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THE SPATIAL LOGIC OF FEAR

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ABSTRACT

Peripersonal space (PPS) is the multimodal sensorimotor representation of the space surrounding the body. This thesis project aims to investigate how this multisensory representation is modulated by emotional faces, particularly salient cue in our environment. In a series of studies, it is investigated how the different emotional expressions may differentially modulate PPS, and which are the mechanisms involved. Study 1 showed that looming neutral, joyful and angry faces gradually facilitated motor responses to the detection of tactile stimuli, as the looming faces approached the participant. In presence of looming fearful faces, the multisensory facilitation remained constant across the different spatial positions, resulting significantly lower in the closest position of the face compared with the neutral condition. Study 2a tested whether the effect found with fearful faces was attributable to a redirection of spatial attention from the face to the peripheral space. Results confirmed that only when a fearful face was looming in the space near the subject, a redirection of attention from the face to the peripheral space was prompted. This would facilitate the motor response to tactile stimuli, associated with visual targets presented in the periphery. This fear attentional effect was not found for neutral and joyful, nor for angry faces, which were tested in Study 2b. The redirection of attention in PPS observed with fearful faces was reflected in the electrophysiological signal associated with face processing, measured in Study 3: the redirection of attention was accompanied by a reduction of the N170 mean amplitude for fearful compared to neutral faces, consistent with a shift of attention away from the centrally presented face towards the peripheral space. Study 4 investigated whether the redirection of attention could also be supported by an increase of the physiological arousal in the space near to the body. The results revealed that the skin conductance response to looming fearful, but not joyful or neutral faces, was modulated by the apparent distance from the participant’s body, maximal in the near and reduced in the far. These results confirm the defensive function of PPS.

CHAPTER 1. Definition and functionalities of PPS in animal and human models

1.1 Introduction

We do not merely exist as objects in space, but rather, we live "spatially" as embodied beings (Patočka, 1998), aware of our spatiality and in constant interaction with it. In this interaction, we produce a functional representation of the space, in a situated manner, as embodied agents in a gravitational environment (Bufacchi & Iannetti, 2016), with our movement possibilities (Noel, Grivatz, et al., 2015) and our intentions (Senna et al., 2019). Diverse contributions challenged the notion of unitary space representation by describing the space as divided into several functional spaces (Jerde et al., 2012; Medendorp et al., 2016).

The first behavioural observations in animals, that provided the idea that the representation of the space near the body was functionally different from other spaces, came from the swiss biologist Heini Hediger (1955), that described how spatial proximity between animals in the zoo determined different behaviours; Hediger called "flight distance", the portion of space close to the animal in which the presence of a potential predator elicits stereotyped defensive reactions. From there, the study of the representation of the special space surrounding the body has gained increasing relevance; the first seminal studies on monkeys attributed the definition of peripersonal space (hereafter PPS) (Rizzolatti et al., 1981a), which was then variously defined, according to the perspective of study, like personal space, reaching space, defensive space, working space… etc. (de Vignemont & Iannetti, 2015). Coello and colleagues (2012) were defining PPS as a space that "contains the objects with which one can interact in the here and now, specifies our private area during social interactions and encompasses the obstacles or dangers to which the organism must pay attention in order to preserve its integrity". In this perspective, PPS describes an area of the space surrounding our body, that is coded in the brain for the purpose of interacting with objects and defending the body from hazards. PPS does not merely coincide with the capability to distinguish the far from the near space by, for instance, reading vergence and binocular disparity cues (Combe & Fujii, 2011; Hadjidimitrakis et al., 2011), but it is linked with a process of integration of multimodal stimuli, that is stronger as much as the encounter with the object is more probable (Hyvärinen & Poranen, 1974). Hyvärinen & Poranen (1974) described the response, in the parietal cortex, to a near visual stimulus, as an anticipated activation, which was measured before the actual tactile stimulus was delivered. The visual information produces an expectation to receive the tactile stimulus which influences the somatosensory experience; the spatiotemporal dynamics of such visual stimulus are extracted to predict its somatosensory consequences (Cléry & Hamed, 2018). Approaching auditory/visual stimuli predictively facilitate tactile processing and enhance tactile sensitivity. This capability to predict the contact with the external event is relevant to anticipate the potential interaction, to promptly prepare an appropriate motor response. For these features, PPS can be defined as a multimodal, sensory-motor, interface between the body and the environment (Rizzolatti et al., 1997); it is multimodal because it implies the coding of multisensory stimuli in body-part centred reference frames (di Pellegrino et al., 1997; Làdavas & Serino, 2008; Serino, 2019); it is sensory-motor because it supports the interaction with an object, by interpreting the sensory information to represent potential approaching or defensive movements (Làdavas & Serino, 2008; Dijkerman & Farnè, 2015; Rizzolatti et al., 1997).

Recently, PPS was further re-defined as a series of graded fields, reflecting the behavioural relevance of actions, which would aim to create or avoid the contact between an external object and the body (Bufacchi & Iannetti, 2018).

In this chapter, it is described how the literature, based on animal and human model, has contributed, historically and conceptually, to the construct of PPS, and it has converged around the definition of a multimodal representation of the space around the body that codes for actions.

1.2 Multimodal features of peripersonal space: monkey studies

1.2.1 Neurophysiological studies of peripersonal space in monkeys

From the early 1980s, the description of multisensory neurons in specific frontoparietal areas of the monkey brain captured the notion of the special neural representation of the near space, compared to the far (Rizzolatti et al., 1981a, b). These bimodal neurons are firing both when a tactile stimulus is delivered on a specific body part, but also when an heteromodal stimulus, that can be visual but also auditory, is presented at a certain distance from that body part; in this case, the visual and the tactile receptive fields of the neuron coincide. Those cells not only respond to tactile and to the visual and/or auditory information (Graziano & Cooke, 2006) but also integrate these multisensory signals (Avillac et al., 2005). Multisensory integration corresponds to the neural process which combines multimodal information to produce a multisensory response, which is significantly different from the summed modality-specific responses (Stein et al., 2010); for instance, the evoked response can be stronger or weaker (super-additive or sub-additive respectively) from the sum of the neural responses produced by the same neuron to each sensory stimulus presented independently (Stanford et al., 2005). The more two stimuli are in spatiotemporal coincidence, the maximal is the multisensory integration. Two stimuli are integrated, in fact, when the system reads the multimodal information as coming from the same source (Cao et al., 2019; Zuanazzi & Noppeney, 2020). Although multisensory integration was firstly defined at the level of the single neuron, its principles have been shown to be applicable in larger neuronal ensembles (EEG on the scalp, see e.g. Cappe et al., 2012), as well as behaviourally, by showing an enhanced sensitivity to tactile target detection (see e.g. Cléry, Guipponi, Odouard, et al., 2015), or speeded reaction times in response to tactile stimuli (see e.g. Noel, Blanke, Magosso, et al., 2018), compared to the unimodal tactile stimulation. Given this, multisensory processing can be more generally redefined as the neural process by which unisensory signals are combined to provide a new representation (Stein et al., 2014). The multimodal interactions, distinctive of PPS, were found in some areas of the frontal lobe, in particular the ventral premotor cortex (Rizzolatti et al., 1981a), of the posterior parietal cortex (Avillac et al., 2007; Duhamel et al., 1998; Leinonen, 1980), and in some subcortical areas (putamen; Graziano & Gross, 1993) (see Figure 1.1 for an overview of the areas of interest).

1.2.1.1 Premotor multimodal interactions

Neurons with PPS properties in the premotor cortex were specifically described in the F4, subregion of inferior area 6 of the ventral premotor cortex. Neurons of area F4, which is known to represent proximal arm movement (Matelli et al., 1985), were shown to be strongly responsive to tactile stimulation, with large receptive fields (RFs) located on the arm, hands and face of the animal, particularly in the peribuccal regions (Gentilucci et al., 1988; Rizzolatti et al., 1981a). Interestingly, most of these neurons (85%), also discharges in response to visual stimuli. Visual RFs of these neurons were shown to be independent of the position of the eyes or the body of the animal and remained anchored to the specific body part. According to the depth of their visual RTs, Rizzolatti and colleagues (1981b) subdivided these bimodal neurons in pericutaneus (54%), firing when visual stimuli were presented about 10 cm from the skin of the animal and distant peripersonal neurons (46%), that were firing when the stimulus was presented at a distance from the skin but still within animal's reach (Rizzolatti et al., 1981b). Graziano et al. (1999) further showed that neurons in this area integrate not only visuo-tactile information but also audio-tactile. Further, these studies highlighted an important feature of PPS neurons: their visual RFs are anchored to the tactile RFs of the specific body part (Graziano et al., 1994) and were independent of the animal's gaze direction (Graziano, Hu, & Gross, 1997).

1.2.1.2 Parietal multimodal interactions

Different parietal areas contribute to an enhanced representation of the near space, in which a significant proportion of neurons shows a preference for visual stimuli located in the surrounding of the animal's body (Hadjidimitrakis et al., 2011; Hamed & Bremmer, 2001; Bhattacharyya et al., 2009; Bremmer et al., 2013; Yang et al., 2011). Importantly, the area VIP, which is located in the fundus of the intraparietal sulcus, other than showing selectivity for monocular disparity (Bremmer et al., 2013; Yang et al., 2011), is also considered one of the two main subregions in the macaque parietal lobe, to display multimodal properties (Graziano & Cooke, 2006; Guipponi et al., 2017, 2013); neurons found in VIP, presented multimodal RFs (Avillac et al., 2005; Colby et al., 1993; Duhamel et al., 1998), and responded to tactile, but also to visual stimuli, mainly presented within a few centimetres from the tactile RF. VIP neurons seem to represent mostly the near space around the face and the head (head centred reference frame), organized along a continuum from the eye to head coordinates (Colby et al., 1993). Importantly, in a fraction of the VIP neurons, the visual and tactile RFs spatially match irrespectively of the eye position, while for the remaining neurons, the relationship between visual and tactile RFs, depended on gaze direction (Avillac et al., 2005).

Multisensory neurons were found also in area 7b of the inferior posterior parietal lobe (Hyvärinen & Poranen, 1974). Notably, the activation of these neurons, which showed a rough somatotopic organization, was dependent on the distance of the visual stimulus from the body part (up to 10 cm). The partial overlap between the tactile and the visual receptive fields of these neurons is thought to be involved in the anticipatory tactile response described before the neuron's tactile RF is touched (Hyvärinen & Poranen, 1974). Unlike VIP neurons, cells in 7b appear to be independent of the position of the arm (Graziano & Gross, 1995), although this is inconsistent with previous findings (Leinonen, 1980).

1.2.1.3 Subcortical multimodal interactions

Classical views on multisensory integration in the late '80s (Bloom et al., 1988) were converging on the model that unimodal signals are first processed in the respective unisensory cortices and then, successively integrated into the secondary areas (Stein, 2012). In the last decades, more models are considering the capability to integrate different neural representations as an intrinsic property of the brain. Seminal single-cell studies in the superior colliculus of the cat (Wallace et al., 1998) demonstrated that multisensory integration happens rather early in the processing of sensory information. Although multisensory encoding was well studied in the superior colliculus, such activity seems not to be devoted to an event near the body. Conversely, the putamen, a subcortical structure of the primate brain, was found to be a relevant structure involved in the processing of visuotactile events in the space around the body (Graziano & Gross, 1993, 1994). Visuotactile neurons in the putamen were showing a somatotopic organization (arm, hand, face), with a rough spatial correspondence (within 10-20 cm) of visual RFs anchored to the tactile one, thus those cells respond only when the stimulated monkey’s arm is under the view, but not when out of view (Graziano & Gross, 1993).

1.2.1.4 A multimodal peripersonal space network

Most of the above-mentioned areas were found to share a distinctive feature, namely the presence of neurons with multimodal RFs, such that multimodal information, not only converge but also are integrated (Avillac et al., 2007). Moreover, these cells respond to perceptual events in different sensory modalities, specifically when occurring within the same spatial frame. For example, they respond to a tactile event on a given body part, as well as to a visual and/or auditory stimulus, but only if it appears near that body part. Interestingly, these areas are also strongly interconnected with each other, frontoparietal multisensory circuits, which directly or indirectly project into the cortico-spinal tract. This multisensory-motor networks (Rizzolatti et al., 1997) are underlying several sensory-motor functions, and PPS neurons form one of the several frontoparietal networks bridging the posterior parietal and the premotor cortex (Avillac et al., 2005; Fogassi et al., 1996; Michaels & Scherberger, 2018) supporting a series of specific sensory-motor functions in the primate brain (i.e., reaching, grasping). The network, particularly important for PPS, is involving the parietal area VIP and the premotor area F4 (Matelli & Luppino, 2001; Rizzolatti et al., 1981a). This network produces all the necessary information to bind together the localization of objects around the body (specifically, the head), with actions toward these objects. Importantly, electrical stimulation of both F4 and VIP induces a similar repertoire of an involuntary eye or head movement with a very short latency (up to 10 ms) (Cooke & Graziano, 2003, 2004; Graziano & Cooke, 2006). For example, micro-stimulation of area VIP produces eye blinking and squinting, ear folding against the head, shoulder shrugging, and the withdrawal of the face from the contralateral side of space in a protective posture (Cooke & Graziano, 2004; Graziano & Cooke, 2006). To note, these areas were not activated by voluntary movements, such as spontaneous eye blink. To sum up the VIP-F4 network seems to be involved in the action of defence and obstacle avoidance behaviour; the parietal VIP is more involved in the construction of the environment anchored to the head, while the premotor F4 is more involved in the production of a reflexive, rapid complex defensive motor pattern, that subserves the function of protection of the body by producing a defensive (closing eyelids, lifting arm/hand in front of the head) or avoidance responses (moving the head away, hand in the back). Thus, the network VIP-F4 is proposed to subserve the PPS representation and protection of the near PPS or safety margin around the body parts, head, and arm/hand unit (Cléry, Guipponi, Wardak et al., 2015).

1.2.2 Looming stimuli and impact prediction to the body

In previous paragraphs, PPS was defined as the neural representation between the body and the environment, that hosts most of the interactions with it, and that is encoded by a dedicated network of frontoparietal areas populated by multimodal neurons, which respond to tactile and visual or auditory stimuli, or both, and mostly when these are perceived at a certain distance from the tactile RF. Importantly, these multimodal neurons showed an enhanced responsivity to looming, rather than static, stimuli (Fogassi et al., 1996). Fast approaching objects are likely to be interpreted as a threat (De Franceschi et al., 2016) and acquire for this reason more ecological relevance than static objects (Romei et al., 2009). Indeed, looming, but not receding (Lewis & Neider, 2015), stimuli are associated with stereotyped fear responses in monkeys (Schiff et al., 1962) and human infants (Ball & Tronick, 1971). At the neural level, it was described that the PPS network (VIP-F4) is particularly sensitive in the detection of dynamic visual stimuli (Cléry et al., 2013) and appears to be involved in intrusive impact prediction to the body.

The objects' dynamicity contains important information for determining the hazard level of the object for the body, or whether it can be beneficial or harmless; for instance, information about motion, direction, velocity, time-to-collision, identity, are analyzed by the brain, to execute the appropriate behavioural responses depending on the context. For instance, most of the VIP neurons have been shown to respond more than twice to stimuli moving in the preferred direction compared to a non-preferred direction (Colby et al., 1993). Another relevant stimulus movement parameter is the speed of travelling of looming stimuli; speed changes produce online expansion of the visual RF in depth in a portion of these neurons in F4; this would suggest that these neurons might compute the time to impact on the body (Fogassi et al., 1996). Because these behavioural effects are induced by visual stimuli and have consequences on the process of touch, this strongly predicts the involvement of a visuotactile convergence network. In a recent fMRI study Cléry and colleagues (2017), tested the hypothesis that the processing of stimuli potentially impacting the face implies a mechanism of multimodal processing. In this study, a visual stimulus looming toward the face, and/or a tactile stimulation on the face, was presented to trained monkeys that were fixating a central point. These visual and tactile stimuli were either presented in isolation or delivered together. When delivered together, the visuotactile spatial and temporal relationships of the tactile and visual stimuli was manipulated, to obtain occasions in which the visual stimulation was predicting, spatially and temporally, the tactile stimulation, and other two occasions in which the visual stimulation was spatially but not temporally predictive and vice versa. They found that impact prediction, namely the anticipation of touch, onto the face, activates a network associated with multisensory convergence and multisensory integration. This multisensory network, composed of prefrontal, parietal, temporal, and occipital-parietal regions, but also striate and extra-striate regions, was particularly activated when the delivery of the tactile stimulus was at the time and location in which the looming visual stimulus would have impacted the body. In particular, the impact prediction to the face involves the parietal-frontal network (VIP/F4), that has been associated with the definition of a defensive PPS (Cooke & Graziano, 2004; Graziano & Cooke, 2006; Graziano et al., 2002). The authors (Cléry et al., 2017) were claiming that the function of the outlined network was to anticipate the consequences of the looming trajectory of the stimulus on the body, by the modulation of the sensitivity to touch. Notably, the activity of the described network was found as highly dependent upon the spatial and temporal predictive information held by the looming visual stimulus.

