, adapting a task used to measure adults' PPS boundaries (Canzoneri, Magosso, & Serino, 2012). Across two studies, run using different perceived sound positions, the results showed that newborns' RTs to audio-tactile stimuli were modulated by the perceived position of the sound presented simultaneously to the tactile information. Specifically, they were significantly shorter when the sound was perceived closer to the body compared to farther away. The modulation of the RTs was very similar to that shown by adults, suggesting that the perceived sound position in whose correspondence the drop of RTs happened could be considered as the boundary of newborns' PPS. Furthermore, such modulation of the RTs was specifically dependent on the presence of a simultaneous auditory and tactile stimulation and was not simply function of the perceived position of the sounds alone. The selective speeding up of the RTs when the sound was perceived closer to the body suggested that at birth the space immediately surrounding the body seems to be already invested of a special salience and characterised by a more efficient integration of multimodal stimuli. Therefore, it might be considered as a rudimentary representation of the PPS, possibly serving, as a working space representation, early interactions between newly born humans and their environment.

Taken together, the results of the presented studies demonstrated that humans show, since the earliest stages of their development, a rudimentary processing of the space surrounding them. Newborns seem, in fact, to already differentiate the space around them, through an efficient discrimination of different moving trajectories and a visual preference for those directed towards their own body, possibly because of their higher adaptive relevance. Furthermore, they seem to integrate multimodal, audio-visual information about stimuli moving in the near space. In this respect, newborns seem to show a facilitated processing of congruent audio-visual

approaching trajectories and, at the same time, their looking behaviour seems to suggests the existence a complex interplay between multisensory integration principles and the behavioural relevance of the stimuli. Finally, newborns' processing of multisensory stimuli seems to be more efficient in a delimited portion of space closest to their bodies, which could possibly be considered as a rudimentary representation of what – in adults – is properly called peripersonal space. These predispositions and rudimentary processing seem to evolve during the first year of life, in parallel with the development of infants' motor skills and of their multisensory integration abilities. In this respect, it seems that after a stage where infants present an unchallenged preference for congruent multimodal stimulation, they eventually show a flexible integration between multisensory integration principles and ethologically salient stimuli, as demonstrated by the fact that their visual preference for unexpected, incongruent audio-visual stimuli is challenged by the simultaneous presence of adaptively relevant stimuli. Overall, then, these findings provide a first understanding of how humans start to process the space surrounding them, which – importantly – is the space linking them with others and the space where their first interactions will take place.

Nevertheless, several aspects of the peripersonal space processing during infancy are yet to be investigated. A first aspect that would be worth studying is the valence of different moving trajectories for newborns. One of the studies summarised above provided evidence on newborns' visual preference for stimuli moving towards their bodies compared to stimuli receding from them or approaching them along a non-colliding trajectory. However, preferential looking paradigms cannot inform on the reason why one stimulus was visually preferred over the other, nor about the positive or negative valence, for the observers, of the stimuli themselves (Banks & Ginsberg, 1985). Therefore, preferential looking data do not offer the opportunity of drawing a definite conclusion on whether newborns' visual preference for stimuli directed towards their bodies was due to interest or threat. A possible way of shedding

light on this standing question would be measuring the physiological responses shown by newborns while they attend stimuli depicting different trajectories. In this respect, a previous study on an adult population showed a facilitation of the autonomic orienting reflex in response to a rising sound, hence considered as an intrinsic warning cue (Bach et al., 2008). In particular, the authors observed a deceleration of the heart rate, mirroring early preattentive stimulus registration processes, and an increase of skin conductance response, reflecting the recruitment of energetic resources (Bach et al., 2008). Possibly, finding in newborns a similar pattern of physiological activation in response to impending collision trajectories might suggest that they attribute a negative, threatening value to such stimuli. On the contrary, the absence of autonomic responses might lead to think that the approaching stimuli were visually preferred by the newborns for being interesting stimuli that might signal an upcoming interaction.

Another possible future direction would be investigating the early peripersonal space representation in relation to the ontogeny of developmental (genetic and neuropsychological) disorders in which the dorsal stream of visual processing seems to show a deficit, such as the Fragile X Syndrome, the Williams syndrome and the Autistic Spectrum Disorders (ASD). Several findings reported a selective deficit of visual motor processing in these disorders (Atkinson et al., 2006; Farzin & Rivera, 2010; Farzin, Whitney, Hagerman, & Rivera, 2008; Gallego, Burris, & Rivera, 2014; Grinter, Maybery, & Badcock, 2010; Spencer et al., 2000), raising the hypothesis that the discrimination of motion trajectories and, hence, the representation of the PPS might be affected as well during infancy. With regards to the ASD in particular, it may be hypothesised that finding a different processing, early in life, of visual trajectories in infants at high risk of developing a disorder within the autistic spectrum might help identify ASD early markers.

Finally, it would be interesting to investigate the connection between the representation of events – such as moving trajectories – that take place in infants' PPS and the representation

of their own bodies. A possible way of doing so would be studying the predictive link between stimuli approaching the body and their tactile consequences on the body. Recently, Kandula and colleagues showed the existence – in adults – of a predictive mechanism that uses visual information about objects moving in the near space to predict the time and location of an impending touch (Kandula, Hofman, & Dijkerman, 2015). In this study, the participants were presented with visual stimuli showing an arm that moved towards either side of their face and whose motion was followed by a tactile stimulation on a cheek. The tactile stimulation could occur at a consistent or inconsistent time with respect to the time-to-contact of the moving arm and on the congruent or incongruent cheek with respect to the motion direction of the arm. The results showed faster RTs in response to the tactile stimuli taking place on the hemispace towards which the arm had moved and at the time-to-contact predicted by the speed of the moving arm. Similarly, Clery and colleagues demonstrated an enhanced tactile sensitivity on the face at the expected time and space of the predicted impact of a looming object (Clery, Guipponi, Odouard, Wardak, & Ben Hamed, 2015). The authors speculated that this sensitivity enhancement could be considered as a crossmodal predictive facilitation linked to the representation of the PPS as a safety area surrounding the body. A paradigm similar to that used by Kandula and colleagues (2015) might be employed with infants in order to investigate the relationship between the impending impact signalled by looming stimuli and the detection of a tactile stimulation on the body. To address this, it might be interesting to measure infants' electrical brain activity in response to expected and unexpected tactile stimuli, predicted or not by looming visual cues. On this note, it has been recently demonstrated that 12-month-old infants showed an increased electrical response for unexpected events during the late stages of processing, but an amplified response for expected events during the early processing stages, suggesting an enhanced processing of predicted events led by selective attention (Kouider et al., 2015). If infants represented looming visual stimuli as reliable predictors of an impending