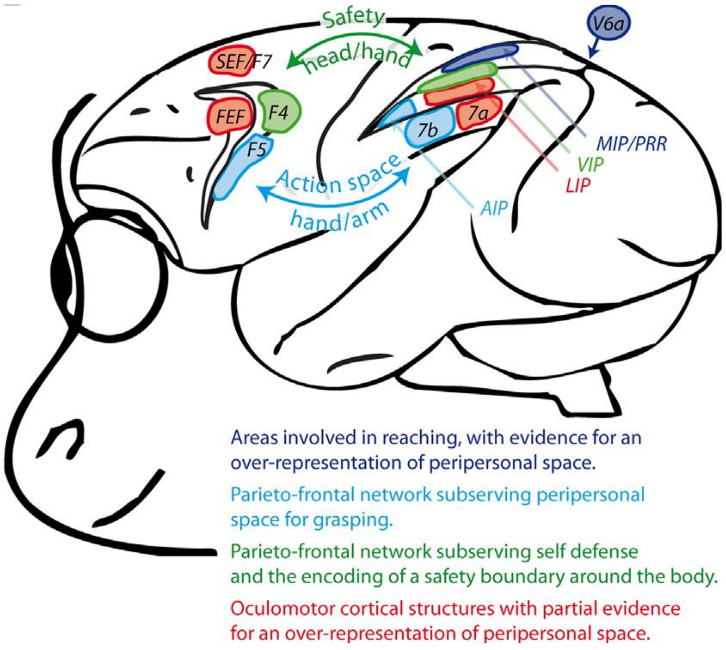


Figure 1.1 Adapted from Cléry, Guipponi, Wardak, et al., 2015. Functional networks associated with enhanced representation of peripersonal space: areas involved in reaching (dark blue), parieto-frontal network subserving peripersonal space for action (cyan), parieto-frontal network subserving self-defence and the encoding of a safety boundary around the body (green), oculomotor structures with partial evidence for an over-representation of peripersonal space (red) (Cléry, Guipponi, Wardak, et al., 2015).

1.3. Multimodal features of peripersonal space: human studies

1.3.1 Neuropsychological studies of peripersonal space in humans

Evidence for discrete brain representations of the space near the body and its part has also come from neuropsychological studies in humans, in which were described similar body part–centred multisensory PPS, as in monkeys (Làdavas, 1998). Patients with right hemisphere lesions, in the posterior parietal regions, often exhibit a deficit known as contralesional extinction (Bender, 1952). In this condition, patients will correctly detect a single stimulus presented in either hemifield, but when stimuli are presented to both hemifields at the same time (double simultaneous stimulation technique; Baylis et al., 2002), they will normally detect only the ipsilesional stimulus, with a deficit in perceiving and reporting the contralesional stimulus. Extinction was reported in various sensory modalities (Bender, 1952; Jacobs & Farnè, 2011), but, importantly, it was also found when the two stimuli applied to the patient were of different modalities; in this case, the phenomenon produced is called cross-modal extinction (di Pellegrino et al., 1997; Farnè & Làdavas, 2000; Làdavas et al., 2000). Two seminal and independent studies by di Pellegrino, Làdavas, and Farnè (1997) and Mattingley and colleagues (1997) described for the first-time cases of patients that were suffering from cross-modal extinction in the tactile or visual modality or both. When a visual stimulus was delivered near the ipsilesional hand, these patients showed an impaired detection of a tactile stimulus on the contralesional hand (visuotactile extinction). Importantly, the visuotactile extinction was not found when the ipsilesional visual stimulus was delivered far from the patient’s hand (di Pellegrino et al., 1997). This result has been attributed to the ‘body-part centred’ multisensory space representation found in the monkey’s brain, by the single-cell studies (Duhamel et al., 1998; Graziano & Gross, 1993; Graziano et al., 1997; Rizzolatti et al., 1981a). Extinction and cross-modal extinction are thought to reflect an unbalanced competition for awareness between concurrent spatial representations for the access to limited attentional resources (Jacobs & Farnè, 2011). The somatosensory representation of the tactually stimulated hand is weaker when simultaneously has to compete with the somatosensory representation of the other hand, activated by visual stimuli presented near the hand (Làdavas, 2002). Importantly, subsequent observations reported that cross-modal extinction is not an all or none phenomenon, in the transition between the near and far space, but, although milder, it is still occurring with ipsilesional stimuli delivered farther from the hand (Farnè & Làdavas, 2000; Làdavas & Pellegrino, 1998). These pieces of evidence were constituting the first suggestion that the transition from near to far space is not abrupt, delimited by the arm's length, but gradual with distance (Longo & Lourenco, 2007). Moreover, the same distance dependence of cross-modal extinction has been reported for the face, both in the visuotactile modality (Farnè, Demattè, et al., 2005; Làdavas, 1998) and in the audio-tactile modality (Làdavas & Farnè, 2000). Lastly, always in analogy with the monkey's PPS literature, cross-modal interactions, showed by the cross-modal extinction phenomenon, were found to be centred on a specific body part (Di Pellegrino et al., 1997). The overall findings showed that crossmodal interactions within the tactile and other modalities, such as auditive or visual, are stronger in the space near the body, and operate in a body part centred coordinate systems. This constitutes the first evidence, in humans, of a multimodal system that was coding the space near the body, similar to which have been found in monkeys (Làdavas, 2002).

1.3.2 Behavioural evidence of peripersonal space in humans

Consistently with monkeys' and neuropsychological literature, the influence of near auditory and visual stimuli on the tactile processing was also described in the healthy population.

One of the paradigms used to assess the change, over space, of multisensory interactions, is the Cross-modal Congruency Task (Spence et al., 2004). In this task, participants were required to make speeded discrimination of two vibrotactile targets based on their upper or lower position, where upper corresponded to a vibration applied to the index finger, and lower, to the thumb. At the same time, participants had also to ignore any visual distractor presented at the same or different position level of the vibration source. Participants' responses were faster and more accurate when the tactile target and the visual cue were presented at the same elevation (congruent condition) with respect to when they were not coupled for the position (incongruent condition); the facilitation of responses to the congruent condition compared with the incongruent condition, is called cross-modal congruency effect (CCE; Driver, 2000). CCE appears to be largest when the visual distractor is presented in the PPS surrounding the hand that receives the target vibration and might, perhaps, be compared to when the visual distractor is moved away from tactually stimulated hand, into its extrapersonal space (Maravita & Spence, 2003). Spatial dependent CCE has been demonstrated also by administering tactile targets and auditory cue (Sperdin & Murray, 2010). Together these findings were demonstrating that the somatosensory processing of tactile stimuli on the body, is affected when a visual or an auditory stimulus is presented near the hand, rather than far. Similar results have also been found in the auditory version of the task (Occelli et al., 2011).

Simpler multimodal interaction tasks have also been used to assess PPS behaviourally. In these tasks, the response required is simply to detect, as fast as possible, a tactile stimulus at the hand, while concurrently task-irrelevant sounds were presented near or far from the stimulated hand. Responses to the detection of the tactile stimulus were normally found faster when the task-irrelevant stimulus was perceived close to the stimulated hand, compared to when the stimulus was perceived far from it (Serino et al., 2007; Serino et al., 2011). This distance-dependent multisensory facilitation of the tactile response times is suggesting that the somatosensory processing of tactile stimuli is influenced more strongly by visual or auditory stimuli when they fall within the PPS, rather than in the extrapersonal space (Làdavas & Serino, 2017). Here, visual or auditory stimuli are presented at two fixed locations, far or close to the body. Based on the notion that neural system representing PPS, both in human (Bremmer et al., 2001; Makin et al., 2007) and in the animal model (Colby et al., 1993; Duhamel et al., 1997; Fogassi et al., 1996; Graziano, Hu, Gross, et al., 1997; Graziano et al., 1999), show a preference for dynamic over static stimuli, Canzoneri, Magosso and Serino (2012) have elaborated a version of the task, in which tactile vibrations at the hand were coupled with dynamic auditory stimuli. In the validation of the task, healthy participants made speeded responses to tactile stimuli applied at the hand while ignoring looming or receding sounds. Tactile stimuli were delivered with different delays from the sound onset; hence, the sound source could be perceived at various distances from the subject’s hand at the time of the tactile stimulation. Reaction times to tactile stimuli at the hand were found to be faster the closer the sound source was perceived. Importantly, the fastening of reaction times to tactile stimuli was not found to be linearly related to the perceived spatial distance of the approaching sound, but rather, responses were facilitated specifically when sounds overcame a limited distance from the body. This critical point, on the looming trajectory, that determines a stronger influence of the dynamic stimulus on the motor response to the tactile stimulus, was considered as a proxy of the boundary of the PPS and was taken as a dependent variable in successive experiments studying different properties of PPS (Ferri et al., 2015 Taffou & Viaud-Delmon, 2014). Interestingly, the distance at which stronger multisensory interactions occurred, was found to be dependent on the stimulated body part, that was closest for the hand (30-45 cm), then face (50-60 cm), and largest for the trunk (70-80 cm) (Serino, Noel, et al., 2015). Interestingly, this modulation appeared only when the auditory stimulus was approaching, but not when it was receding, with the exception of the hand, which still showed spatial-dependent multisensory facilitation also for the receding condition. Here, the human behavioural responses, as well as the neuronal responses described in the monkey's brain, were found to depend upon similar factors; for instance, human PPS was found to be body-part centred (Fogassi et al., 1992, 1996; Gentilucci et al., 1983; Graziano et al., 1994), to vary according to the specific body part stimulated (i.e., the trunk or the face), or to be sensitive to the spatiotemporal dynamics of the stimuli (i.e. direction tuning: approaching versus receding; Fogassi et al., 1996; Graziano, Hu, Gross, et al., 1997). The concept of a not unitary but modular PPS, with representations centred around body parts, was first reported in patients with extinction (Farnè, Demattè et al., 2005). Also, Serino, Noel, et al. (2015) observed that the separated PPS representations were not fully independent from each other: hand-centred and face-centred PPS were both integrated with the larger trunk-centred PPS. To conclude, behavioural evidence confirmed the existence of body part specific PPS representations, that could be interpreted as a mechanism in support of object-body interaction, that could be either approaching or avoiding an object or reacting to a potential threat.

1.3.3 Neuroimaging studies of peripersonal space in humans

Other than behavioural, many neuroimaging studies have described the PPS mechanisms at the neural level in support of the homologies with the monkeys' PPS. A network of human brain areas in the premotor and posterior parietal cortices was targeted, as in the monkey's brain, to be the candidate to host PPS neural representation (see for reviews, Cléry, Guipponi, Wardak, et al., 2015; Grivaz et al., 2017). Specifically, a frontoparietal multisensory motor network was described in reference to the hand, the face, and other body parts, such as lower limbs (Huang et al., 2012). Here below, the main recent findings, that concern the PPS around the hand and the face, are described.

Makin and colleagues (2007), in an fMRI study on eleven healthy participants, compared BOLD responses to visual stimuli approaching a near-the-hand target or a far target (70 cm); they localized areas in the IPS and the lateral occipital complex (LOC), that represented the visual space near the hand. Furthermore, they were able to determine the sensory contributions, visual or proprioceptive, to the representation of hand-centred space, with a dissociation between the posterior and the anterior IPS. IPS areas were more active in the conditions in which the hand was visible, even when it was replaced with a dummy-hand, thus visual information had a predominant role over proprioception. Conversely, the anterior IPS was found to use more multisensory information in representing the peri-hand space; it was found to have a higher BOLD response in the condition in which the hand was not retracted, even if not visible.

The highlighted cortical and subcortical sites were also confirmed by Brozzoli and colleagues (2011), by using a repetition suppression paradigm in an fMRI scanner. This paradigm is grounded on the assumption that the repeated presentation of identical stimuli elicits a reduced evoked signal in the neuronal population selective to that specific stimulus feature (Avidan et al., 2002); consequently, with this paradigm, it is possible to target subpopulation of neurons within a single voxel that exhibit selectivity to a specific feature. In this study (Brozzoli et al., 2011), it was found that the IPS, the inferior parietal lobule (IPL; supramarginal gyrus) (Grivaz et al., 2017), the dorsal and ventral premotor cortex, the cerebellum, and as well the putamen, exhibited selective BOLD adaptation to the presentation of objects moving near the hand. Importantly, this effect was not found when the stimulus was presented in a farther position (100 cm) or when the hand was withdrawn from the object. Moreover, Gentile and colleagues (2011), further showed that these areas and in particular the left anterior IPS, the insula, the dorsal premotor cortex and the subcortical putamen were showing super-additive responses to visual stimuli administered at the hand. Altogether these studies were quite convergent in indicating that the network of premotor and parietal areas, plus the putamen and the cerebellum, are representing the PPS around the hand.

A more direct proof of the involvement of these areas in the PPS representation of the space around the hand is represented by the TMS study by Serino and colleagues (2011). By using a low-frequency repetitive TMS (rTMS) they were able to induce virtual lesions in the left ventral premotor cortex (vPMc), in the posterior parietal cortex (PPC), around the IPS, and in V1, as a control area. Healthy subjects performed a tactile detection task, while concurrently ignoring sounds that were presented either close to, or far from, the tactually stimulated hand (100 cm). They found that, when the rTMS was not applied, responses to tactile target that were concomitant with close sounds, were faster, compared to when the sound was far, and this effect was found to be specific to a hand centred-reference frame (no longer found when the arm was kept backwards), moreover this facilitation was also found while rTMS was applied over V1. Critically, virtual lesions to vPMc and PPC, overrode the facilitation effect of the near, compared to far sounds, by inhibiting the audio-tactile interaction around the hand. These results further highlighted the central role of the vPMc and PPC in constructing a multisensory representation of the space around the hand.

Nonetheless, other studies were dedicated to the investigation of the neural representation of the peri-space around body parts other than the hand, such as the face area. Bremmer and colleagues (2001), presented to healthy subjects lying in an fMRI scanner, moving visual, tactile, or auditory stimuli around the face. They observed an increased neural activity evoked by tactile stimulation at the face, overlapped with activity evoked by stimuli in the other two modalities, when moving, but not when stationary. This pattern was found in the depth of the IPS, in the vPMc, and in the lateral inferior postcentral cortex. These findings came in support of the claim that the polymodal motion processing in humans and in monkeys, is supported by the same areas. In particular, the activation in the depth of the IPS was considered the human equivalent of the macaque area VIP (Avillac et al., 2007; Duhamel et al., 1998; Grivaz et al., 2017). These results were further confirmed by Sereno and Huang (2006), which mapped the organization of a multisensory representation of the face, in the parietal area, with a particular interest in the superior part of the postcentral gyrus. In this area, they found aligned maps of tactile and visual stimuli presented near the face. Further, the authors (Sereno and Huang, 2006), showed that visual stimuli were coded in spatial coordinates centred on the face and not on the retina.

All together these pieces of evidence are in support of the existence, in humans, of a mechanism that codes specifically for the space around the body, which is mainly located in the premotor cortex and the posterior parietal cortex, as also supported by the meta-analysis conducted by Grivaz and colleagues (2017). The authors highlighted different clusters of brain areas which were consistently activated during the PPS tasks (Figure 1.2). These clusters were concentrated in the left and the right superior parietal cortex, in the right and the left temporoparietal cortex, and the right and the left premotor cortex. Grivaz and colleagues (2017) proposed that the superior parietal cluster could be considered as the human homologue of the monkey’s superior parietal lobule (SPL, area 5; Graziano et al., 2000). Moreover, this cluster of superior parietal areas of the right hemisphere also included a portion of the IPS, that was proposed to be the homologue of the monkey VIP. VIP area, as pointed out before, is involved in the multisensory representation of the space near the face (Avillac et al., 2007; Duhamel et al., 1998).

The temporoparietal cluster of areas includes multimodal association regions known to process and integrate visual, auditory, vestibular, and tactile information (Driver & Noesselt, 2008). The activity of these regions in the temporoparietal cortex, which mainly overlaps with the monkey inferior parietal lobule (IPL) and area 7b, possibly reflects the multimodal processing of tactile and the visual and auditory modalities associated with PPS (Macaluso & Driver, 2005). These areas were also shown to be sensitive to the spatial feature of the different sensory inputs (Corbetta et al., 2000; Mayer et al., 2004).

Lastly, the premotor cluster of areas is associated with action coding and constitutes a key region of multisensory convergence. The authors (Grivaz et al., 2017) proposed that the identified ventral premotor areas, particularly of the right hemisphere, may correspond to the ventral premotor region, namely the F4 (Rizzolatti et al., 1981a) or polysensory zone (Graziano & Cooke, 2006) in the macaque brain. Interestingly, Grivaz and colleagues (2017), by using a meta-analytic coactivation technique, showed that these clusters were extensively interconnected with each other, with two main patterns of functional connectivity, the first involving the IPL and IPS regions with primary somatosensory regions, and the second, involving the SPL and premotor regions.

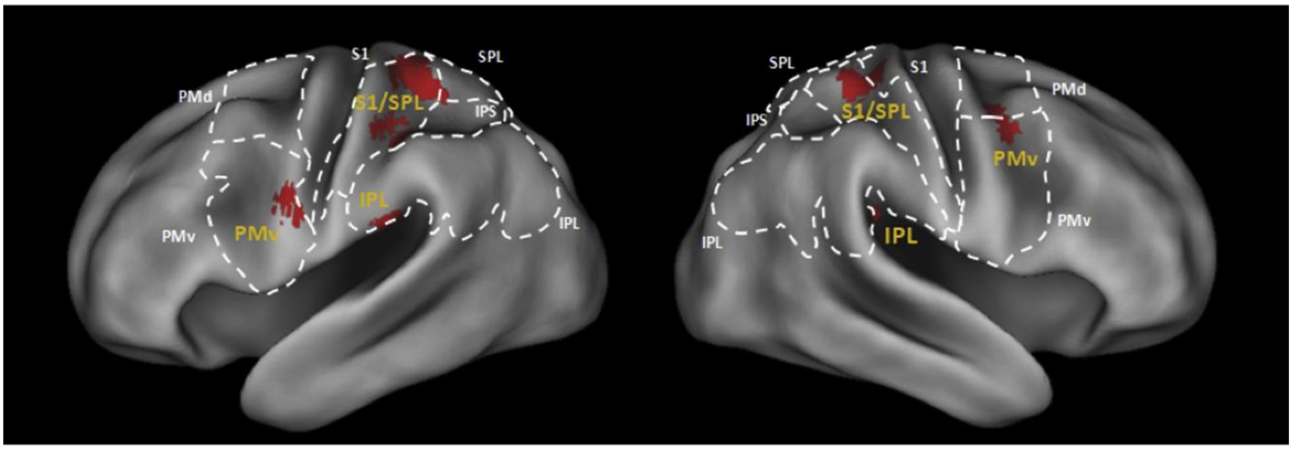


Figure 1.2 From Grivaz et al. (2017). Brain areas showing consistent activation across the different fMRI studies on PPS representation in humans from the meta-analysis conducted by Grivaz et al. (2017) (SPL superior parietal lobule, S1 primary somatosensory cortex, IPL inferior parietal lobule, IPS intraparietal sulcus, PMv/d ventral/dorsal premotor cortex).

1.4 Conclusions

In this chapter, the main literature on animal and human model, that gave rise to the concept of PPS, as the neural representation of the space near the body, was reviewed. Neurons that were identified to participate directly in the PPS representation, fire when a tactile stimulus is presented on a specific body part, but also when a visual or an auditory stimulus is presented close to the specific body part; this polymodal cells, have thus audio or visual RFs which partially overlap with the tactile RFs; consequently, these neurons respond best to stimuli presented near the skin surface, and their gradient of firing diminishes as the distance increases. When stimuli are in the far space, only a weak response is induced. Since some of these neurons seem to respond more to dynamic looming stimuli, more than static, it was proposed that they might be involved in the computation of the time to impact on the body. Importantly, these multimodal RFs, are centred on the specific body part, and not determined by, for instance, retinal, or other egocentric reference systems. In the monkey brain, neurons that presented these features were found particularly in frontoparietal, well connected, areas. The VIP-F4 circuit is associated with a movement of defence and withdrawal, which gives the PPS a function of protection, with the preservation of a space of safety around the body.

Seminal neuropsychological studies on cross-modal extinction enlightened for the first-time important features of the PPS in humans; these studies were showing visuotactile and audio-tactile interactions, stronger near the body and operating in a body part-centred coordinate system. These features were further confirmed by behavioural studies in healthy humans, that measured the somatosensory processing of tactile stimuli on the body in terms of a speeded reaction times. The multisensory facilitation of the motor responses to tactile stimuli was higher when the tactile stimulus was coupled with a visual or an auditory stimulus, and more so when this stimulus was closer to the tactually stimulated body part. Neuroimaging studies identified areas in the human brain within the intraparietal and premotor cortices, coding for the space near the body and responding to multisensory stimuli in PPS.

CHAPTER 2. Modulations of peripersonal space

2.1. Introduction

As seen in the previous chapter, specific areas of the brain code for the near space around the body, in particular, a set of neurons in the intraparietal sulcus (Duhamel et al., 1998), in the ventral premotor areas (Rizzolatti et al., 1981a) present multimodal RFs, whose extension is taken as a proxy of the PPS. In the multisensory PPS, tactile and visual or auditory stimuli are more strongly integrated, and this process follows the multisensory integration principle (Murray & Wallace, 2011). This principle states that signals from two modalities in spatiotemporal proximity are integrated with an advantage in responsiveness. The amount of multisensory response enhancement that normally results from the simultaneous presentation of visual and tactile stimuli (Noel, Łukowska et al., 2015) is expected to positively correlate with the proximity of the visual stimulus to the tactually stimulated body part.

Although PPS was described as constituted by receptive fields spatially linked to a margin surrounding the body, PPS is not a static representation. The proximity-dependent modulation of multisensory integration might be more or less gradual, as it is assumed that the spatial criteria for jointly processing two events in different modalities (Noel et al., 2016) depends upon a wide realm of factors. If PPS is considered as the output of a sensory-motor computation that links the body with the environment, it can be expected to involve body disposition, in its motor possibilities and physical constraints, and the sensory-motor experience; nonetheless it should also be modulated by the environmental features of the stimulus: that are, not only its spatiotemporal dynamics but also its valence and significance for the fitness of the individual. Moreover, PPS is also expected to be affected by higher-level social factors and personality traits.

The dynamic adjustment of this representation, beyond all these different factors, makes PPS a fundamental function of the body-brain in interaction with the environment, in a goal-driven behaviour. Such a mechanism would also be seminal in subserving defensive reactions against threats. The dual model of PPS proposed by de Vignemont and Iannetti (2015) is based on the idea that there might be at least two distinct PPS systems. The distinction would be based on the function: PPS for a goal-directed action and PPS for bodily protection. These two PPS functions require different sensory and motor processes (de Vignemont & Iannetti, 2015).

In this chapter, classical and more recent contributions, that described PPS modifications, are reviewed. The discussion is anchored to the functional distinction between the PPS for goal-directed actions and the defensive PPS. Besides, along with the discussion, the definition of multisensory PPS as distinct from the constructs of reaching space and interpersonal space is stressed.

2.2. Peripersonal Space for the purpose of acting

PPS for a goal-directed action also called working space, is subserved by the network of parietal-frontal areas, that bind multimodal information to generate an appropriate motor program. Although it does not coincide with the reaching space, this mechanism has appeared to play a role in grasping and reaching actions. Most of the goal-directed actions are deliberate and purposeful, voluntary and sensitive to objects affordances and sensitive to the progress of the ongoing action (Brozzoli et al., 2009). The modulation of PPS for goal-directed action might require the involvement of plastic motor mechanisms. PPS modulation was observed after training or repeated exposure to a given sensory-motor context (i.e. tool use, limb immobilization). Also, PPS for a goal-directed action may be capable of instantaneous non-motor mediated adjustment. In some cases, the subject has to infer the proximity of a certain stimulus to its body, by targeting far spaces as representative of the body itself; it is the condition of looking oneself reflected into a mirror or projected on a shadow on the ground. In this case, the remapping of PPS, onto these relevant areas, is abrupt and does not require action mediation. Another situation in which PPS for goal-directed actions is modulated is when the subject is no longer alone in acting but has to take into consideration the presence of others.

2.2.1 Motor-driven reorganization of Peripersonal Space

2.2.1.1 Extended peripersonal space with the use of a tool

One of the fundamental features of PPS for goal-directed actions is that it can be plastically shaped through the motor experience. One way to modify motor experience is to alter the coupling of the body movement with its environmental outcome; tool-use represent the classical way to create this condition. By modifying the action space, with tool-use, the subject can also act over a space which would be out-of-reach with bare arms. The tool has in this context the function of prolongation of the arm, and it is used to produce an action, deliberate and purposeful, with direct consequences, in achieving a specific goal. The effects of tool-use on PPS were variously studied in the context of repeated use of a rake to retrieve objects (Iriki et al., 1996; Maravita et al., 2002), or to simply perform a pointing task toward visual stimuli (Berti & Frassinetti, 2000; Hunley et al., 2017; Maravita et al., 2001); also, the effects on PPS were examined in the condition of two tools, one per each arm, that could be crossed or not over the body midline (Holmes et al., 2007; Maravita et al., 2002). The seminal work of Iriki et al. (1996) showed, in monkeys, that prolonged use of a rake to retrieve distant food, enlarged the receptive fields of bimodal cells of the anterior bank of IPS. Neurons, that were firing when a visual stimulus was approaching the hand, become, after the tool-training, responsive to visual stimuli approaching the tip of the tool.

Neuropsychological studies first demonstrated, in humans, PPS plasticity related to tool-use (Farnè, Bonifazi, et al., 2005; Farnè, Iriki, et al., 2005; Farnè & Làdavas, 2000; Berti & Frassinetti, 2000). In the study by Farnè and Làdavas (2000), visual extinction was investigated in a group of right brain-damaged patients. When the patient was holding a tool, ipsilaterally to his right lesion, and visual stimuli were presented at the tip of that tool, a stronger contralesional tactile extinction was induced. Thus, the tool-use condition affected the distance from the body at which visual stimuli need to be, to interfere with the tactile stimuli detection on the controlesional hand. Importantly, this effect was observed only after the patient interacted with the tool for a certain amount of time, in this case, 5 minutes of retrieving far objects. This result constitutes evidence of an extension of the peri-hand space representation (Farnè & Làdavas, 2000**;** Maravita et al., 2001). To note, PPS extension is temporary: after a certain time of tool non-use (5–10 min), cross-modal extinction was comparable to the pre-tool use condition (Farnè & Làdavas, 2000).

Importantly, the active use of the tool seems needed to extend PPS representation. The study conducted by Farnè, Iriki, and Làdavas (2005), showed that the passive holding of the tool failed to modulate PPS, even when the holding was prolonged in time. Results that were consistent with the evidence in monkey parietal cells, whose RFs were elongated after active but not passive tool use (Hihara et al., 2003; Iriki et al., 1996; Obayashi et al., 2000). The active use of the tool to act in the far space poses the question of whether the PPS modifications are extended along with the tool, in a continuum hand-tool configuration (expansion hypothesis), or rather, these PPS modification would cover only the functional tip of the tool, being projected onto the location tapped by the tip (projection hypothesis). In support of the first hypothesis of an expansion of the visuotactile integrative area along the tool axis, comes from neuropsychological studies with right brain-damaged patients (Farnè, Bonifazi, et al., 2005; Farnè, Serino, et al., 2007). These studies tested whether, after tool-use, cross-modal extinction could be observed at different locations along the tool axis. Cross-modal extinction was equally observed at the middle and at the distal portions of the used tool. Conversely, if the PPS was projected to prioritize certain regions of space, the mechanisms that support such modulation would be more likely to be attentional, with its focus that shifts at the tip of the tool (Holmes et al., 2008). Therefore, multisensory interactions increase selectively for stimuli presented at the sector of space where the tool is used (Farnè, Bonifazi, et al., 2005), and not toward tool parts that do not directly support the interactions.

Evidence of PPS assessed in healthy subjects proved multisensory interactions between stimuli on the body and external stimuli presented in the correspondent functional part of the tool (Brozzoli et al., 2009; Canzoneri et al., 2013; Maravita et al., 2001). Altogether these results were in support of the interpretation that PPS was extended toward space where the individual interacted with the object (Làdavas & Serino, 2008). Serino, Canzoneri, et al. (2015) propose a possible mechanism to explain the tool-use meditated PPS extension. According to the authors, this PPS modulation has to be attributed to a mechanism of multimodal integration, between the visual/auditory stimulus and the temporally synchronized tactile information derived by the tool manipulation (Serino, Canzoneri, et al., 2015). With tool-use, a new multimodal pattern is produced. Somatosensory inputs at the hand and visual/auditory inputs that fall in the tool action space (that may also coincide with space far from the subject) are now likely to be jointly processed, as they were belonging to the same event. In this condition, PPS is expanded via tool-use. With this interpretation, it derives that tool-use per se might not be necessary to extend PPS, but it may be sufficient to reproduce a pattern of stimulation which is synchronous and multimodal. In support of this claim is the evidence by Bassolino and colleagues (2010), which demonstrated that PPS can be extended not only by the use of a solid tool but also without being physically connected with the far space, in case of mouse cursor manipulation.

2.2.1.2 Peripersonal space does not coincide with the reaching space

Tool-use expands PPS, and, enlarges the reaching space (ARS; arms' reaching space), that is the space, reachable by the subject by extending the arm without leaning (Coello et al., 2008). ARS is normally assessed by reaching tasks, in which subjects are asked to explicitly judge the reachability of a certain distant target or to perform the actual reachability movement (Coello et al., 2008). Although the construct of ARS unarguably captures a distinction between far/unreachable and near/reachable spaces, it does dissociate from the multisensory PPS (Bufacchi & Iannetti, 2018; Cléry, Guipponi, Wardak, et al., 2015; Serino, 2019). This dissociation is present both at the neuroanatomical level and at the level of the behavioural performance. ARS and PPS seem not to coincide at the neural level. Namely, when multisensory stimuli are delivered within ARS, do activate PPS areas, but only if presented close to the hand (Brozzoli et al., 2011; Graziano et al., 1994). ARS is coded by a frontoparietal network, that includes area F2 and area MIP, in the medial part of the intraparietal sulcus (Bhattacharyya et al., 2009; Colby & Goldberg, 1999; Colby, 1998). These areas are connected with the “reaching areas” of the dorsal visual stream, V6 and V6a (Pitzalis et al., 2015). This network is distinguished from the F4-VIP network in which multisensory PPS neurons have been described, and more functionally linked with defence and obstacle avoidance behaviour.

In a series of five experiments, Zanini and colleagues (2020) provided a behavioural demonstration that PPS does not coincide with ARS. Results were showing that PPS is smaller than ARS and that the PPS multisensory facilitation depends upon the hand position, while ARS does not. They found that the proximity of the visual stimulus to the hand, and not their reachability, predicts the increase in multisensory facilitation. Visual boosting of touch is hand-centred and follows the changes in hand position.

2.2.2 Non-motor-driven reorganization of Peripersonal Space

A special case of interaction with stimuli that are in the far space but are coded as they were in the near space, is constituted by mirrors and shadows of the body. For instance, a distant mirror can create the condition in which stimuli located near the body are reflected and perceived far from the body. In monkeys, Iriki and colleagues (Iriki et al., 1996), trained the animals in retrieving objects by viewing their hand projected in a video monitor. Bimodal neurons, normally responding to stimuli delivered on monkey’s real hand, were activated when visual were stimuli presented near to the virtual image of the hand. In humans, Maravita, Spence, Clarke, Husain, and Driver (2000) observed that a patient, who suffered from cross-modal extinction, failed to perceive tactile stimuli at the hand when simultaneously he saw visual stimuli through a mirror. In this condition, PPS is extended toward the far locations which represent the near relevant area around the body. This modification appeared to be abrupt and does not require action mediation. A similar case is represented by body shadows. Pavani and Castiello (2004), by adopting a cross-modal congruency task, demonstrated that subjects' tactile discrimination of stimuli at the hand, was affected by the presentation of stimuli when presented far from the participant's hand, but near the shadow projected by the hand. This body shadow, which constitutes a representation of the space near the body, has to be spatiotemporally synchronized with the movement of the real hand, as well as perfectly mimicking its shape.

2.2.3 Space of cooperation: effect of joint actions and presence of others on Peripersonal Space

PPS for goal-directed actions can be affected by the presence of another agent, with whom it would be likely to interact. Factors that go from joint actions to higher-level social manipulations produce effects that are targeted as social modulations of PPS (Heed et al., 2010; Pellencin et al., 2018; Teneggi et al., 2013; Teramoto, 2018). Converging electrophysiological data, in monkeys, and neuroimaging data, in humans, are showing that PPS neurons fire not only in response to the visuotactile stimulation in their PPS but are also reactive to stimuli in the PPS of others. For instance, Ishida and colleagues (2009), recorded bimodal VIP neurons in the macaque which were responding to visual stimuli presented close to the animal's hand but also when applied to the body of the experimenter facing the animal. In humans, Teramoto and colleagues (2018), showed that the detection of a tactile stimulus at the hand is faster when the visual stimulus is close to the stimulated hand, but also when close to the hand of another person facing the participant. Consistently, Heed and colleagues (2010), demonstrated that the observation of others' sensory-motor experience is remapped onto the subject's representation. In their visuotactile interaction task, participants had to discriminate the position of two tactile stimuli, while ignoring visual distractors. The task could be performed with a partner which responded instead to the visual distracters. Only if the partner was in the participant’s PPS, the joint execution of the task reduced the interference of the visual stimuli onto the tactile discrimination task, compared to when the participant performed the task alone. At the neural level, ventral premotor cortex seems differentially activated, not only according to the distance of an object from the participant’s hand but also to another person’s hand (Brozzoli et al., 2013). Thus, the brain seems to represent also the PPS around other people, by remapping multisensory information around the body of the others into one’s PPS. This remapping ability strongly varies as a function of the similarity between the individual and the other. Maister and colleagues (2015), showed that after synchronous visuotactile stimulation, inducing enfacement illusion (Tajadura-jiménez et al., 2013), auditory stimuli presented close to the other person’s body and close to the subject’s body, did similarly affect tactile processing on the subject’s body. At a difference with Maister and colleagues (2015), in which shared sensory experiences elicited a remapping of the other’s PPS, Teneggi, Canzoneri, di Pellegrino and Serino (2013), showed an expansion of PPS only by implying the mere presence of other individuals. Importantly, this effect was achieved only through positive cooperative interaction with the other, rather than an unfair uncooperative one. Lastly, Pellencin and colleagues (2018) showed that when subjects performed a visuotactile interaction task in the social context of someone else standing in front of them, PPS was expanded, that is that subjects were faster in processing tactile stimuli on their body when a visual stimulus occurred close to the other’s body. This effect was found only when subjects faced a moral other, but not when immoral. The manipulation was based on a mere social impression that did not require any effective interaction. The stressed PPS functionality of detecting potential physical interactions, between one’s own body and external stimuli, is relevant to construct a space representation, also within a possible cooperative context.

2.3. Peripersonal Space for the purpose of defence

PPS that subserves also the function of bodily protection was defined by Graziano and Cooke (2006) as a “margin of safety”. It acts as an anticipatory sensory-motor interface, necessary for the early detection of potential threats for the integrity of the body, and to drive defensive reactions to them. In monkeys, the electrical micro-stimulation of PPS regions induces a behavioural defence and avoidance repertoire of the entire defensive movement (Cooke & Graziano, 2004; Graziano & Cooke, 2006). These modulations of PPS are categorically different from the motor-driven modulation described in the case of tool use, that requires a repeated exposure or training but acts online as a function of the current stimulation. Defensive PPS modulations are expected to be abrupt and involuntary, to fit the unpredictable environment. Its protective function mainly requires the rapid detection of what can be considered a threat. Notably, the dynamics of the defensive PPS would depend upon many different factors, from the low-level to the high-level features of the stimulus, such as its spatiotemporal features and its affective saliency. Also, defensive PPS dynamics would be modulated by the subjects' idiosyncrasies in the sensitivity to threat, for example in the case of anxiety traits. This capability to reshape dynamically to predict online possible collision with stimuli, to prepare a potential motor response, is essential to sustain a protective function for the body.