collision and, hence, of a tactile stimulation, we could expect a similar modulation of the event-related potentials following touches that were, or were not, signalled by the previous looming of a visual stimulus.

The investigation of the abovementioned aspects of the peripersonal space representation, along with the findings outlined by the studies presented in this manuscript, will offer the opportunity to better understand how both typically and atypically developing infants represent the space immediately surrounding their bodies, which is the space where they will learn to protect themselves from dangers and the space were all their interactions, social and not, will take place.

REFERENCES

Abrams, R. A., & Christ, S. E. (2005). The onset of receding motion captures attention: comment on Franconeri and Simons (2003). *Perception and Psychophysics, 67*(2), 219-223.

Abrams, R. A., & Christ, S. E. (2006). Motion onset captures attention: a rejoinder to Franconeri and Simons (2005). *Perception and Psychophysics, 68*(1), 114-117.

Atkinson, J., & Braddick, O. (1989). Development of basic visual functions. In A. Slater, & G. Bremner, *Infant development* (pp. 7-41). London: Lawrence Erlbaum Associates.

Atkinson, J., Braddick, O., Rose, F. E., Searcy, Y. M., Wattam-Bell, J., & Bellugi, U. (2006). Dorsal-stream motion processing deficits persist into adulthood in Williams syndrome. *Neuropsychologia, 44*, 828-833.

Bach, D. R., Schächinger, H. N., Esposito, F., Di Salle, F., Lehmann, C., Herdener, M., Scheffler, K, & Seifritz, E. (2008). Rising Sound Intensity: An Intrinsic Warning Cue Activating the Amygdala. *Cerebral Cortex, 18*, 145-150.

Bahrick, L. E., & Lickliter, R. (2000). Intersensory Redundancy Guides Attentional Selectivity and Perceptual Learning in Infancy. *Developmental Psychology, 36*(2), 190-201.

Bahrick, L. E., & Lickliter, R. (2012). The role of intersensory redundancy in early perceptual, cognitive, and social development. In A. Bremner, D. J. Lewkowicz, & C. Spence (Eds.), *Multisensory Development* (pp. 183-205). Oxford, England: Oxford University Press.

Bahrick, L. E., Lickliter, R., & Flom, R. (2004). Intersensory Redundancy Guides the Development of Selective Attention, Perception, and Cognition in Infancy. *Current Directions in Psychological Science, 13*(3), 99-102.

Ball, W., & Tronick, E. (1971). Infant Responses to Impending Collision: Optical and Real. *Science, 171*, 818-820.

Banks, M. S., & Ginsberg, A. P. (1985). Infant visual preferences: A review and new theoretical treatment. In H. W. Reese, *Advances in child development & behavior* (Vol. 19, pp. 20-246). New York: Academic Press.

Bassolino, M., Serino, A., Ubaldi, S., & Làdavas, E. (2010). Everyday use of the computer mouse extends peripersonal space representation. *Neuropsychologia, 48*, 803-811.

Beer, A. L., Plank, T., & Greenlee, M. W. (2011). Diffusion tensor imaging shows white matter tracts between human auditory and visual cortex. *Experimental Brain Research, 213*(2-3), 299-308.

Beer, A. L., Plank, T., Meyer, G., & Greenlee, M. W. (2013). Combined diffusion-weighted and functional magnetic resonance imaging reveals a temporal-occipital network involved in auditory-visual object processing. *Frontiers in Integrative Neuroscience, 7*(5).

Begleiter, H., Gross, M. M., & Kissin, B. (1967). Evoked cortical responses to affective visual stimuli. *Psychophysiology, 3*(4), 336-344.

Begleiter, H., Gross, M. M., Porjesz, B., & Kissin, B. (1969). The effects of awareness on cortical evoked potentials to conditioned affective stimuli. *Psychophysiology, 5*(5), 517-529.

Berlyne, D. B. (1958). The influence of the albedo and complexity of stimuli on visual fixation in the human infant. *British Journal of Psychology, 49*(4), 315-318.

Billington, J., & Wilkie, R. M. (2011). Neural processing of imminent collision in humans. *Proceedings of the Royal Society B: Biological Sciences, 278*, 1476–1481.

Bornstein, M. H. (1985). Colour-name versus shape-name learning in young children. *Journal of Child Language, 12*(2), 387-393.

Bower, T. G., Broughton, J. M., & Moore, M. K. (1970). Infant responses to approaching objects: An indicator of response to distal variables. *Perception and Psychophysics, 9*, 193-196.

Bremner, A. J., Holmes, N. P., & Spence, C. (2008). Infants lost in (peripersonal) space? *Trends in Cognitive Sciences, 12*(8), 298-305.

Bremner, A. J., Lewkowicz, D. J., & Spence, C. (2012). The multisensory approach to development. In A. J. Bremner, D. J. Lewkowicz, & C. Spence (Eds.), *Multisensory Development* (pp. 1-26). Oxford, England: Oxford University Press.

Bremner, A. J., Mareschal, D., Lloyd-Fox, S., & Spence, C. (2008). Spatial Localization of Touch in the First Year of Life: Early Influence of a Visual Spatial Code and the Development of Remapping Across Changes in Limb Position. *Journal of Experimental Psychology, 137*(1), 149-162.

Brozzoli, C., Cardinali, L., Pavani, F., & Farnè, A. (2010). Action-specific remapping of peripersonal space. *Neuropsychologia, 48*, 796-802.

Brozzoli, C., Ehrsson, H. H., & Farnè, A. (2014). Multisensory Representation of the Space Near the Hand: From Perception to Action and Interindividual Interactions. *The Neuroscientist, 20*(2), 122-135.

Brozzoli, C., Gentile, G., Bergouignan, L., & Ehrsson, H. H. (2013). A Shared Representation of the Space Near Oneself and Others in the Human Premotor Cortex. *Current Biology, 23*, 1764-1768.

Brozzoli, C., Pavani, F., Urquizar, C., Cardinali, L., & Farnè, A. (2009). Grasping actions remap peripersonal space. *NeuroReport, 20*, 913-917.

Bushnell, E. W., & Boudreau, J. P. (1993). Motor Development and the Mind: The Potential Role of Motor Abilities as a Determinant of Aspects of Perceptual Development. *Child Development, 64*, 1005-1021.

Canzoneri, E., Magosso, E., & Serino, A. (2012). Dynamic Sounds Capture the Boundaries of Peripersonal Space Representation in Humans. *PLoS ONE, 7*(9), 1-8.

Canzoneri, E., Ubaldi, S., Rastelli, V., Finisguerra, A., Bassolino, M., & Serino, A. (2013). Tool-use reshapes the boundaries of body and peripersonal space representations. *Experimental Brain Research, 228*, 25-42.

Cappe, C., Thelen, A., Romei, V., Thut, G., & Murray, M. M. (2012). Looming Signals Reveal Synergistic Principles of Multisensory Integration. *The Journal of Neuroscience, 32*(4), 1171-1182.

Cappe, C., Thut, G., Romei, V., & Murray, M. M. (2009). Selective integration of auditory-visual looming cues by humans. *Neuropsychologia, 47*(4), 1045-1052.

Cappe, C., Thut, G., Romei, V., & Murray, M. M. (2010). Auditory-visual integration of auditory-visual looming cues by humans: timing, topography, directionality and sources. *Journal of Neuroscience, 30*, 12572-12580.

Carretié, L., Hinojosa, J. A., Martín-Loeches, M., Mercado, F., & Tapia, M. (2004). Automatic Attention to Emotional Stimuli: Neural Correlates. *Human Brain Mapping, 22*, 290-299.

Carver, L. J., & Vaccaro, B. G. (2007). 12-month-old infants allocate increased neural resources to stimuli associated with negative adult emotion. *Developmental Psychology, 43*(1), 54-69.

Cecere, R., Romei, V., Bertini, C., & Làdavas, E. (2014). Crossmodal enhancement of visual orientation discrimination by looming sounds requires functional activation of primary visual areas: A case study. *Neuropsychologia, 56*, 350-358.

Clery, J., Guipponi, O., Odouard, S., Wardak, C., & Ben Hamed, S. (2015). Impact Prediction by Looming Visual Stimuli Enhances Tactile Detection. *The Journal of Neuroscience, 35*(10), 4179-4189.

Coello, Y., Bourgeois, J., & Iachini, T. (2012). Embodied perception of reachable space: how do we manage threatening objects? *Cognitive Processing, 13 (Suppl 1)*, S131-S135.

Colombo, J., & Mitchell, D. W. (2009). Infant visual habituation. *Neurobiology of Learning and Memory, 92*, 225-234.

Costantini, M., Ambrosini, E., Tieri, G., Sinigaglia, C., & Committeri, G. (2010). Where does an object trigger an action? An investigation about affordances in space. *Experimental Brain Research, 207*, 95-103.

Csibra, G., & Johnson, M. H. (2007). Investigating event-related oscillations in infancy. In M. de Haan (Ed.), *Infant EEG and event related potentials* (pp. 289-304). Hove, England: Psychology Press.

Csibra, G., Kushnerenko, E., & Grossmann, T. (2008). Electrophysiological Methods in Studying Infant Cognitive Development. In C. A. Nelson, & M. Luciana (Eds.), *Handbook of developmental cognitive neuroscience* (2nd ed., pp. 247-262). Cambridge, MA: MIT Press.

da Haan, M., & Thomas, K. M. (2002). Applications of ERP and fMRI techniques to developmental science. *Developmental Science, 5*(3), 335–343.

de Haan, M., & Nelson, C. A. (1997). Recognition of the mother's face by six-month-old infants: A neurobehavioral study. *Child Development, 68*(2), 187-210.

de Vignemont, F., & Iannetti, G. D. (2015). How many peripersonal spaces? *Neuropsychologia, 70*, 327-334.

di Pellegrino, G., & Làdavas, E. (2015). Peripersonal space in the brain. *Neuropsychologia, 66*, 126-133.

Dolcos, F., & Cabeza, R. (2002). Event-related potentials of emotional memory: Encoding pleasant, unpleasant, and neutral pictures. *Cognitive, Affective, & Behavioral Neuroscience, 2*(3), 252-263.

Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature, 415*, 429-433.

Fagard, J., Spelke, E., & von Hofsten, C. (2009). Reaching and grasping a moving object in 6-, 8-, and 10-month-old infants: Laterality and performance. *Infant Behavior and Development, 32*, 137-146.

Fantz, R. L. (1956). A method for studying early visual development. *Perceptual and motor skills, 6*, 13-15.

Fantz, R. L. (1957). Form preferences in newly hatched chicks. *Journal of Comparative and Physiological Psychology, 50*(5), 422-430.

Fantz, R. L. (1958a). Depth discrimination in dark-hatched chicks. *Perceptual and Motor Skills, 8*, 47-50.