2.3.1 Stimulus driven reorganization of Peripersonal Space: low-level factors

According to Bufacchi and Iannetti (2018), PPS is functionally defined as a series of graded receptive fields which reflect the relevance of potential actions with the purpose of creating or avoiding the object's contact with the body. It is not an in-or-out space and cannot be solely defined by the metrical proximity with the body. This multisensory system, adapted to the detection and reaction to events with a possible collision with the body, is expected to be sensitive also to other features of the environment. This fine-tuning to the dynamics of the environment constitutes one of the most important features to sustain the function of bodily protection. Relevant parameters are the movement direction of the stimulus and its travelling speed.

Concerning the direction, Colby, Duhamel and Goldberg (1993) reported that the most of the monkey's VIP neurons were found to fire when a stimulus moves in a preferred direction with respect to the animal (straight toward or from above to the eyes of the animal), showing similar response properties of the cells described in the visual MT (middle temporal area). Also, some neurons were shown to prefer receding stimuli (Duhamel et al., 1998).

Many PPS neurons were also found to be selective for the speed of travelling. Neurons in VIP prefer higher speeds (Colby et al., 1993), at a difference with neurons found in MT which are sensitive to a wider range of different speeds, including slower speeds. Speed sensitive neurons were also found in the monkey’s inferior premotor cortex (area F4) by Fogassi and colleagues (1996). In particular, the RFs of most of these neurons were found to increase in depth as a function of the speed of the looming stimulus. The effect of speed on PPS was also observed at the behavioural level in humans by Noel, Blanke, Magosso et al. (2018), which demonstrated that the speed of approaching sounds significantly modulated the size of PPS around the face and the trunk. In this study, healthy subjects performed a tactile detection task (at the face or the trunk), while ignoring task-irrelevant looming sounds that could vary in speed of travelling (slow 25 cm/s; fast 75 cm/s). PPS was defined as the central point of a fitted linear function (Serino, Noel, et al., 2015); for the face, it was approximately at 52 cm when the looming sound was set at 25 cm/s, but when the speed was set at 75 cm/s (the triple of the slow condition), the boundary of the peri-face was recorded at around 77 cm. Similar results were found for the trunk which showed also a shift in the central point, from approximately 83 cm to 103 cm at the highest speed.

2.3.2 Stimulus driven reorganization of Peripersonal Space: the salience of the stimulus

Other than the low-level spatiotemporal features of the stimulus, also the semantically relevant content is modulating PPS. The affective salience of a stimulus is defined by the specific high-level features which match the motivational importance of approaching pleasure or avoiding pain. The effect of affective salient stimuli on visual attention is already well known. Many studies have demonstrated that attention allocation is prioritized by affective salient stimuli compared with neutral, even when task-irrelevant (Astudillo et al., 2018; Calvo & Nummenmaa, 2008; Knight et al., 2007). The motivational relevance of an object in PPS is determined both by the object per se and its spatiotemporal dynamics (i.e., whether it is close or far, looming or receding, fast or slow).

Although there are quite consistent and convergent data on the low properties of PPS, how the affective salience intersects the computation of the safety margins around the body is still quite unexplored. Those mechanisms are expected to involve a long-range top-down synchronization mechanism (Cléry, Guipponi, Wardak, et al., 2015), involving likely the orbitofrontal cortex, the colliculus and the amygdala (Tamietto & Gelder, 2010), that would weigh the multimodal parieto-premotor PPS computation (Cléry, Guipponi, Wardak, et al., 2015; Talsma, 2015). Attention to space might be a determinant function in support of the dynamic non-motor modulation of PPS.

The highly dynamic context-dependent nature of space representation has been already demonstrated in the visual modality. In particular, in the monkey’s parietal cortex (LIP area; Hamed et al., 2002) and the visual MT extrastriate (Womelsdorf et al., 2006), visual RFs of neurons appeared to dynamically change as a function of attention. In humans, attention modulated the perceived size of an object (Anton-Erxleben et al., 2007) and affected depth representation (Guan & Qian, 2020). Cléry and colleagues (Cléry, Guipponi, Wardak, et al., 2015) proposed that similar mechanisms might also underlie stimulus-driven changes of PPS, through a differential weighted integration of the context-dependent incoming information (visual, tactile, proprioceptive, auditory stimuli).

Vagnoni and colleagues (2012) directly tested whether the perception of a looming stimulus was modulated by its affective salience. In their task, subjects were exposed to looming images that could depict either threatening (snakes and spiders) or non-threatening animals (butterflies and rabbits). After the image disappeared, they were asked to judge the time in which the stimulus would have collided with the subject’s body. Results were showing that time-to-collision was underestimated for threatening compared to non-threatening stimuli. Such an effect would have the adaptive effect of inducing faster reactions to threats on a collision course with the observer. Moreover, this effect was higher, the more the stimuli were judged as threatening. The effect of the stimulus salience was also studied in multi-modal tasks, implying tactile detection (de Haan et al., 2016; Ferri et al., 2015; Spaccasassi et al., 2019; Taffou & Viaud-Delmon, 2014). Typically, those studies investigate how multimodal facilitation in the detection and response to the tactile stimuli on the body is modulated by the distance of a looming auditory or visual stimulus (e.g. objects, animals, sounds). This effect of distance in tactile responses is examined in interaction with the affective saliency of that looming stimulus. Typically, the dynamics of PPS can be described by adapting two non-exclusive approaches.

The first describes the modulation of PPS in terms of an expansion/restriction, by looking at the critical point in space (see Canzoneri et al., 2012 for the methodology) were looming stimuli more strongly facilitate tactile responses. An example derives from Taffou & Viaud-Delmon (2014), who demonstrated that PPS was extended in the presence of a threatening (sound of a growling dog) with respect to a more neutral stimulus (sound of sheep bleating). Importantly, this effect was found specifically in cynophobic participants. The feared element elicited an anticipated reaction, in the sense that the sound of barking dogs influenced tactile detection earlier in time during the looming than neutral sounds.

According to the second approach, PPS can be also described by observing the graduality over space of the tactile responses facilitation, exerted by the visual/auditory stimulus presentation and expected to vary within a certain degree as it approaches (Noel et al., 2016; Salomon et al., 2017). A sharp change in tactile response times over distance would depict a strong effect of the looming stimulus entering the PPS; a less sharp transition, instead, indicates a shallower effect of the proximity (Van der Stoep, Nijboer, et al., 2015). For instance, de Haan and colleagues (2016), demonstrated that when an approaching stimulus is considered as harmful by the subject, responses to tactile stimuli at the hand were more modulated by its distance from the subject, with respect to a non-threatening one. Since threatening stimuli bias visual attention toward their location (Öhman, Flykt, & Esteves, 2001; Vuilleumier & Schwartz, 2001), the location of that stimulus has more relevance in determining the strength of the visuotactile integration. Thus, the closer the threatening stimulus is, the faster were the subjects in responding to tactile stimuli; conversely, non-threatening stimuli exerted a shallower effect of the distance in facilitating tactile responses. This distance-dependent facilitation would allow for a more precise prediction of the consequences of the threatening stimulus' contact.

Also, and orthogonally to the saliency factor, studies have manipulated the positive and negative valence of those stimuli (Ferri et al., 2015; Spaccasassi et al., 2019) that corresponds to their perceived pleasantness or unpleasantness (Kensinger et al., 2006). Sounds that elicit a negative emotion (e.g. brown noise) or have a negative connotation (e.g. woman screaming) induce an expansion of PPS, compared to neutral, or positive (Ferri et al., 2015). In this study, the effect of stimulus-driven arousal is likely to play a relevant role, given that seeing or hearing alerting approaching stimuli induces an early preparation to respond to them, in this case, faster response times to tactile stimuli at farther distances. In this respect, Spaccasassi and colleagues (2019) directly controlled for the perceived arousal level of stimuli, while looking at the pure effect of the valence, in modulating visuo-tactile interaction in space. Interestingly, in a second experiment, they studied the effect, on visuo-tactile interaction in PPS of the learned valence, that was acquired during an instrumental conditioning task. They found that approaching valenced stimuli were more facilitating tactile responses at farther distances from the body; importantly this effect was found for both negative and positive valenced stimuli and for both intrinsic and learned valence, with respect to neutral stimuli.

Moreover, personality factors or internal states of the individual, appear to influence PPS (see for a review, Cléry & Hamed, 2018). Idiosyncrasies in the level of anxiety and fear of a specific stimulus were shown to increase the defensive response magnitude (Spaccasassi & Maravita, 2020; Sambo & Iannetti, 2015) and the PPS extension (de Vignemont & Iannetti, 2015). For instance, anxiety for closed spaces appears to specifically enlarge the representation of near space, when measured with a line bisection task (Lourenco et al., 2011). As seen before, approaching threatening visual stimuli, such as spiders in de Haan et al. (2016), or auditory, as the looming sound of a growling dog in Taffou & Viaud-Delmon (2014), affected PPS representation, at a difference with emotionally neutral stimuli. Importantly, this effect was found only in participants that showed phobias for the specific stimulus presented, arachnophobia and cynophobia, respectively.

Taken together these studies are showing that arousing stimuli, particularly when potentially harmful, modulate PPS, which subserves the function of protecting the body against threats (de Vignemont & Iannetti, 2015; Graziano & Cooke, 2006; Sambo & Iannetti, 2013). Anxious individuals, which have an increased tendency to perceive a situation as alarming, show, compared to non-anxious individuals, an enlarged PPS, as an increased protection around the body.

2.3.3 Peripersonal Space does not coincide with Interpersonal Space

In social psychology, the space around the body is functionally defined as the area that individuals maintain around themselves, defined interpersonal space (InterPS). An intrusion of someone’s InterPS is expected to provoke discomfort or even a reaction of withdrawal (Hayduk, 1983), together with an experience of threat for the subject’s psychological or physical integrity. InterPS is commonly assessed by a stop distance task, in which participants are asked to stop an approaching person at a distance they judge as no more comfortable (Iachini et al., 2014). InterPS was shown to change as a function of different contextual and individual factors; for example, anxiety-inducing and stressful situations, induce individuals to stay further away from each other (Dosey & Meisels, 1969; Iachini et al., 2015). PPS and InterPS are two conceptualizations of space that have been sometimes treated as overlapping (e.g. de Vignemont & Iannetti, 2015; Iachini et al., 2014; Kennedy et al., 2009). Nonetheless, the two spaces might not be fully functionally coincident (Patané et al., 2017, 2016).

Pellencin and colleagues (2018) directly tested whether the measures of multisensory PPS and InterPS under the same experimental manipulation, that corresponded to the condition of facing a moral versus an immoral other. As seen previously, when facing a moral other, PPS was expanded. Congruently, the moral other was perceived as less intrusive when approaching: IterPS was reduced in the moral condition. This result was consistent with previous studies manipulating morality (Iachini et al., 2015). PPS and interpersonal distance were both similarly affected by social manipulation and maybe both reflect a similar social outcome: the behavioural intention to interact. However, the interpersonal distance, measured as a comfort zone, and the PPS central point did not correlate with each other. The two spaces may reflect, in fact, two different mechanisms. The InterPS does more reflect a desire of vicinity or repulsion of the interaction, with an affective connotation which relies on a more social affiliative motivational system. Conversely, social PPS might reflect the motor component preparation of joint interaction with the other person. Nonetheless, the two mechanisms may partially overlap (Serino, 2019). PPS system in social context would be relevant to detect the physical interaction between one’s and the other’s body, seminal for action preparation and defence; this, in turn, would be relevant to regulate the InterPS as the processing of the social space between individuals. This suggestion (Serino, 2019) has still to be fully investigated, although there are already data on a possible dissociation between the InterPS and the reaching space (Patané et al., 2017).

2.4. Conclusions

In this chapter, the main contributions, to the factors modulating PPS, are reviewed. The discussion is organized around the functional distinction between the PPS for goal-directed actions and the defensive PPS according to the dual model of PPS proposed by de Vignemont and Iannetti (de Vignemont & Iannetti, 2015). The modulation of PPS for goal-directed action might require the involvement of plastic motor mechanisms. PPS modulation was observed after training or repeated exposure to a given sensory-motor context (i.e. tool use, limb immobilization). Also, PPS for a goal-directed action may be capable of instantaneous non-motor mediated adjustments such as in cases in which the body was reflected in a mirror or projected in a shadow. Another situation in which PPS for goal-directed actions is modulated is when the subject acts together or in presence of another individual. PPS that subserves the function of bodily protection acts as an anticipatory sensory-motor interface, necessary for the early detection of potential threats for the integrity of the body, and to drive defensive reactions to them. Defensive PPS modulations are expected to be abrupt and involuntary, to fit the unpredictable environment. The dynamics of the defensive PPS would depend upon many different factors, from the low-level (i.e., proximity, speed, direction of looming) to the high-level features of the stimulus (i.e., affective saliency and valence). Also, defensive PPS dynamics would be modulated by the subjects' specific sensitivity to threat, for example in the case of anxiety traits. Multisensory PPS was also distinguished from the constructs of arm reaching space (ARS) and interpersonal space (InterPS), by considering the different cognitive functions that they may subserve, as well as their dissociation at the neural and at the behavioural level.

CHAPTER 3. Facial emotional expressions in the peripersonal space

3.1. Introduction

Space representation is the fundamental function that frames perception and grounds any interactions with the environment. As described in the previous chapters, PPS corresponds to the representation of the space around the body computed around specific body parts, by the integration of the visual or auditory processing of a stimulus in the environment, with the somatosensory processing of tactile stimuli on the body. PPS multisensory integration is ruled by spatiotemporal principles (Murray & Wallace, 2011; Noel et al., 2016) which may be weighted by the preferential selection of attention.

Attention is the function that continuously and dynamically selects, from all the available information, a particular stimulus, such as a location, a feature or an object, which gains dedicated processing resources (Talsma et al., 2010). *Spatial attention* is the mechanism of attentional selection based on spatial location, which can affect not only the processing of information from a single modality but also the process of multimodal interactions (Macaluso, 2012; Talsma, 2015; Tang et al., 2016; Van der Stoep, Spence, et al., 2015). Multisensory performance improvements are affected by spatial attention when stimuli are presented in locations attended by the subject, compared to unattended (Tang et al., 2016). The process that describes how attentional focus is shifted from one location, feature, object, to another, is defined as attentional orienting. This process might be mainly driven by both bottom-up, stimulus-driven, or top-down, goal-driven, factors. A stimulus can be preferentially processed because it is novel, unexpected, or because its physical features deviate significantly from the other competing stimuli or features (exogenous attention). On the other side, a weak stimulus may be preferentially processed because it meets the current goal and expectation of the subject (endogenous attention). A complex network of frontoparietal areas (Chica et al., 2014) is involved in the endogenous and exogenous shift of spatial attention. Endogenous attention, involved in the voluntary orienting, is generally associated with a dorsal frontoparietal area, including, bilaterally, the superior parietal sulcus, the intraparietal sulcus and the region of the frontal eye fields of the prefrontal cortex. Exogenous attention, on the other hand, would involve the ventral areas of this frontoparietal network with lateralization on the right hemisphere. They include the right temporoparietal junction, the right ventral frontal cortex, the middle and inferior frontal gyrus (Fox et al., 2006; Tang et al., 2016). This network is particularly activated during attentional shifts when attention is captured away from its locus by the unexpected appearance of a stimulus. Exogenous attention appears of seminal importance as a "circuit breaker" (Corbetta & Shulman, 2002), which flexibly interrupts the endogenous monitoring of a certain portion of space when an unexpected salient event requires the reorienting of attention.

Emotional signals provide another factor that biases attentional orienting and preferential processing of information (emotional attention; Pourtois et al., 2013; Vuilleumier et al., 2001). The emotional and motivational value of the stimulus is not only determined by its specific physical features but also, by the influence of internal factors or some previous knowledge on perceptual processing (Pourtois et al., 2013). This attentional function was found to involve, predominantly, the amygdala, as a generator of saliency signal, and its strong connections with sensory areas, as well as the widely interconnected prefrontal areas (Palermo & Rhodes, 2007; Pourtois et al., 2013).

Exogenous, endogenous and emotional factors of attentional selectivity (Pourtois et al., 2013), in interplay with the PPS multisensory integration, are possibly at the base of the dynamic reshaping of the defensive PPS, driven by low-level features (i.e., proximity, speed or direction of movement, size) but also by the affective salience of the stimulus (i.e., threatening stimulus). Emotional facial expressions are salient stimuli that affect the orienting of emotional attention (Vuilleumier, 2005). A still unaddressed question is whether emotional facial expressions may also affect PPS dynamics. Moreover, since the different emotional expressions differ in valence, arousal level, and their motivational and communicative components, a second question would be whether and how the different emotional expressions would differentially modulate PPS.

In this chapter, it is first described how emotional facial expressions can be considered salient stimuli able to potentially influence the orienting of emotional attention, with a reference to the possible neural correlates that may underlie this process. Moreover, a paragraph is dedicated to the attentional effects of fearful faces, which represent an interesting case, as they signal a possible upcoming threat, but do not constitute the threat. In the second part of the chapter, the research questions, that base the studies described in the present thesis, are formulated.