Fantz, R. L. (1958b). Visual discrimination in a neonate chimpanzee. *Perceptual and Motor Skills, 8*, 59-66.

Fantz, R. L. (1958c). Pattern vision in young infants. *The Psychological Record, 8*, 43-47.

Fantz, R. L. (1961a). A method for studying depth perception in infants under six months of age. *The Psychological Record, 11*, 27-32.

Fantz, R. L. (1961b). The origin of form perception. *Scientific American, 204*(5), 66-72.

Fantz, R. L., & Ordy, J. M. (1959). A visual acuity test for infants under six months of age. *The Psychological Record, 9*, 159-164.

Fantz, R. L., Ordy, J. M., & Udelf, M. S. (1962). Maturation of pattern vision in infants during the first six months. *Journal of Comparative and Physiological Psychology, 55*(9), 907-917.

Farnè, A., Pavani, F., Meneghello, F., & Làdavas, E. (2000). Left tactile extinction following visual stimulation of a rubber hand. *Brain, 123*, 2350-2360.

Farroni, T., Csibra, G., Simion, F., & Johnson, M. H. (2002). Eye contact detection in humans from birth. *PNAS, 99*, 9602-9605.

Farroni, T., Johnson, M. H., Menon, E., Zulian, L., Faraguna, D., & Csibra, G. (2005). Newborns' preference for face-relevant stimuli: effects of constrast polarity. *PNAS, 102*, 17245-17250.

Farroni, T., Menon, E., & Johnson, M. H. (2006). Factors influencing newborns' preference for faces with eye contact. *Journal of Experimental Child Psuchology, 95*, 298-308.

Farroni, T., Menon, E., Rigato, S., & Johnson, M. H. (2007). The perception of facial expressions in newborns. *European Journal of Developmental Psychology, 4*, 2-13.

Farroni, T., Simion, F., Umiltà, C., & Dalla Barba, B. (1999). The gap effect in newborns. *Developmental Science, 2*(2), 174-186.

Farzin, F., & Rivera, S. M. (2010). Dynamic object representations in infants with and without fragile X syndrome. *Frontiers in Human Neuroscience, 4*, 12.

Farzin, F., Whitney, D., Hagerman, R. J., & Rivera, S. M. (2008). Contrast detection in infants with fragile X syndrome. *Vision Research, 48*, 1471-1478.

Ferri, F., Tajadura-Jiménez, A., Väljamäe, A., Vastano, R., & Costantini, M. (2015). Emotion-inducing approaching sounds shape the boundaries of multisensory peripersonal space. *Neuropsychologia*.

Field, D. T., & Wann, J. P. (2005). Perceiving time to collision activates the sensorimotor cortex. *Current Biology, 15*(5), 453-458.

Filippetti, M. L., Johnson, M. H., Lloyd-Fox, S., Dragovic, D., & Farroni, T. (2013). Body Perception in Newborns. *Current Biology, 23*, 2413-2416.

Filippetti, M. L., Orioli, G., Johnson, M. H., & Farroni, T. (2015). Newborn Body Perception: Sensitivity to Spatial Congruency. *Infancy*, 1-11.

Finisguerra, A., Canzoneri, E., Serino, A., Pozzo, T., & Bassolino, M. (2015). Moving sounds within the peripersonal space modulate the motor system. *Neuropsychologia, 70*, 421-428.

Flom, R., & Bahrick, L. E. (2007). The Development of Infant Discrimination of Affect in Multimodal and Unimodal Stimulation: The Role of Intersensory Redundancy. *Developmental Psychology, 43*(1), 238-252.

Foxe, J. J., McCourt, M. E., & Javitt, D. C. (2003). Right hemisphere control of visuospatial attention: line-bisection judgments evaluated with high-density electrical mapping and source analysis. *Neuroimage, 19*, 710-726.

Franconeri, S. L., & Simons, D. J. (2003). Moving and looming stimuli capture attention. *Perception & Psychophysics, 65*(7), 999-1010.

Franconeri, S. L., & Simons, D. J. (2005). The dynamic events that capture visual attention: A reply to Abrams and Christ (2005). *Perception & Psychophysics, 67*(6), 962-966.

Freiberg, K., Tually, K., & Crassini, B. (2001). Use of an auditory looming task to test infants' sensitivity to sound pressure level as an auditory distance cue Authors . *British Journal of Developmental Psychology, 19*(1), 1-10.

Friedman, S. (1972). Habituation and recovery of visual response in the alert human newborn. *Journal of Experimental Child Psycholoy, 13*(2), 339-349.

Gallego, P. K., Burris, J. L., & Rivera, S. M. (2014). Visual motion processing deficits in infants with the fragile X premutation. *Journal of Neurodevelopmental Disorders, 6*(29).

Gamberini, L., Seraglia, B., & Priftis, K. (2008). Processing of peripersonal and extrapersonal space using tools: Evidence from visual line bisection in real and virtual environments. *Neurpsychologya, 46*, 1298-1304.

Gentile, G., Petkova, V. I., & Ehrsson, H. H. (2011). Integration of Visual and Tactile Signals From the Hand in the Human Brain: An fMRI Study. *Journal of Neurophysiology, 105*, 910-922.

Ghazanfar, A. A., Neuhoff, J. G., & Logothetis N, K. (2002). Auditory looming perception in rhesus monkeys. *PNAS, 99*(24), 15755-15757.

Gibson, E. J. (1988). Exploratory behavior in the development of perceiving, acting and the acquiring of knowledge. *Annual Review of Psychology, 39*, 1-41.

Grassi, M., & Darwin, C. J. (2006). The subjective duration of ramped and damped sounds. *Perception & Psychophysics, 68*(8), 1382–1392.

Grassi, M., & Pavan, A. (2012). The subjective duration of audiovisual looming and receding stimuli. *Attention, Perception & Psychophysics, 74*, 1321–1333.

Graziano, M. S., & Cooke, D. F. (2006). Parieto-frontal interactions, personal space, and defensive behavior. *Neuropsychologia, 44*(6), 845-859.

Graziano, M. S., Reiss, L. A., & Gross, C. G. (1999). A neuronal representation of the location of nearby sounds. *Nature, 397*, 428-430.

Graziano, M. S., Yap, G. S., & Gross, C. G. (1994). Coding of visual space by premotor neurons. *Science, 266*(5187), 1054-1057.

Grinter, E. J., Maybery, M. T., & Badcock, D. R. (2010). Vision in developmental disorders: Is there a dorsal stream deficit? *Brain Research Bulletin, 82*, 147-160.

Guthrie, D., & Buchwald, J. S. (1991). Significance Testing of Difference Potentials. *Psychophysiology, 28*(2), 240-244.

Hall, D., & Moore, D. (2003). Auditory neuroscience: the salience of looming sounds. *Current Biology, 13*, R91-R93.

Heed, T., Habets, B., Sebanz, N., & Knoblich, G. (2010). Others' Actions Reduce Crossmodal Integration in Peripersonal Space. *Current Biology, 20*, 1-5.

Hershenson, M. (1964). Visual discrimination in the human newborn. *Journal of Comparative and Physiological Psychology, 58*(2), 270-276.

Hoehl, S., & Striano, T. (2008). Neural processing of eye gaze and threat-related emotional facial expressions in infancy. *Child Development, 79*(6), 1752–1760.

Hoehl, S., & Wahl, S. (2012). Recording Infant ERP Data for Cognitive Research. *Developmental Neuropsychology, 37*(3), 187-209.

Iarocci, G., & McDonald, J. (2006). Sensory Integration and the Perceptual Experience of Persons with Autism. *Journal of Autism and Developmental Disorders, 36*(1), 77-90.

Iriki, A., Tanaka, M., & Iwamura, Y. (1996). Coding of modified body schema during tool use by macaque postcentral neurons. *Neuroreport, 7*, 2325-2330.

Ishida, H., Nakajima, K., Inase, M., & Murata, A. (2010). Shared mapping of own and others' bodies in visuotactile bimodal area of monkey parietal cortex. *Journal of Cognitive Neuroscience, 22*, 83-96.

Johnson, M. H. (1990). Cortical maturation and the development of visual attention in early infancy. *Journal of Cognitive Neuroscience, 2*(2), 81-95.

Johnson, M. H. (2000). Functional brain development in infants: Elements of an interactive specialization framework. *Child Development, 71*, 75-81.

Johnson, M. H. (2001). Functional brain development in humans. *Nature Reviews Neuroscience, 2*, 475-483.

Johnson, M. H. (2005). Subcortical face processing. *Nature Reviews Neuroscience, 6*, 766-774.

Johnson, M. H. (2011a). *Developmental Cognitive Neuroscience: an Introduction* (3rd ed.). John Wiley & Sons.

Johnson, M. H. (2011b). Interactive specialization: a domain-general framework for human functional brain development?. *Developmental Cognitive Neuroscience, 1*(1), 7-21.

Johnson, M. H., & Morton, J. (1991). *Biology and Cognitive Development: The Case of Face Recognition.* Oxford: Blackwell.

Johnson, M. H., de Haan, M., Oliver, A., Smith, W., Hatzakis, H., Tucker, L. A., & Csibra, G. (2001). Recording and Analyzing High-Density Event-Related Potentials With Infants Using the Geodesic Sensor Net. *Developmental Neuropsychology, 19*(3), 295-323.

Johnson, M. H., Dziurawiec, S., Ellis, H., & Morton, J. (1991). Newborns' preferential tracking of face-like stimuli and its subsequent decline. *Cognition, 40*, 1-19.

Johnson, M. H., Senju, A., & Tomalski, P. (2015). The two-process theory of face processing: Modifications based on two decades of data from infants and adults. *Neuroscience and Biobehavioral Reviews, 50*, 169-179.

Kandula, M., Hofman, D., & Dijkerman, H. C. (2015). Visuo-tactile interactions are dependent of the predictive value of the visual stimulus. *Neuropsychologia, 70*, 358-366.

Kayed, N. S., & van der Meer, A. L. (2000). Timing strategies used in defensive blinking to optical collisions in 5- to 7-month-old infants. *Infant Behavior and Development, 23*, 253-270.

Kayed, N. S., & van der Meer, A. L. (2007). Infants' timing strategies to optical collisions: A longitudinal study. *Infant Behavior and Development*, 50-59.

Kayser, C., Petkov, C. I., & Logothetis, N. K. (2009). Multisensory interactions in primate auditory cortex: fMRI and electrophysiology. *Hearing Research, 258*(1-2), 80-88.

Konczak, J., & Dichgans, J. (1997). The development toward stereotypic arm kinematics during reaching in the first 3 years of life. *Experimental Brain Research, 117*, 346-354.

Kouider, S., Long, B., Le Stanc, L., Charron, S., Fievet, A. C., Barbosa, L. S., & Gelskov, S. V. (2015). Neural dynamics of prediction and surprise in infants. *Nature Communications, 6*(8537).

Kushnerenko, E., Ceponiene, R., Balan, P., Fellman, V., Huotilainen, M., & Näätänen, R. (2001). Maturation of the auditory event-related potentials during the first year of life . *Neuroreport, 13*(1), 47-51.

Làdavas, E. (2002). Functional and dynamic properties of visual peripersonal space. *Trends in Cognitive Sciences, 6*(1), 17-22.

Làdavas, E., di Pellegrino, G., Farnè, A., & Zeloni, G. (1998). Neuropsychological evidence of an integrated visuotactile representation of peripersonal space in humans. *Journal of Cognitive Neuroscience, 10*(5), 581-589.