3.2. Emotional faces as salient stimuli

3.2.1 Salience, valence and arousal as features of an affective stimulus

Salience is defined as the quality by which an aspect of the environment stands out relative to its surrounding. A salient stimulus is more likely capturing attention and it is more efficiently individuated (Talsma et al., 2010); both stimulus-driven and cognitive/affective factors determine stimulus salience (Niu et al., 2012). Stimulus driven factors are related to low-level feature discontinuities that typically arise from the contrast between the object and the context (i.e. a red dot among green dots; a flickering stimulus on a static background).

Affective salience also influences the reflexive allocation of attention (Knight et al., 2007). The attentional bias for affectively salient stimuli determines a preferential perception and enhanced memory when attentional resources are limited, as well as greater likelihood to attract attention when viewed in complex scenes (Niu et al., 2012; de Cesarei and Codispoti, 2008). The affective salience is determined by the valence and the arousal components. The valence refers to the perceived hedonistic value of the stimulus, and it is expressed by a continuum that goes from pleasant to unpleasant. Arousal instead refers to the intensity of the stimulus in provoking a state of restlessness, excitement and agitation in the subject; it is expressed by a continuum that varies from calming to exciting.

3.2.2 Emotional facial expressions are salient stimuli

Particularly salient stimuli in our environment are the emotional facial expressions (Öhman et al., 2001; Vuilleumier, 2005). Faces provide diverse information about others, including identity and several emotional and motivational aspects. Emotional faces have shown to influence the orienting of emotional attention, leading to a preferential perception and enhanced processing of the emotional face (Vuilleumier & Pourtois, 2007). Emotional facial expressions can be judged as positive (i.e., expressions of joy) or negative valenced (i.e., expressions of fear or anger), more or less arousing (i.e, a neutral or a very angry face). Importantly, other than these two dimensions, emotional faces are intrinsically identified by their emotional and motivational value; they may be informative about the state of the social or physical environment; for instance, they may communicate the intentions of the other or the presence of a threat in the surrounding. The informative value of the emotional expressions can be increased and interpreted eventually with additional information, such as gaze cueing (Carlson, 2016) or contextual factors, such as a threatening environment (Wieser & Keil, 2014). Due to this intrinsic emotional and motivational value, emotional facial expressions are of particular interest, among other salient stimuli, for two reasons. First, two emotional facial expressions, equally valenced and arousing, might prompt differential effects on the motivational adaptive behaviour of the observer (see the case of fearful and angry faces below). Second, the effect on attention of emotional expressions can be decomposed in two functional steps: first, as salient stimuli, emotional faces are expected to influence the orientation of emotional attention toward the emotional face; second, once processed, emotional faces may continuously stay on the face or on the face location, or rather be diverted to the surrounding, including surrounding locations; in this case, attention may be diffused or shifted in avoidance of the face.

3.2.2.1 Emotional faces processing and emotional attention: the role of the amygdala

The capturing of attention by emotionally salient stimuli (Öhman, 2005) is essential for flexible and adaptive behaviour. This attentional capability requires the integration of spatial information, with information about the emotional face (Yamaguchi & Onoda, 2012). Together with other two main regions, the inferior frontal gyrus (IFG) and the superior parietal sulcus (STS), the amygdala (AMG) (Aggleton, 1992; Fusar-poli, Placentino, Carletti et al., 2009; Hariri et al., 2002; LeDoux, 2014; Mende-siedlecki et al., 2012; Palermo & Rhodes, 2007; Pessoa & Adolphs, 2010; Sabatinelli et al., 2011) is one of the most important structures involved in the processing of emotional facial expressions. These regions would be involved in understanding the other's actions and in the extraction of the invariant aspects of the emotional information (Uono et al., 2017; Carvajal et al., 2013). Damage or interruption of these regions impaired the recognition of facial expression (Adolphs et al., 1999; Dal Monte et al., 2013). In particular, the STS, connected with the AMG (Pitcher et al., 2017), appeared to be a key region sensitive to dynamic social stimuli, including biological motion, actions, gaze and vocalizations (Basil et al., 2013; Nummenmaa & Calder, 2009), as well as dynamic facial features of emotional expressions (Engell & Haxby, 2007).

Importantly, through direct or indirect connections to somatosensory, parietal and frontal areas (LeDoux, 2014; Phan et al., 2002; Phelps, 2006; Vuilleumier et al., 2001), the AMG seems implicated in the orienting of attention that leads to enhanced perceptual processing of the emotional stimuli (Pourtois et al., 2013; Williams et al., 2006). Connections, via the AMG, to visual areas, such as the fusiform face area, would be implicated in the perceptual enhancement of emotional facial expressions (Phan et al., 2002; Pourtois et al., 2013; Vuilleumier et al., 2001).

Moreover, emotional biases that influence perception and attention would also be exerted by indirect amygdala's projections. AMG projects to basal nuclei in the forebrain, from which cholinergic pathways reach the frontal, parietal and sensory cortices. Cholinergic pathways have been found to strongly modulate attention which enhances, and sustains in time, the neuronal discharge (Parikh & Sarter, 2008); also, this pathway is implicated in the disengage of the current attentional focus to promote the efficient shift towards emotional information (Vuilleumier, 2005). In particular, the orbitofrontal cortex and the posterior parietal cortex seem involved in the spatial orienting toward threat-related stimuli. Lastly, the AMG seems to be indirectly implicated in the control of the emotional attention through other neurotransmitter pathways implicated in the arousal response (via locus coeruleus and noradrenaline; Pourtois et al., 2013).

3.2.3 The special (spatial) case of fearful faces on emotional attention

Among the other emotional expressions, fearful faces represent a special case of salient stimuli. Together with angry faces, fearful faces are negative valenced and normally judged as very arousing. Both emotional expressions demand immediate attention from the observer to prepare a fight or flight reaction (Vuilleumier, 2005). At difference with angry faces, fearful faces are not intrinsically threatening, but they signal a potential upcoming danger in the environment, without specifying its nature or location (Stoyanova et al., 2007; Valk et al., 2015). Fearful faces were found to enhance basic perceptual processes such as contrast and orientation sensitivity and spatial resolution (Bocanegra & Zeelenberg, 2009, 2011; Phelps, 2006; Phelps et al., 2005). As a consequence, a fearful face may act as a cue that prompts heightened perceptual sensitivity to threat in the environment. Fear cues may serve to engage scanning of the environment prompting a shift of attention away from the fearful face, to promote search of the threat (Stoyanova et al., 2007). On the other side, angry faces can represent an immediate, imminent threat, which may involve an urgent defensive action (Grillon & Charney, 2011; Sarlo & Munafò, 2010; Valk et al., 2015). The observation of angry body expressions was found to activate premotor cortex more than fearful expressions (Pichon et al., 2009). Fearful faces require exploration before action, while angry faces ask for immediate action. This difference in the communicative component of angry and fearful faces might be reflected also in a specific deployment of attention (Juncai et al., 2017). Fearful faces, but not angry faces, would diffuse attention to peripheral targets in an attentional blink paradigm (Taylor & Whalen, 2014), even when those objects are task-irrelevant (Berggren & Derakshan, 2013) or non-threatening (Becker, 2009). Studies assessing the attentional bias of fearful faces with the dot-probe task (MacLeod et al., 1986) revealed that fearful faces appear to strongly draw attention to the side of the emotional stimulus, facilitating the detection of a subsequent target (Carlson & Mujica-Parodi, 2015; Carlson & Reinke, 2008, 2010), similarly to other visual threats (Fox et al., 2002; Koster et al., 2004; MacLeod et al., 1986). Interestingly, Torrence and colleagues (2017) found that the attentional bias in the case of fearful faces was more consistent at shorter intervals between the appearance of the face and the appearance of the dot (SOA <300 ms). This result would suggest that the capture of attention by fearful facial expressions is quick but short-lived (see also Holmes et al., 2005). The rapid holding of attention may be supporting the redirection of attention from the face to other locations, to identify the location of the threat. In the same study, Torrence and colleagues (2017) showed that joyful faces, which do not signal a presence of a threat but a positive cooperative intention, were slower in capturing attention compared with fearful faces, but they attracted subject's attention also at longer intervals between the appearance of the face and the appearance of the dot (Torrence et al., 2017).

All these evidence would support the hypothesis that fearful faces, compared with other emotional expressions, would elicit enhanced environmental monitoring of the peripheral space (Taylor & Whalen, 2014; Wieser & Keil, 2014), seminal to support the perceptual processing of upcoming threats that could be everywhere. Threat evaluation would produce increased arousal which would lead to a generalized increase in vigilance and attention (Phelps et al., 2005; Whalen, 1998).

3.3. Emotional faces in space: knowns and unknowns

3.3.1 Emotional faces in the defensive Peripersonal Space

Spatial and selective types of attention are central functions, seminal for efficient detection and localization of danger's signals in the environment (Wieser & Keil, 2020). Attentional biases elicited by emotional expressions are likely to influence the defensive PPS in the prediction of possible sensory consequences of encountering the threat (i.e. impact prediction; Cléry & Hamed, 2018) and in the support of action preparation. Importantly, in this perspective, emotional faces should not only be conceived as an isolated stimulus, but in the egocentric perspective of the subject: not only the emotional expression would affect PPS, but also its position with respect to the subject's body. Previous studies considered as a factor the position of emotional facial expression with respect to the subject's body (Cartaud et al., 2018; Ruggiero et al., 2017; Vieira et al., 2017) on the comfort distance judgments to assess interpersonal space. Particularly angry expressions, compared with joyful and neutral, were found to increase comfort distance judgments (Cartaud et al., 2018; Ruggiero et al., 2017; Vieira et al., 2017). Anger prompts avoidant behaviours to protect against a potential violation.

3.3.2 Open issues and research questions

It is still unknown how the multisensory PPS would be affected by emotional faces; in particular, whether an approaching human face showing an emotional facial expression, that could be either negative (fearful and angry) or positive (joyful), would differentially modulate PPS representation compared to the same face with a neutral expression. Given the important adaptive function of PPS, it is expected that salient cues, such as emotional faces, would be a factor in differentially modulating PPS, with respect to neutral faces, and whether there is a difference between the different emotions. This research project would aim to assess whether emotional facial expressions affect PPS multisensory dynamics; second, whether the different emotional expressions, that differ in their valence, arousal level and communicative value, may differentially modulate PPS, and which are the mechanisms involved.

In a first study, it will be asked whether looming emotional faces would affect the multisensory facilitation of stimuli at the body. It will be investigated the effect of looming fearful, joyful or angry facial expressions, compared with the effect of a neutral facial expression. A second study will investigate the hypothesis that emotional modulations of PPS are driven by the differential distribution of spatial attention elicited by the emotional faces. Joyful and fearful faces will be compared with neutral faces. Spatial attention is expected to be differentially distributed not only according to the emotion displayed but also depending on the face position with respect to the subject. Specifically, fearful faces, looming in the near space of the subject, are expected to prompt a redistribution of attention from the face to the peripheral space. To check whether this effect would not merely depend on the negative valence or the arousing component of the stimulus, the effect of angry faces on spatial attention in PPS will be also tested. A third and a fourth study would investigate the physiological correlates of this attentional mechanisms, both by looking at the electrophysiological response of the attentional effect on emotional faces when looming toward the subject, but also by asking whether this effect in PPS would be supported by a differential increase of the autonomic response.

3.3.2.1 A multimodal interaction task

In these studies, although with some variations, a well-validated experimental paradigm to assess PPS (Canzoneri et al., 2012; Serino, Noel, et al., 2015) will be adopted. This paradigm has two fundamental features. It is multimodal and it implies dynamic stimuli in space. First, it is multimodal because it studies the interactions between modalities, tactile and visual, whose one of the two is the target to detect (tactile), and the other must be ignored (visual). Subjects are always asked to provide speeded responses to tactile stimuli delivered at the body, to their cheeks, while watching the task-irrelevant visual stimuli, in this case, human emotional faces. Second, visual stimuli are not static, but they are presented as moving in space. They always appear as looming toward the subject, from the distant space, in a far position in-depth, from which they linearly approach, at a constant speed, until they are closer to the subject. PPS is studied as the degree of multisensory facilitation of the responses to tactile stimuli (fastening of response times), as the face approaches the subject.

The facial emotional stimulus has a double function in this paradigm. From one side it is the visual stimulus that moves in space; thus, it is expected, by following the rule of multisensory integration, to facilitate the responses to the tactile stimuli (responses evoked by the face-tactile compound). Second, it determines the emotional condition: the face would display an emotional expression of fear, anger or joy, but also no expression, neutral. The interaction between the factors of emotion and distance of the face from the subject would explain the variance of the responses to the tactile stimuli.

3.4. Conclusions

In this chapter, it is described how emotional faces can be considered salient stimuli possibly modulating the defensive PPS. Highly informative, emotional faces were found to strongly modulate perception and attentional mechanisms. A very interesting case is represented by fearful faces, that signal an environmental threat whose location is unknown. As a consequence, it is expected that an adaptive function of fearful faces would be to enhance the perceptual processing of stimuli in the face surrounding, potentiating the detection of an upcoming possible harmful event. Angry faces, although similarly negative, represent a direct threat asking for immediate action.

Emotional expressions of joy, on the other side, would signal no presence of threats in the environment and possibly an approach bias. All these communicative features of the different emotional faces not only differ in their arousal level or their valence (positive or negative) but also in their motivational and affective value: these factors would have a particular effect on the dynamic reshaping of the defensive PPS. Studies described in this manuscript aim to address the question of whether emotional stimuli affect PPS and to describe which are the possible mechanisms involved.

CHAPTER 4. Dynamics of Peripersonal Space when facing emotional expressions

4.1. Introduction

PPS is the multimodal sensory-motor interface that mediates the interaction between the individual and the environment. The extent of PPS is defined by the location in space where multisensory signals from bodily and external stimuli are integrated, with a gain in responsiveness to multisensory stimuli (multisensory facilitation). PPS extent varies according to both the participants’ action possibilities and the characteristics of the external events, such as the affective salience of a stimulus. Study 1 aims to investigate whether such spatially dependent multisensory integration is modulated by the affective salience of human-like facial expressions.

4.2. Study 1: Dynamics of Peripersonal Space when facing emotional expressions

4.2.1 Introduction

Previous studies have been shown that PPS is a dynamic representation. Social interactions (Heed et al., 2010; Pellencin et al., 2018; Teneggi et al., 2013; Teramoto, 2018) and the perceived valence of external stimuli have been shown to modulate PPS. A growing amount of studies showed that the salience of a stimulus moving in space (i.e. object, animal, sound) has an impact on the PPS sensorimotor mechanism (de Haan et al., 2016; Ferri et al., 2015; Lloyd et al., 2006; Spaccasassi et al., 2019; Taffou & Viaud-Delmon, 2014; Vagnoni et al., 2015). The mechanisms that underlie these overt dynamic changes in PPS are relying on the interaction between bottom-up multimodal processes (multisensory integration between tactile and visual/auditory stimuli) and top-down processes, involving attention (Talsma, 2015). Particularly salient stimuli in our environment are the emotional facial expressions and abundant empirical evidence has converged to indicate that processing of emotional faces can exert strong influences on attentional mechanisms (Pourtois & Vuilleumier, 2006). However, no evidence shows how the perception of another person conveying emotional information affects the multisensory representation of PPS.

This study aims to investigate whether seeing an approaching fearful, angry or joyful face would differentially affect multisensory PPS than a neutral facial expression. To assess PPS, a modified version of a multimodal interaction task is adopted (Pellencin et al., 2018; Serino, Noel, et al., 2015). In this task, participants are asked to respond as quickly as they can to tactile stimuli administered on their body (i.e., on their cheeks), while an external stimulus, visual in this case, appears to approach the participant from distant space. Tactile stimulation is delivered at various delays from the onset of the visual stimulus, so that touch coincides with the perception of the external object at different distances from the participant. Several studies showed that tactile processing is significantly boosted (compared with unimodal tactile processing) when an external stimulus is within a certain distance from the body, and this effect can be used to estimate the extent of the PPS representation (Serino, 2019). In the present task, the neutral external stimulus used in previous studies is substituted with a social stimulus, i.e., an avatar's face approaching the participant in virtual reality. The facial expression of the virtual face is modulated to convey a negative emotion (i.e. fear or anger, in different conditions), a positive emotion (i.e. joy) or an emotionally neutral expression; it is tested whether the space-dependent modulation of responses to the tactile stimulus is affected by the facial expression of the approaching face (i.e. proximity effect). Since a fearful expression is a physiologically more salient cue than neural, joyful and angry expressions, supporting an evolutionary function for survival in asserting the presence of an environmental threat, which is not the face *per se*, it can be predicted that responses to tactile stimuli should not be influenced by the position of a fearful face, as it approaches the body. Instead, when approaching neutral, joyful or angry faces are presented, faster responses to tactile stimulation in near than in far space are expected, with no differences between the different facial expressions, since attention is expected to stay on the face as it approaches.

4.2.2 Methods

4.2.2.1 Participants

Sixty healthy participants (30 females, 30 males; mean age 26±5) were recruited for this study. None of the participants reported any history of neurological or psychiatric disorders, and all were naive to the purpose of the study. The experiment was conducted in accordance with the principles of the 1964 Declaration of Helsinki and approved by the ethical committee “Commission cantonale d'éthique de la recherche sur l'être humain” in Vaud, Switzerland (Project-ID 2017-01588). The sample size was determined via a power analysis conducted in G*Power 3.1 software (Faul et al., 2007); the affective modulation of PPS was expected to have a medium to large effect size (Pellencin et al., 2018); the alpha was set at 0.05 and the power was set at 0.95. For a repeated measure within-factor analysis of variance (ANOVA) with no covariates, it was determined that a sample size of twenty subjects per group would be enough to detect the effect.