Làdavas, E., Zeloni, G., & Farnè, A. (1998). Visual peripersonal space centred on the face in humans. *Brain, 121*, 2317-2326.

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1997). Motivated attention: affect, activation, and action. In P. J. Lang, R. F. Simons, & M. Balaban (Eds.), *Attention and Emotion: Sensory and Motivational Processes* (pp. 97-135). Mahwah, NJ: Erlbaum.

Lawrence, R. D., Carrello, C., & Pastore, R. E. (1987). Relative effectiveness of three stimulus variabiles for locating a moving sound source. *Perception, 16*, 175-186.

Leo, F., Romei, V., Freeman, E., Làdavas, E., & Driver, J. (2011). Looming sounds enhance orientation sensitivity for visual stimuli on the same side as such sounds. *Experimental Brain Research, 213*, 193-201.

Lewkowicz, D. (2008). Perception of Dynamic and Static Audiovisual Sequences in 3- and 4-Month-Old Infants. *Child Development, 79*(5), 1538-1554.

Lewkowicz, D. J. (2014). Early Experience & Multisensory Perceptual Narrowing. *Developmental Psychobiology, 56*(2), 292-315.

Lewkowicz, D. J., & Ghazanfar, A. A. (2006). The decline of cross-species intersensory perception in human infants. *PNAS, 103*(17), 6771-6774.

Lewkowicz, D. J., & Ghazanfar, A. A. (2009). The emergence of multisensory systems through perceptual narrowing. *Trends in Cognitive Sciences, 13*(11), 470-478.

Lewkowicz, D. J., Leo, I., & Simion, F. (2010). Intersensory Perception at Birth: Newborns Match Nonhuman Primate Faces and Voices. *Infancy, 15*(1), 46-60.

Libertus, K., & Landa, R. J. (2013). The Early Motor Questionnaire (EMQ): a parental report measure of early motor development. *Infant Behavior and Development, 36*(4), 833-842.

Libertus, K., & Needham, A. (2004). Face preference in infancy and its relation to motor activity. *International Journal of Behavioral Development, 38*(6), 529-538.

Libertus, K., & Needham, A. (2010). Teach to reach: the effects of active vs. passive reaching experiences on action and perception. *Vision Research, 50*(24), 2750-2757.

Libertus, K., & Needham, A. (2011). Reaching experience increases face preference in 3-month-old infants. *Developmental Science, 14*(6), 1355-1364.

Lloyd-Fox, S., Blasi, A., & Elwell, C. (2010). Illuminating the developing brain: The past, present and future of functional near infrared spectroscopy. *Neuroscience and Biobehavioral Reviews, 34*, 269-284.

Longo, M. R., & Lourenco, S. F. (2006). On the nature of near space: Effects of tool use and the transition to far space. *Neuropsychologia, 44*, 977-981.

Longo, M. R., Trippier, S., Vagnoni, E., & Lourenco, S. F. (2015). Right hemisphere control of visuospatial attention in near space. *Neuropsychologia, 70*, 350-357.

Lourenco, S. F., Longo, M. R., & Pathman, T. (2011). Near space and its relation to claustrophobic fear. *Cognition, 119*, 448-453.

Luck, S. J. (2014). *An Introduction to the Event-Related Potential Technique* (2nd ed.). London, England: The MIT Press.

Maier, J. X., & Ghazanfar, A. A. (2007). Looming biases in monkey auditory cortex. *Journal of Neuroscience, 27*(15), 4093-4100.

Maier, J. X., Chandrasekaran, C., & Ghazanfar, A. A. (2008). Integration of bimodal looming signals through neuronal coherence in the temporal lobe. *Current Biology, 18*, 963-968.

Maier, J. X., Neuhoff, J. G., Logothetis, N. K., & Ghanzafar, A. A. (2004). Multisensory Integration of Looming Signals by Rhesus Monkeys. *Neuron, 43*, 177-181.

Makin, T. R., Holmes, N. P., & Zohary, E. (2007). Is that near my hand? Multisensory representation of peripersonal space in human intraparietal sulcus. *The Journal of Neuroscience, 27*(4), 731-740.

McCulloch, D. L. (2007). Visual evoked potentials in infants. In M. De Haan (Ed.), *Infant EEG and Event-Related Potentials* (pp. 39-76). Hove, England: Psychology Press - Taylor & Francis Group.

Middlebrooks, J. C., & Green, D. M. (1991). Sound Localization by Human Listeners. *Annual Review of Psychology, 42*, 135-139.

Morton, J., & Johnson, M. H. (1991). CONSPEC and CONLERN: A Two-Process Theory of Infant Face Recognition. *Psychological Review, 98*(2), 164-181.

Murray, M. M., Thelen, A., Thut, G., Romei, V., Martuzzi, R., & Matusz, P. J. (2016). The multisensory function of primary visual cortex in humans. *Neuropsychologia, 83*, 161-169.

Náñez, J. (1988). Perception of Impending Collision in 3-to 6-Week-Old Human Infants . *Infant Behavior and Development, 11*, 447-463.

Neuhoff, J. G. (1998). Perceptual bias for rising tones. *Scientific Correspondence, 395*(6698), 123-124.

Neuhoff, J. G. (2001). An Adaptive Bias in the Perception of Looming Auditory Motion. *Ecological Psychology, 13*(2), 87-110.

Noel, J. P., Grivaz, P., Marmaroli, P., Lissek, H., Blanke, O., & Serino, A. (2015). Full body action remapping of peripersonal space: the case of walking. *Neuropsychologia, 70*, 375-384.

Olofsson, J. K., Nordin, S., Sequeira, H., & Polich, J. (2008). Affective picture processing: An integrative review of ERP findings. *Biological Psychology, 77*, 247-265.

Olsho, L. W., Koch, E. G., Carter, E. A., Halpin, C. F., & Spetner, N. B. (1988). Pure-tone sensitivity of human infants. *The Journal of the Acoustical Society of America, 84*, 1316-1324.

Orekhova, E. V., Stroganova, T. A., Posikera, I. N., & Elam, M. (2006). EEG theta rhythm in infants and preschool children. *Clinical Neurophysiology, 117*, 1047–1062.

Reid, V. M., Hoehl, S., Landt, J., & Striano, T. (2008). Human infants dissociate structural and dynamic information in biological motion: Evidence from neural systems. *Social Cognitive and Affective Neuroscience, 3*(2), 161-167.

Ricciardi, E., Bonino, D., Pellegrini, S., & Pietrini, P. (2014). Mind the blind brain to understand the sighted one! Is there a supramodal cortical functional architecture? *Neuroscience & Biobehavioural Reviews, 41*, 64-77.

Rigato, S., Begum Ali, J., van Velzen, J., & Bremner, A. J. (2014). The Neural Basis of Somatosensory Remapping Develops in Human Infancy. *Current Biology, 24*, 1224-1226.

Rizzolatti, G., Scandolara, C., Matelli, M., & Gentilucci, M. (1981). Afferent properties of periarcuate neurons in macaque monkeys. II. Visual responses. *Behavioural Brain Research, 2*, 147-163.

Rochat, P., & Goubet, N. (1995). Development of Sitting and Reaching in 5- to &Month-Old Infants. *Infant Behaviour and Development, 18*, 53-68.

Romei, V., Murray, M. M., Cappe, C., & Thut, G. (2009). Preperceptual and Stimulus-Selective Enhancement of Low-Level Human Visual Cortex Excitability by Sounds. *Current Biology, 19*, 1799-1805.

Rosenblum, L. D., Carello, C., & Pastore, R. E. (1987). Relative effectiveness of three stimulus variables for locating a moving sound source. *Perception, 16*, 175-186.

Rosenblum, L. D., Wuestefeld, A. P., & Saldaña, H. M. (1993). Auditory looming perception: Influences on anticipatory judgments. *Perception, 22*, 1467-1482.

Rossini, J. C. (2014). Looming motion and visual attention. *Psychology and Neuroscience, 7*(3), 425-431.

Sambo, C. F., & Iannetti, G. D. (2013). Better Safe Than Sorry? The Safety Margin Surrounding the Body Is Increased by Anxiety. *The Journal of Neuroscience, 33*(35), 14225–14230.

Schiff, W., & Oldak, R. (1990). Accuracy of judging time to arrival: Effects of modality trajectory and gender. *Journal of Experimental Psychology: Human Perception and Performance, 16*, 303-316.

Schiff, W., Caviness, J. A., & Gibson, J. J. (1962). Persistent fear responses in rhesus monkeys to the optical stimulus of "looming". *Science, 36*(3520), 982-983.

Schlauch, R. S., Ries, D. T., & DiGiovanni, J. (2001). Duration discrimination and subjective duration for ramped and damped sounds. *Journal of the Acoustical Society of America, 109*, 2880-2887.

Schmuckler, M. A., Collimore, L. M., & Dannemiller, J. L. (2007). Infants' Reactions to Object Collision on Hit and Miss Trajectories. *Infancy, 12*(1), 105-118.

Schupp, H. T., Cuthberg, B. N., Bradley, M. M., Cacioppo, J. T., Ito, T., & Lang, P. J. (2000). Affective picture processing: The late positive potential is modulated by motivational relevance. *Psychophysiology, 37*, 257-261.

Schupp, H. T., Junghöfer, M., Weike, A. I., & Hamm, A. O. (2004). The selective processing of briefly presented affective pictures: An ERP analysis. *Psychophysiology, 41*, 441-449.

Seifritz, E., Neuhoff, J. G., Bilecen, D., Scheffler, K., Mustovic, H., Schächinger, H., Elefante, R, & Di Salle, F. (2002). Neural Processing of Auditory Looming in the Human Brain. *Current Biology, 12*, 2147-2151.

Serino, A., Annella, L., & Avenanti, A. (2009). Motor properties of peripersonal space in humans. *PLos ONE, 4*, e6582.

Serino, A., Bassolino, M., Farnè, A., & Làdavas, E. (2007). Extended Multisensory Space in Blind Cane Users. *Psychological Science, 18*, 642-648.

Shams, L., Kamitani, Y., & Shimojo, S. (2000). Illusions: what you see is what you hear. *Nature, 408*(6814), 788.

Simon, O., Mangin, J. F., Cohen, L., Le Bihan, D., & Dehaene, S. (2002). Topographical layout of hand, eye, calculation, and language-related areas in the human parietal lobe. *Neuron, 33*, 475-487.

Slater, A. (2002). Visual perception in the newborn infant: issues and debates. *Intellectica*, 57-76.

Smith, N. K., Cacioffo, J. T., Larsen, J. T., & Chartrand, T. L. (2003). May I have your attention, please: Electrocortical responses to positive and negative stimuli. *Neuropsychologya, 41*, 171-183.

Spears, W. C. (1966). Visual preference in the four-month old infant. *Psychonomic Science, 4*, 237-238.

Spencer, J., O'Brien, J., Riggs, K., Braddick, O., Atkinson, J., & Wattam-Bell, J. (2000). Motion processing in autism: evidence for a dorsal stream deficiency. *NeuroReport, 11*(12), 2765-2767.

Tajadura-Jiménez, A., Väljamäe, A., & Vastfjall, D. (2008). Emotional bias for the perception of rising tones. *The Journal of the Acoustical Society of America, 123*, 3245.

Taylor, M. J., & Baldeweg, T. (2002). Application of EEG, ERP and intracranial recordings to the investigation of cognitive functions in children. *Developmental Science, 5*(3), 318–334.

Teneggi, C., Canzoneri, E., di Pellegrino, G., & Serino, A. (2013). Social modulation of peripersonal space boundaries. *Current Biology, 23*(5), 406-411.