4.2.2.2 Task and experimental procedure

The experiment was implemented in ExpyVR software (available online at http://lnco.epfl.ch/ framework for designing and running experiments in virtual reality) and ran on a Windows-based PC (Dell XPS 8930, Dell, Round Rock, Texas, USA). The tactile stimuli consisted of vibrations delivered bilaterally at the participants' cheeks by a pair of electrodes (Precision MicroDrives shaftless vibration motors, model 312-101, 3V, 60 mA, 150 Hz, 5 g). The motor had a surface area of 113 mm2 and reached maximal rotation speed in 50 ms. This device was activated for 100 ms during tactile stimulation.

Visual stimuli were stereoscopically presented by a head-mounted display (HMD, Oculus Rift SDK, Oculus VR, 100° field of view, 60 Hz), and consisted in avatar faces (see Figure 4.1) expressing fear, joy, anger or neutral. The expression was manipulated ad hoc to render the desired features of facial expression by Poser software (vers. 10; Smith Micro Software, Aliso Viejo, California, USA). Stimuli implemented in the study were chosen through a validation procedure (see Paragraph 4.2.2.3).

To assess the PPS representation, we adopted a modified version of the visuo-tactile task described by Serino and colleagues (Serino, Noel, et al., 2015; Pellencin et al., 2018). In this study, participants sat on a comfortable chair in a quiet room and were exposed to visual stimuli rendered in 3D on a neutral grey background. All the visual objects consisted of looming avatar faces with different facial expressions. Stimuli appeared to approach the participants (see Figure 4.1): on each trial, the virtual face moved in the sagittal plane for 3 s from an initial apparent position of ≈ 220 cm from the participant to a position at ≈ 10 cm from the participant, where the face remained still for 1 s.

The task consisted of 168 trials. In 47% of the trials, the looming face was coupled with a tactile vibration (multimodal trials, visuotactile trials) delivered at five different temporal delays from the appearance of the face (D1=2.5 s; D2= 2 s; D3= 1.5 s; D4=1 s; D5=0.5 s). In this manner, the position of the face at the time of tactile stimulation appeared to be closer and closer to the participant as the delay before tactile stimulation increased (D1 ≈ 45 cm, the nearest point; D2 ≈ 80 cm; D3 ≈ 115 cm; D4 ≈ 150 cm; D5 ≈ 185 cm, the farthest point). In 24% of the trials, there was no virtual face (unimodal, tactile-only trials), and tactile stimulation was delivered alone at one of the temporal delays. Another 24% of the trials were visual-only trials, in which the approaching face was shown, but no tactile stimulation was provided. The remaining 5% were attentional trials, consisting of similar faces marked with a red dot on the forehead that participants were asked to detect by signalling to the experimenter with a vocal response. Condition presentation was randomized. The ITI could vary from 0 to 1 s (±0.2 s). The entire task was split into two sub-blocks of 84 trials. Each sub-block lasted approximately 7 minutes. Between the two, a little pause was introduced to prevent fatigue.

The sixty participants (gender-balanced) were randomly assigned to the three experimental groups: 20 to the Joyful-Faces Group (JF-Group), other 20 to the Fearful-Faces Group (FF-Group), other 20 to the Angry-Faces Group (AF-Group). After signing the consent form, participants seated on a comfortable chair, in a sound-attenuated room. Vibrators were then attached bilaterally on the cheeks with medical tape and virtual reality headset was mounted on the head of the participant. Before the task began, the lenses focus of the Oculus VR was manually adjusted by each participant until a clear vision was reported. During the task, participants made speeded simple responses to the tactile stimulation by pressing a button placed on the table in front of the participant with their right hand. All participants repeated the entire task twice. Firstly, in the Neutral condition, in which only neutral faces were shown, and secondly the Emotion condition, in which only emotional faces were shown joyful, fearful or angry, respectively to the assigned group. The Emotion condition always followed the Neutral condition, to avoid a possible carry-over effect. The experiment never exceeded 60 minutes.

4.2.2.3 Visual stimuli validation

All face stimuli, joyful, fearful, angry and neutral, were created and validated together in a pre-experimental phase of the study. Face stimuli consisted of 3D avatar faces created with ‘Poser 10’ (http://my.smithmicro.com/poser-3d-animation-software.html) that displayed a joyful, fearful, angry or neutral expression.

To select the faces to be included in the experiments, 60 naïve participants (30 females; mean age 29±10 SD) were instructed to rate 20 two-dimensional pictures of emotional faces. Of those, 5 represented versions for each emotional expression, namely joyful, fearful, angry, and neutral. Pictures were presented on a computer screen. For each picture, participants were asked to rate the emotion, the intensity, and the arousal level, on three rating scales presented below the picture. For the emotion rating, participants selected the word that best matched the emotional expression of each face, among seven possible alternatives (i.e., fear, joy, anger, disgust, sadness, surprise, neutral), by placing an ‘‘X’’ on the selected one. For the intensity measurement, participants rated, on a 10-points Likert scale, how strongly that emotion was expressed (0=lowest intensity; 9=highest intensity) by placing an ‘‘X’’ on the selected point of the scale. Lastly, for the arousal measurement, participants were asked to rate the arousal level generated by each stimulus, on a 10-point Likert scale (0=not at all arousing; 9=extremely arousing), by placing an ‘‘X’’ on the selected point of the scale. The order of presentation of the pictures was randomized across participants.

This procedure allowed to select 2 joyful, 2 fearful, 2 angry and 2 neutral facial expressions for which the highest percentage of participants correctly identified the facial emotion (mean hit rate for joyful faces, 95%; fearful faces, 80%; angry faces, 92%; neutral faces, 80%), which also showed the highest perceived intensity and the highest perceived arousing effect. To check whether the mean ratings for intensity and arousal were significantly different between the joyful, fearful, angry, and neutral faces, repeated-measures ANOVA was conducted with mean intensity and mean arousal scores.

The analysis on intensity level showed that ratings were different across emotions [F (3,177) = 140.11; p<0.01; η_p^2=0.70]. Post-hoc Bonferroni corrected showed that all emotions were judged as more intense than the neutral expressions (Neutral faces: m=2.39, sem=0.26; Joyful faces: m=5.62, sem=0.13; Fearful faces: m=7.12, sem=0.18; Angry faces: m=6.66, sem=0.17; all p<0.01); moreover fearful and angry expressions were judged as more intense than the joyful (all p<0.01). Importantly, fearful faces did not differ in the intensity level from the angry faces (p=0.51).

The analysis on arousal level showed that ratings were different across emotions [F (3,177) = 87.76; p<0.01; η_p^2=0.60]. Post-hoc Bonferroni corrected showed that all emotions were judged as more arousing than the neutral expressions (Neutral faces: m=1.53, sem=0.20; Joyful faces: m=3.89, sem=0.28; Fearful faces: m=5.08, sem=0.30; Angry faces: m=4.76, sem=0.28; all p<0.01); moreover fearful and angry expressions were judged as more arousing than the joyful (all p<0.01). Importantly, fearful faces did not differ in the arousing level from the angry faces (p=1).

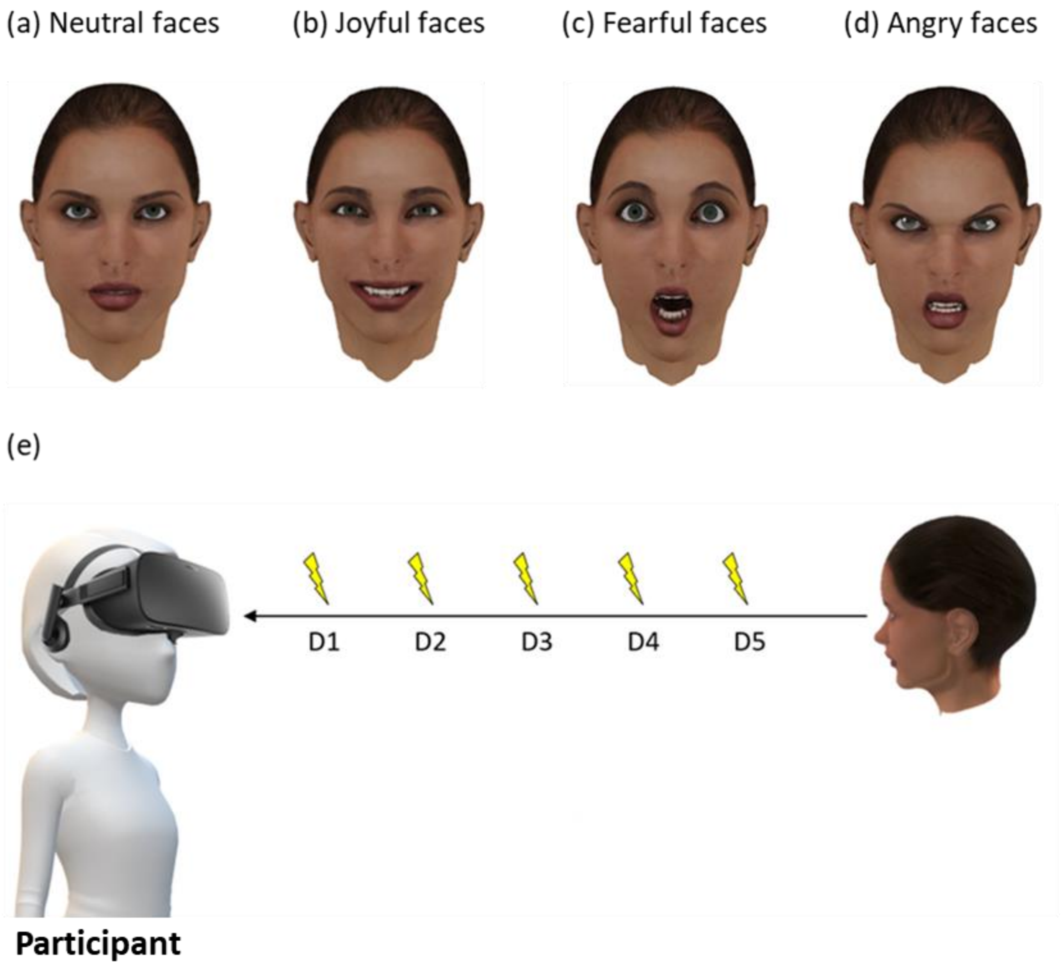


Figure 4.1. Upper panel. Visual Stimuli. Example of a neutral (a), joyful (b), fearful (c) and angry (d) facial expression of the virtual avatar's faces. Lower panel (e). The virtual scenario. At each trial, a face was approaching the participant, from the far to its proximity, covering always the same distance at the same time. Tactile stimulation could be delivered with different delays from the beginning of the trial. Thus, the position of the face at the time of the tactile stimulation resulted at different distances from the participant's body (D1, D2, D3, D4, D5).

4.2.3 Results

To study whether the salience of an emotional expression could influence PPS representation, we analyzed the spatial modulation of visuo-tactile interactions in the presence of a neutral, joyful, fearful or an angry face. Responses to tactile stimuli were also compared across the different distances where the approaching avatar face was perceived at the time of tactile stimulation (D1, D2, D3, D4 and D5). Since participants were extremely accurate at the task, rates of false alarms and omissions were very low, i.e., 0.14 % and 1.45 % respectively. For this reason, the performance was analyzed in terms of reaction times (RTs) only, as in previous versions of the task (e.g., Canzoneri et al., 2012; Serino, Noel, et al., 2015). RTs exceeding more than 2 standard deviations from the mean RT of each block were considered outliers and trimmed from the analyses (1% of trials on average in all conditions). For each subject, mean RTs to tactile targets were calculated for every spatial distance (from D1 to D5) separately for the Neutral and the Emotion conditions.

To provide a general measure of multisensory processing in PPS, in line with previous studies (e.g., Noel, Łukowska et al., 2015; Serino, Noel, et al., 2015), we computed a baseline-corrected RT index: for each subject, the averaged RT in the unimodal condition was subtracted from the mean RT in the multimodal condition at each distance of the visual stimulus at a time of the tactile stimulation. This correction is also used to control for a possible expectation effect due to the different temporal delays of tactile stimulation (Kandula et al., 2017). Baseline-corrected RTs were submitted to repeated measures ANOVAs with Distance (D1; D2; D3; D4; D5) and Condition (Neutral; Emotion) as the within-subjects factors, and Group (JF-Group; FF-Group; AF-Group) as a between-subjects factor. Post-hoc analyses were conducted with Bonferroni corrections and the significance threshold was set at $p < 0.05$. The magnitude of effect size was expressed by partial eta-squared (η_p^2).

The ANOVA (see Figure 4.2) showed an effect of the factors Group [$F(2,57)=4.57$; $p=0.01$; $\eta_p^2=0.14$], Condition [$F(1,57)=18.41$; $p<0.01$; $\eta_p^2=0.24$] and Distance [$F(4,228)=59.25$; $p<0.01$; $\eta_p^2=0.51$]. There was also a significant interaction between Distance and Condition [$F (4,228) =4.80$; $p<0.01$; $\eta_p^2=0.08$]. Since all the effects were further characterized by a significant three-way interaction [$F(8,228)=2.29$; $p=0.02$; $\eta_p^2=0.07$], in order to explore significant effect, we firstly decompose the three-way interaction into separate ANOVAs, one for each group.

Results from the JF-Group showed a main effect of Condition [F(1,19)=5.62; p=0.03; η_p^2=0.23], in which baseline-corrected RTs in the Neutral faces condition were overall faster than in the Joyful faces condition (Neutral: m=-25.13, sem=6.56; Joyful: m=-14.58; sem=5.59). Moreover there was an effect of Distance [F(4,76)=14.47; p<0.01; η_p^2=0.43], in which baseline-corrected RTs in D1 were significantly faster than baseline-corrected RTs in D3, D4 and D5 (all p<0.01), while values in D2 were significantly faster than in D4 and D5 (all p<0.01). All other comparisons were not significant (p>0.12) (D1: m=-36.45, sem=5.12; D2: m=-29.61, sem=4.79; D3: m=-18.17, sem=5.13; D4: m=-9.35, sem=4.75; D5: m=-5.71, sem=3.54). Importantly, no significant interaction was found between Distance and Condition [F(4,76)=0.05; p=0.99; η_p^2<0.01], indicating that responses to tactile stimuli speeded up as the face approached the participant, similarly when the face showed a neutral or joyful expression.

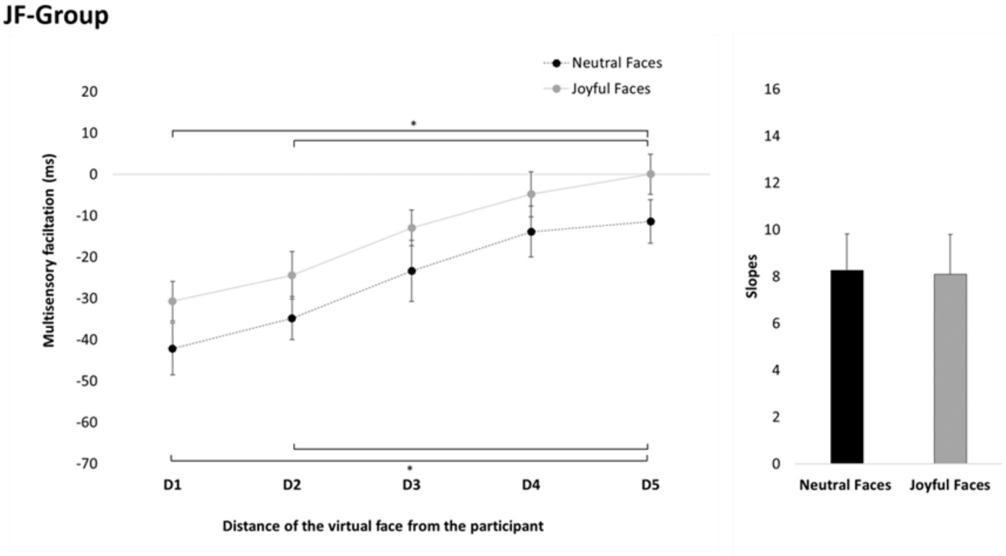
On the contrary, results from the FF-Group showed no effect of Condition [F(1,19)=1.60; p=0.22; η_p^2=0.08], a significant effect of Distance [F(4,76)=14.69; p<0.01; η_p^2=0.44] and, importantly, a significant two-way interaction [F(4,76)=7.30; p<0.01; η_p^2=0.28]. In the Neutral condition, baseline-corrected RTs in D1 were significantly faster than baseline-corrected RTs in D3, D4 and D5 (p<0.01), while values in D2 were significantly faster than in D4 and D5 (all p<0.01) (D1: m=-40.62, sem=5.40; D2: m=-26.53, sem=5.12; D3: m=-16.09, sem=4.93; D4: m=-8.89, sem=4.94; D5: m=1.57, sem=6.44). Conversely, in the Fearful condition, none of the values in the distance conditions were different from the others (all p>0.82) (D1: m=-17.55, sem=5.06; D2: m=-14.71, sem=4.24; D3: m=-16.21, sem=4.73; D4: m=-6.19, sem=6.04; D5: m=-9.01, sem=5.25). Thus, the effect of distance was different according to whether the face presented was neutral or fearful. While in the Neutral condition, responses were gradually facilitated as the face approached the subject, in Fearful faces condition, responses were facilitated at each distance, with no further modulation as the face approached.

Results from the AF-Group showed a main effect of Condition [F(1,19)=23.98; p<0.01; η_p^2=0.56], whereby baseline-corrected RTs in the Neutral Faces condition were overall faster than in the Angry Faces condition (Neutral: m=-37.69, sem=6.81; Angry: m=-24.96; sem=6). Moreover there was an effect of Distance [F(4,76)=34.24; p<0.01; η_p^2=0.64] whereby baseline-corrected RTs in D1 and in D2 were significantly faster than baseline-corrected RTs in D3, D4 and D5 (all p<0.01), while values in D3 were significantly faster than in D5 (p<0.01). All other comparisons were not significant (p>0.2) (D1: m=-52.92, sem=5.68; D2: m=-44.11, sem=5.66; D3: m=-29.52, sem=4.67; D4: m=-19.59, sem=4.39; D5: m=-10.49, sem=4.72). Importantly, no significant interaction was found between Distance and Condition [F(4,76)=1.41; p=0.24; η_p^2<0.07]. Thus, responses to tactile stimuli speeded up as the face approached the participant, independently on whether the face was neutral or angry.

To provide a more synthetic index of the change in PPS representation induced by the nature of emotional faces, baseline-corrected RTs were fitted as a function of the distance of the visual stimulus by means of a linear function. For each subject, in each condition, the slope value was extracted from the parameters that described the linear fits (de Haan et al., 2016). Given that RTs are expected to be faster the closer the approaching face is to the participant, slope values represent a measure of how strongly the tactile processing was influenced by the location of the face (de Haan et al., 2016; Noel et al., 2016; Salomon et al., 2017). Steeper slopes (higher values) indicate stronger multisensory integration effect for faces entering the PPS; conversely, flatter slopes (lower values) indicate a shallower effect of the proximity (Van der Stoep, Nijboer, et al., 2015). Slope values (see Figure 4.2) were submitted to a 2 X 3 mixed ANOVA with Condition (Neutral; Emotion), as a within-subjects factor, and Group (JF-Group; FF-Group; AF-Group), as between-subject factor. Results showed a significant main effects of Group [F(2,57)=3.35; p=0.04; η_p^2=0.11] and Condition [F(1,57)=13.23; p<0.01; η_p^2=0.19], that were further explained by a significant two-way interaction Group X Condition [F(2,57)=5.58; p<0.01; η_p^2=0.16]. While slope values for the JF-Group and the AF-Group did not change when the face was neutral as compared to joyful or angry (all p=1), for the FF-Group slope values were flatter when the faces were fearful compared to when they were neutral (JF-Group: Neutral: m=8.25, sem=1.56; Joyful: m=8.09, sem=1.70; FF-

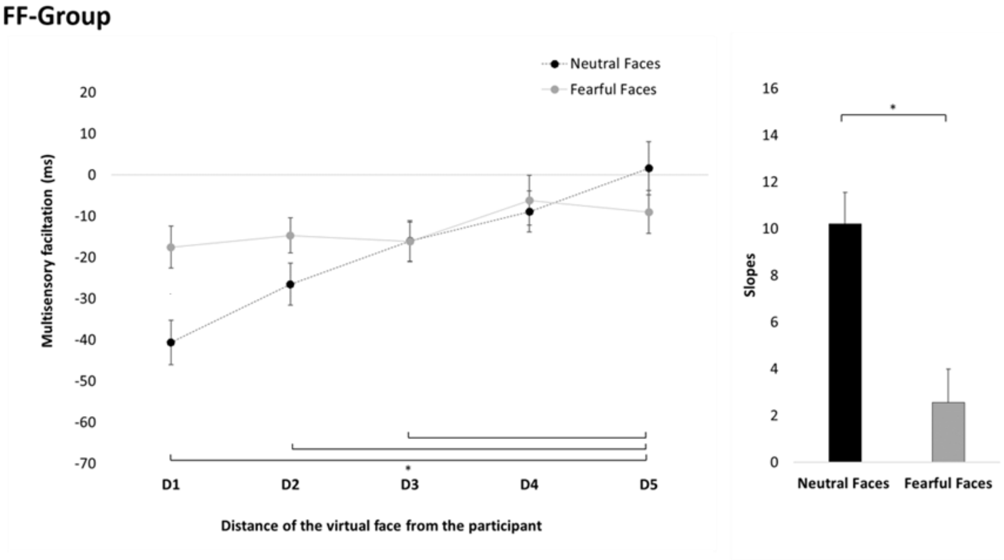
Group: Neutral: m=10.20, sem=1.35; Fearful: m=2.55, sem=1.43; AF-Group: Neutral: m=12.15, sem=1.65; Angry: m=9.72, sem=1.22). Importantly, slopes values in the neutral conditions of the three groups were not different (all p=1).

(a)



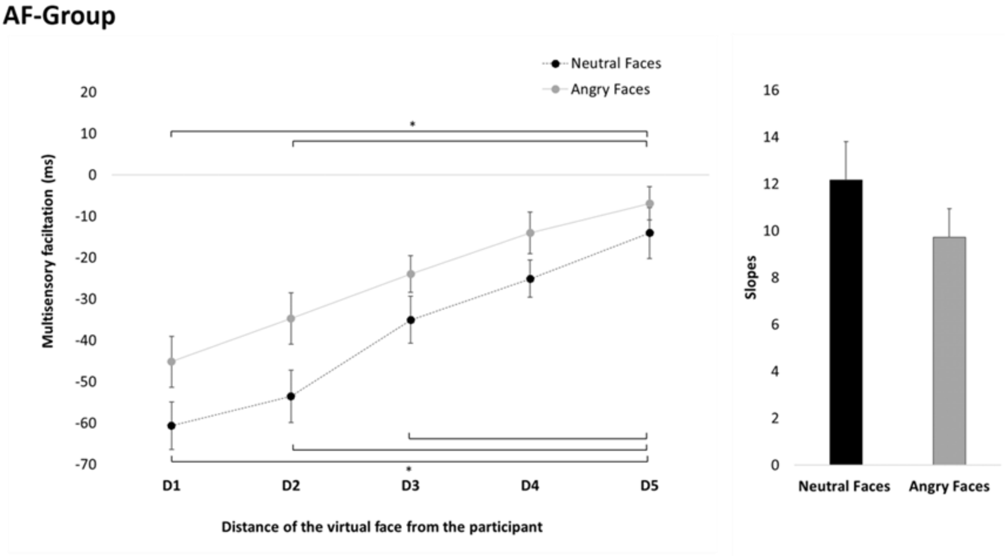
JF-Group

(b)



FF-Group

(c)



AF-Group

Figure 4.2. Baseline-corrected RTs are reported as a function of distances (D1, D2, D3, D4, D5) of the visual stimulus in the Neutral (Neutral faces; dashed black line) and in the Emotion (Joyful faces; Fearful faces; Angry faces; continuous grey line) conditions. Error bars represent S.E.M.. Asterisks are signalling the main significant comparisons. The histograms represent the slope values. Panel (a) refers to the JF-Group. The spatial modulation of RTs in the Neutral condition was not distinguishable from the Emotion condition: baseline-corrected RTs tended to decrease with the proximity of the avatar's face from the participant. Slopes values in the two conditions were not different. Panel (b) refers to the FF-Group. In the Neutral condition, baseline-corrected RTs tends to decrease with the increase of the proximity of the face to the body. In the Emotion condition, no difference was found between the distance conditions. Slopes in the Emotion condition were flatter than slopes in the Neutral condition. Panel (c) refers to the AF-Group. The spatial modulation of RTs in the Neutral condition was not distinguishable from the Emotion condition: baseline-corrected RTs tended to decrease with the proximity of the avatar's face from the participant. Slopes values in the two conditions were not different.

4.2.4 Discussion

PPS is the representation of the space surrounding the body (Rizzolatti et al., 1997), and its extent can be defined by the portion of space in which multisensory information between bodily and external stimuli has a higher probability of being integrated (Noel, Łukowska et al., 2015). The defensive-like function of the PPS is intrinsic to the plasticity of this representation, as PPS representation was demonstrated to be highly linked to the mechanisms dedicated to self-body protection (Cléry, Guipponi, Wardak, et al., 2015; de Vignemont & Iannetti, 2015; Graziano & Cooke, 2006; Lourenco et al., 2011; Sambo & Iannetti, 2013; Sambo et al., 2012) and to be sensitive to stimulus salience (de Haan et al., 2016; Ferri et al., 2015; Spaccasassi et al., 2019; Taffou & Viaud-Delmon, 2014; Vagnoni et al., 2012).

In this study, we assessed whether this spatially dependent form of multisensory integration was modulated by emotional facial expressions. To this aim, we adapted a well-validated multimodal interaction task (Pellencin et al., 2018; Serino, Noel, et al., 2015): 60 healthy participants were asked to respond to tactile stimuli delivered to their cheeks at five possible delays while watching approaching 3D avatar faces showing joyful, fearful, angry or neutral expressions.

Approaching fearful faces, compared to neutral, joyful and angry faces, had a different effect on PPS. Neutral, joyful and angry faces facilitated responses to tactile stimuli in a manner that was gradually affected by the proximity of the approaching face: the closer the face was to the participant at the time of touch delivery, the faster the participant responded to tactile stimulation. Conversely, when the avatar face showed a fearful expression, the participants' responses to touch did not speed up any further as the face approached their body.

Multisensory neurons mapping PPS are sensitive to the spatio-temporal dynamics of objects in the environment, and it is known that stimuli related to the body (in this case, a tactile vibration) and external events that occur near the body (the approaching avatar's face) are highly likely to be jointly processed (Serino, 2019). The information from this joint processing is directly transferred to the motor system to prompt appropriate responses (Finisguerra et al., 2015; Makin et al., 2009; Serino et al., 2009). RTs represent, in this sense, a proxy for the relevance of actions aiming to avoid or promote contact (Bufacchi & Iannetti, 2018), and this relevance increases, gradually, as a function of the object's proximity to the body (Canzoneri et al., 2012; Kandula et al., 2015; Serino, Noel, et al., 2015). In the present study, in particular with neutral, joyful and angry faces, the transition between farther and nearer positions in space was continuous, rather than discrete; this evidence would suggest that a step-like proximity function is an inadequate description of PPS (Bufacchi & Iannetti, 2018). The lack of a specific border is in line with the notion that PPS is based on a sequence of graded receptive fields; while the response magnitude of some neurons increases rapidly, most neurons show a less steep response gradient (Colby et al., 1993) and present receptive fields which extend beyond the animal's reaching distance (Colby et al., 1993; Graziano, Hu, Gross, et al., 1997), encompassing a much larger area than commonly reported (see Bufacchi & Iannetti, 2018, for a review).

Crucially, the gradual increase of visuotactile interactions in PPS, serving a defensive purpose, interacted with the salience of the stimulus. While an approaching emotional face (i.e. neutral, joyful or angry) becomes gradually more relevant as a function of its proximity to the body, a stimulus very relevant for survival, as a fearful face, primes sensorimotor interactions independently of the distance from the observer, i.e. the spatially modulated multisensory facilitation remains constant in the space considered in the present study. An approaching fearful face triggered an evolutionary meaningful preparation to respond when the face was presented in the far, or the near space, similarly. Notably, the effect found for fearful faces does not seem to reflect a generic response to negative stimuli, as it was not observed for angry faces, but it is related to the capability of specific facial expressions to warn of potential dangers.

This interaction between the proximity and the saliency of the stimulus on the multimodal PPS interactions is assumed to be mediated by long-range connections involving the functional areas for threat detection and emotion processing and the PPS frontoparietal circuits. The amygdala, with its connections to somatosensory, parietal and frontal areas (Palermo & Rhodes, 2007), constitutes a central structure for perception and recognition of emotional facial expressions (Adolphs et al., 2005), and plays a major role in the attentional orientation toward threats (Cisler & Koster, 2010; Peck et al., 2013; Vuilleumier, 2005), integrating not only emotional but also spatial information. The present results seem to support the hypothesis of a functional connection between the neural structures dedicated to processing affective stimuli and those representing PPS, affirming once more the defensive function of PPS (Graziano & Cooke, 2006). An indirect demonstration of such a connection comes from the work of Åsh and colleagues (2014): conditioned threats were more resistant to extinction processes when they invaded PPS than when they were distant. With an fMRI study, De Borst and colleagues (2018) provided further support for this result. Participants, laying in the scanner, had to passively observe an approaching male aggressor. Through intersubject correlation analysis, the authors found that the activity in the emotion-related structures (amygdala, ACC, insula) was more synchronized across participants when the threat was near, but only when it was perceived as directed towards themselves (the first-person perspective was prompted in a pre-experimental session). Moreover, from effective connectivity analyses, they found direct neural connections from the left intraparietal sulcus (considered a key area of the PPS network; Grivaz et al., 2017) to the right anterior cingulate cortex, and from that structure to the right amygdala and the left anterior cingulate cortex, when stimuli were presented in a first-person rather than a third-person perspective. All these findings suggest that the amygdala and the emotion-related structures contribute to PPS representation, in the context of emotionally relevant stimuli (Belkaid et al., 2015).

Fear, expressed by another human, is considered a particular kind of threatening stimulus, as it does not constitute a direct danger (as a weapon, a poisonous spider, or an angry face), but it communicates a potential environmental risk, whose source is unknown (Fanselow & Pennington, 2018). It is acknowledged that viewing fearful facial expressions affects basic perceptual processes (Bertini et al., 2017, 2020; Bocanegra & Zeelenberg, 2011; Cardini et al., 2012; Phelps et al., 2006), as well as spatial attentional processes (Carlson & Reinke, 2008). It is adaptive to rapidly orient spatial attention to others’ expressions of fear and, in the absence of any other information about the location of the potential threat (e.g., eye gaze directed towards the threat), the individual is prompted to scan the surrounding environment to detect the source of the threat (Juncai et al., 2017; Torrence et al., 2017). It was demonstrated, indeed, that fearful expressions strengthen the representation of contextual threat, eliciting vigilance in the visual periphery (Wieser & Keil, 2014). Thus, it is possible to hypothesize that in our task, an approaching fearful face did not modulate tactile responses because spatial covert attention might have been redirected away, so that response times to tactile stimulation were no longer modulated by the apparent location of the fearful face. On the contrary, neutral, joyful or angry faces, which do not advert attention from their position, became more and more relevant as their proximity increased. Therefore, attention was maintained on the approaching neutral, joyful or angry face, which further modulated tactile reaction times as a function of its position in space.

Thus, the results of the present study stress that PPS and emotional processing are closely related, and dedicated studies are needed to explore the mechanisms that underlie these instantaneous adjustments to the ongoing low-level (sensory and motor) and the emotional context, probably mediated by spatial attentional factors.

4.3. Conclusions

This first study aimed to observe the effect of emotional faces on the multisensory PPS. It was highlighted that fearful faces had a differential effect on PPS with respect to the other emotional and neutral faces; at the difference with the latter, in presence of looming fearful faces, responses to tactile stimuli were less facilitated as the face was approaching the participants; this effect was observable in the nearest, but not in farther face’s positions. Importantly, this pattern was not found with angry faces, resulting not attributable to the negative, versus positive, valence of the stimulus. To explain this result, it is hypothesized the intervention of a differential distribution of spatial attention. When fearful faces were entering the PPS, spatial attention might have been redirected away from the face location to the surrounding space; in this way, face location was less relevant to determine the facilitation of the motor response to tactile stimuli, as the face intruded the PPS. On the other hand, with other facial expressions, attention might remain on the looming face without being redirected. This effect would result specific for fearful faces, in accordance with their adaptive role of signalling a potential threat and promoting a scanning of the environment.

CHAPTER 5. The spatial logic of fear

5.1. Introduction

Study 1 demonstrated that PPS representation is modulated by emotional facial expressions. Approaching joyful and angry faces did not differ with respect to neutral faces in modulating the reactivity to tactile stimuli. Participants were faster in responding to a tactile stimulus when this was co-occurring with the presentation of the face, and this facilitation was increasing gradually, as the face was closer to the participant. Fearful faces showed a completely different pattern. Unlike the other emotions displayed, response to tactile stimuli was independent of the position of the fearful face. Also, when the fearful face was in the very proximity of the participant, responses to tactile stimuli resulted significantly less facilitated with respect to neutral. This result was discussed by hypothesizing that the different emotional expressions were differently modulating spatial attention in PPS. As positive valenced stimuli, joyful faces are not expected to motivate the observer in engaging any defensive action preparation; also, by signalling an approach bias and perhaps a cooperative intention, a joyful face would quite likely hold attention along its approaching movement. On the other side, angry faces are an important signal of social threat that calls for attention to remain focused on the face as it approaches. In this sense, the effect on attention of joyful and angry faces, although the first positively and the second negatively valenced, would be similar. Both emotional expressions motivate the individual to pose continuous attention to the approaching stimulus. Similarly, neutral faces, even though not particularly valenced, can be considered as salient stimuli, as they carry different important information about the individual (i.e., identity and personality traits) and the environment (i.e., no presence of threat); moreover, when presented as looming toward the subject, this stimulus is expected to become more and more relevant as it approaches; also in the case of neutral faces, attention is expected to remain on the face. Multisensory facilitation of responses to tactile stimuli was thus determined by the position of the face, with respect to the subject, similarly when it was joyful, angry or neutral. Contrariwise, fearful faces are hypothesized to trigger a completely different attentional pattern with respect to the other emotions considered. As fearful faces were looming and intruding PPS, they would have prompted a redirection of spatial attention from the face location to the surrounding space of the face. Thus, in PPS, the attentional focus has probably not privileged the fearful face location; therefore, the somatosensory processing of tactile stimuli was no longer affected by the co-occurrence of the face presentation and not affected by its position. The hypothesized redirection of attention in PPS would reflect the adaptive function of fearful faces, that is to motivate the engage of sources in the preparation of a defensive reaction to a menace that could be anywhere and whose nature is unspecified; this process would primarily require the disengage of attentional sources from the fearful face, to potentiate the processing of the surrounding space.

Study 2a is designed to test whether different emotional expressions differently affected PPS through a differential distribution of spatial attention. A first experiment (EXPERIMENT 1) will test the hypothesis that joyful and neutral faces do not redistribute attention when they intrude PPS. A second experiment (EXPERIMENT 2) would test whether fearful faces in PPS, compared to neutral, are associated with a redirection of attention from the face location to the periphery.