Tharpe, A. M., & Ashmead, D. H. (2001). A longitudinal investigation of infant auditory sensitivity. *American journal of audiology, 10*, 104-112.

Thelen, E., & Spencer, J. P. (1998). Postural Control During Reaching in Young Infants: A Dynamic Systems Approach. *Neuroscience and Biobehavioral Reviews, 22*(4), 507-514.

Thelen, E., Corbetta, D., & Spencer, J. P. (1996). Development of Reaching During the First Year: Role of Movement Speed. *Journal of Experimental Psychology, 22*(5), 1059-1076.

Trehub, S. E., Schneider, B. A., Thorpe, L. A., & Hudge, P. (1991). Observational measures of auditory sensitivity in early infancy. *Developmental Psychology, 27*, 40-49.

Tucker, D. M. (1993). Spatial sampling of head electrical fields: The geodesic sensor net. *Electroencephalography and Clinical Neurophysiology, 87*, 154-163.

Tyll, S., Bonath, B., Schoenfeld, M. A., Heinze, H., Ohl, F. W., & Noesselt, T. (2013). Neural basis of multisensory looming signals. *Neuroimage*, 13-22.

Vagnoni, E., Lourenco, S. F., & Longo, M. R. (2012). Threat modulates perception of looming visual stimuli. *Current Biology, 22*(19), R826-827.

Vagnoni, E., Lourenco, S. F., & Longo, M. R. (2015). Threat modulates neural responses to looming visual stimuli. *European Journal of Neuroscience, 42*, 2190-2202.

van der Meer, A. L., Fallet, G., & van der Weel, F. R. (2008). Perception of structured optic flow and random visual motion in infants and adults: a high-density EEG study. *Experimental Brain Research, 186*, 493-502.

van der Meer, A. L., Svantesson, M., & van der Weel, F. R. (2012). Longitudinal Study of Looming in Infants with High-Density EEG. *Developmental Neuroscience, 34*, 488–501.

Van der Stoep, N., Nijboera, T. C., Van der Stigchel, S., & Spence, C. (2015). Multisensory interactions in the depth plane in front and rear space: A review. *Neuropsychologia, 70*, 335-349.

van der Weel, F. R., & van der Meer, A. L. (2009). Seeing it coming: infants' brain responses to looming danger. *Naturwissenschaften, 96*, 1385–1391.

Vetter, P., Smith, F. W., & Muckli, L. (2014). Decoding sound and imagery content in early visual cortex. *Current Biology, 24*(11), 1256-1262.

von Hofsten, C. (1979). Development of visually directed reaching: the approach phase. *Journal of Human Movement Studies, 5*, 160-178.

von Hofsten, C. (1980). Predictive Reaching for Moving Objects by Human Infants. *Journal of Experimental Child Psychology, 30*, 369-382.

von Hofsten, C. (1991). Structuring of Early Reaching Movements: A Longitudinal Study. *Journal of Motor Behaviour, 23*(4), 280-292.

von Hofsten, C. (2004). An action perspective on motor development. *TRENDS in Cognitive Sciences, 8*(6), 266-272.

von Hofsten, C., & Rönnqvist, L. (1988). Preparation for Grasping an Object: A Developmental Study. *Journal of Experimental Psychology: Human Perception and Performance, 14*(4), 610-621.

Von Mühlenen, A., & Lleras, A. (2007). No-Onset Looming Motion Guides Spatial Attention. *Journal of Experimental Psychology: Human Perception and Performance, 33*(6), 1297-1310.

Waberski, T. D., Gobbelé, R., Lamberty, K., Buchner, H., Marshall, J. C., & Fink, G. R. (2008). Timing of visuo-spatial information processing: electrical source imaging related to line bisection judgements. *Neuropsychologia, 46*, 1201-1210.

Walker-Andrews, A. S., & Lennon, E. M. (1985). Auditory-Visual Perception of Changing Distance by Human Infants. *Child Development, 56*(3), 544-548.

Weir, C. (1976). Auditory frequency sensitivity in the neonate: A signal detection analysis. *Journal of Experimental Child Psychology, 21*, 219-225.

Weir, C. (1979). Auditory frequency sensitivity of human newborns: Some data with improved acoustic and behavioral controls. *Perceptual Psychophysics, 26*, 287-294.

Werner, L. A. (2002). Infant auditory capabilities. *Current Opinion in Otolaryngology & Head and Neck Surgery, 10*, 398-402.

Werner, L. A. (2007). Human auditory development. In R. Hoy, P. Dallos, & D. Oertel (Eds.), *The Senses: A Comprehensive Reference* (Vols. 3 - Audition, pp. 871-894). St. Louis: Elsevier.

Werner, L. A., & Gillenwater, J. M. (1990). Pure tone sensitivity of 2- to 5-week-old infants. *Infant Behaviour and Development, 13*, 355-375.

Wetherford, M. J., & Cohen, L. B. (1973). Developmental Changes in Infant Visual Preferences for Novelty and Familiarity. *Child Development, 44*, 416-424.

Yonas, A. (1981). Infants' responses to optical information for collision. In R. N. Aslin, J. R. Alberts, & M. R. Petersen, *Development of perception: Vol. 2. The visual system* (pp. 313-334). New York: Academic Press.

Yonas, A., Bechtold, A. G., Frankel, D., Gordon, R. F., McRoberts, G., Norcia, A., & Sternfels, S. (1977). Development of sensitivity to information for impending collision. *Perception & Psychophysics, 21*(2), 97-104.

Yonas, A., Pettersen, L., & Lockman, J. (1979). Young infants' sensitivity to optical information for collision. *Canadian Journal of Psychology, 33*, 268-276.

Zmyj, N., Jank, J., Schütz-Bosbach, S., & Daum, M. M. (2011). Detection of visual–tactile contingency in the first year after birth. *Cognition, 120*(1), 82-89.