Study 2b is dedicated to the investigation of the spatial dynamics triggered by angry faces in PPS. The hypothesis is that the redirection of attention, found with fearful faces, is not a generic reaction to threat, nor it is attributable to the negative valence or the arousal level of the emotion expressed. At a difference with what predicted for fearful faces, angry faces are not expected to trigger any redistribution of spatial attention when approaching the subject, similarly to neutral faces. In the case in which angry faces will not replicate the effect on spatial attention hypothesized with fearful faces, it will be concluded that the effect hypothesized for fearful faces is attributable to the specific emotional component of the expression of fear.

5.2. Study 2a: The spatial logic of fear

5.2.1 Introduction

It is adaptive to preferentially orient attention toward cues of threat in the environment, that can be variously represented by a wide range of stimuli such as scenes, words, emotional faces (Yiend, 2010). Attentional biases were found to depend upon the affective salience of the stimulus defined by its arousal and valence components. Arousing and negatively valenced stimuli attract spatial attention (Cisler & Koster, 2010; Koster, Crombez, Van Damme, et al., 2004; Yiend, 2010). As argued before, one of the PPS functions is to protect the body from potential threats occurring within PPS (i.e. avoiding a spider running toward the hand; de Vignemont & Iannetti, 2015), thus it quite likely that attentional biases would also mediate PPS modulations driven by the affective salience of a stimulus (Cléry, Guipponi, Wardak, et al., 2015). This hypothesis is also sustained by the evidence that attention does affect perception, as well as perceptual judgments of distance and size of a stimulus in space (Anton-Erxleben et al., 2007; Kreutzer et al., 2015; Wright et al., 2011).

Among the realm of stimuli that provide a cue of threat, facial expressions of fear constitute a special case: they are not intrinsically threatening or harmful for the observer, but they do communicate the potential presence of a threat in the environment. The information conveyed by a fearful face has an intrinsic ambiguity that needs to be interpreted. Without any additional information such as eye gaze or other information in the context (i.e., shared signal hypothesis by Adams & Kleck, 2005), it would be adaptive for the subject to prepare a reaction to a threat that might be anywhere. One first strategy might be allocating attentional resources in the surrounding of the face to potentiate the processing of an eventual upcoming harmful event. Also, this process becomes more likely in the proximity of the body, where the threat is imminent, and the reaction is more urgent. This attentional dynamic triggered by the fearful face would in turn affect multisensory interactions (De Meo et al., 2015; Talsma, 2015). Previous literature has described that fearful faces act as an exogenous cue that exerts a strong influence on selective attention; in fact, healthy subjects covertly and reflexively orient attention toward the fearful face location; this dynamic in the attentional focus is inferred by measuring the change in the behavioural performance or the neural response to subsequent target that appear at the same face location (Brosch et al., 2011; Carlson & Aday, 2018; Carlson & Reinke, 2008; Pourtois & Vuilleumier, 2006; Vuilleumier & Pourtois, 2007). Other pieces of evidence have shown that the capture of spatial attention by fearful faces is rapid but short-lived (Holmes et al., 2005; Torrence et al., 2017), probably to support the functional reallocation of attention to detect the potential upcoming threat.

Study 2a would explore the different dynamics of spatial attention in PPS prompted by the different emotional expressions of joy (EXPERIMENT 1) and fear (EXPERIMENT 2) compared with neutral faces. In two experiments the effect of the redirection of spatial attention on PPS is measured with a tailored paradigm that consists in detecting tactile stimuli at the cheeks while watching task-irrelevant emotional faces will approach the subject. Faces will be looming across two different portions of space, one very far and one near the subject. To test the spatial dynamics of attention, another visual element is introduced: close to the face location or in the space surrounding it, a ball, with the function of an “attentional probe”, would appear simultaneously with the delivery of the tactile stimulation. The ball can appear in the space immediately surrounding the emotional/neutral face or more in the periphery of the face. The assumption is that the fleeting attention, prompted by the fearful face in PPS, is engaged by the ball appearance; this attentional bias is expected to be stronger when the ball appears in a location that the subject is more likely to be scanning (i.e., the periphery of the fearful face). The engagement of attention will, in turn, modulate the magnitude of the multisensory interactions. The more the ball attracts attention, the more the somatosensory processing of tactile stimuli are influenced by the ball appearance; this relation is measurable by looking at the motor facilitation of the response to tactile stimuli.

5.2.2 Experiment 1: Joyful faces

EXPERIMENT 1 will contrast the effect of neutral and joyful faces on the distribution of spatial attention in PPS. The hypothesis is that both with joyful and neutral faces in PPS, attention is focused on the approaching face (or space immediately surrounding it). Therefore, it is expected to find facilitation of the responses to tactile stimuli that depends on the distance of the face from the participant's body: participants are expected to respond faster to the tactile stimulation when faces are in near, as opposed to far space (PPS effect). Also, since attention is expected to remain on the face, balls that appear close to it are expected to further facilitate the tactile responses, compared to when they appear more in the periphery.

5.2.2.1 Methods

Participants

Twenty-three healthy participants with no history of neurological or psychiatric disorder were recruited (12 females; age: M ± SD = 29.78±3.84 years). The experiment was conducted in accordance with the principles of the Declaration of Helsinki and approved by the Bioethics Committee of the University of Bologna. Each participant gave written informed consent before participating and after being informed about the procedure of the experiment. The sample size was determined via a power analysis conducted in G*Power 3.1 software (Faul et al., 2007); the modulation of spatial attention in PPS was expected to have a medium to large effect size (Torrence et al., 2017; Valdés-Conroy et al., 2014); the alpha was set at 0.05 and the power was set at 0.95. For a repeated measure within-factor analysis of variance (ANOVA) with no covariates, it was determined that a sample size of twenty-three would be enough to detect the effect.

Task and experimental procedure

The experiment was implemented in ExpyVR software (available online at http://lnco.epfl.ch/ framework for designing and running experiments in virtual reality) and ran on a Windows-based PC (Dell XPS 8930, Dell, Round Rock, Texas, USA). The tactile stimuli consisted in vibrations delivered bilaterally at the participants' cheeks by a pair of electrodes (Precision MicroDrives shaftless vibration motors, model 312-101, 3V, 60 mA, 150 Hz, 5 g). The motor had a surface area of 113 mm2 and reached maximal rotation speed in 50 ms. This device was activated for 100 ms during tactile stimulation. The visual stimuli were avatar joyful or neutral faces (see Figure 4.1 A-B). The expression was manipulated ad hoc and validated in a preliminary study (see Chapter 4, Paragraph 4.2.2.3).

At the beginning of each trial (T0), an avatar face with a neutral or joyful expression appeared centrally on the visual field, either in the space near to (≈115 cm) or far from (≈220 cm) the participant, by relaying stereoscopically to the head-mounted display (HMD, Oculus Rift SDK, Oculus VR, 100° field of view, 60 Hz) worn by the participant. The face then moved toward the participant on the sagittal plane for a total of 3000 ms until its final position (Near: ≈10 cm; Far: ≈115 cm) where it remained still for 1000 ms (T2). Importantly, 2000 ms after the beginning of the trial (T1), the tactile stimulation was delivered bilaterally, and, simultaneously, a static checkerboard ball appeared for 250 ms, either ≈1° (ball central) or ≈10°(ball peripheral) to the left or right of the face (left and right sides counterbalanced among trials; Figure 5.1). Thus, at T1, touch coincides with the perception of the ball and of the face, at different distances from the participant (at ≈45 cm, in the near, and ≈150 cm in the far). The ITI was set at 2100 ms (+/- 100 of jitter). Distances of near and far spaces were calibrated as previously done in Serino, Noel, et al. (2015). During the task, participants made speeded simple responses to the tactile stimulation by pressing a button placed on the table in front of the participant with their right hand.

There was a total of 320 experimental trials, equally divided among the 8 experimental conditions (i.e. 40 trials per condition): Face Emotion: Neutral / Joyful; Space: Far / Near; Ball Position: Central / Peripheral. There were also an additional 100 trials, introduced to decrease task predictability: in 80 trials no vibration was delivered and in 20 trials, no ball was shown. Importantly, the only aspect of the task that was lateralized was the presentation of the ball, which could be either on the left or right with respect to the central position of the face. However, the side of the presentation is not a factor of interest for the present design and left/right presentation trials were therefore pooled. The entire experiment was split into 5 blocks of 84 trials each, in which the conditions were pseudo-randomized such that each block presented an equal number of each condition. The experiment lasted approximately one hour, and participants could rest between blocks to prevent fatigue.

After signing the consent form, participants seated on a comfortable chair, in a sound-attenuated room. Vibrators were then attached bilaterally on the cheeks with medical tape, and participants then wore the virtual reality headset. Before starting the task, lens focus was adjusted for each participant to ensure clear vision.

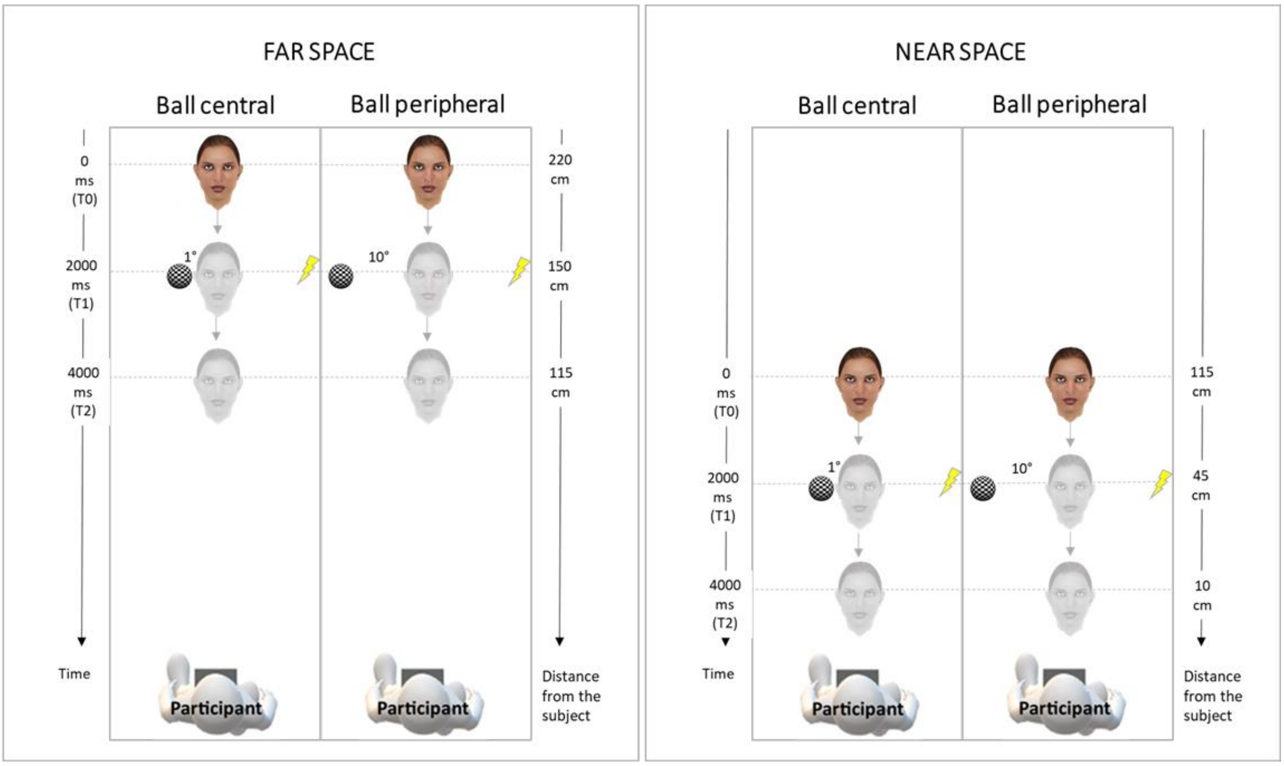


Figure 5.1. Experimental paradigm. At T0, a looming face could appear in the far space (left panel) or the near-space (right panel) with respect to the participant. From T0 until T2, the face approached the participant at a constant speed. At T1 a tactile stimulus is delivered simultaneously to the appearance of a ball with a checkboard pattern. Both in the near and the far space conditions, the ball could appear 1° (Ball Central) or 10° (Ball Peripheral) apart from the face, on the left or the right side of the face's frontal plane.

5.2.2.2 Results

The rate of omissions was low (M=1.6% SD=2.4). For this reason, the performance was analysed in terms of reaction times (RTs) only, as previously done in e.g., Canzoneri et al. (2012). Trials with RTs exceeding more than 2 standard deviations from the mean RT of each block were considered as outliers and excluded from the analyses (M=4.5%. SD=3.01). For each participant, mean RTs were calculated for each condition and used for analysis.

A 2x2x2 RM ANOVA (Face Emotion: Neutral / Joyful; Space: Far / Near; Ball Position: Central / Peripheral) was conducted to test whether looming joyful vs. neutral faces induced a change in PPS representation (i.e. a difference in RTs to tactile stimulation) through a different distribution of spatial attention, probed by the ball appearing centrally or peripherally from the face. Results showed a significant main effect of Face Emotion [F(1,22)=4.99; p=0.03; η_p^2=0.18]; participants responded faster to Joyful than Neutral faces (Joyful faces: M=372.73 ms; SEM=11.35; Neutral faces: M=377.66 ms; SEM=11.84). There was also a significant main effect of Space [F(1,22)=72.95; p<0.01; η_p^2=0.77]; participants responded faster to faces in the Near than Far space (Near: M=360.93 ms; SEM=11.68; Far: M=389.45 ms; SEM=11.32). It is also found a significant main effect of Ball Position [F(1,22)=6.32; p=0.02; η_p^2=0.22]; participants responded faster when the ball was central as opposed to peripheral to the face (Central: M=373.46 ms; SEM=11.52; Peripheral: M=376.94 ms; SEM=11.68).

Moreover, there was a significant Face Emotion by Space interaction [F (1,22) =5.59; p=0.03; η_p^2=0.20]. Newman-Keuls post-hoc comparisons revealed that when faces appeared in Far space, participants responded faster to Joyful than Neutral faces (Joyful faces: M=384.87 ms; SEM=22.14; Neutral faces: M=394.04 ms; SEM=23.34; p<0.01). On the contrary, when faces appeared in Near space, there was no significant difference in RTs between Joyful and Neutral faces (Joyful faces: M=360.58 ms; SEM=23.21; Neutral faces: M=361.29 ms; SEM=23.76; p=0.78). No significant three-way Face Emotion by Space by Ball position interaction was found [F (1,22) =1.59; p=0.22; η_p^2=0.07].

Responses to tactile stimuli were facilitated when faces were near to, as opposed to far from, the participant (PPS effect). Besides, joyful faces facilitated response to tactile stimuli compared to neutral faces (salience effect), in the far but not in the near space. Finally, central, as opposed to peripheral, balls facilitated response to tactile stimuli, regardless of the emotional expression of the face or the distance of the face from the participant (see Figure5.2).

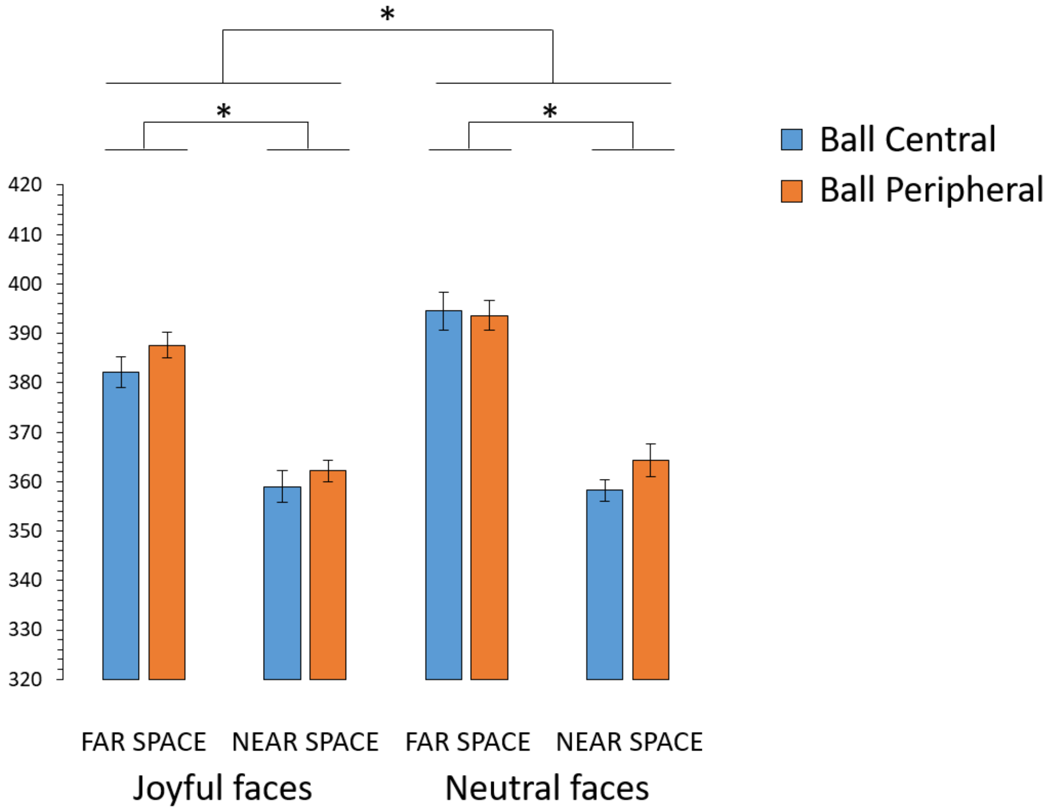


Figure 5.2. Results of Experiment 1. The bar graph shows the main effect of Distance. Responses to tactile stimuli are facilitated (faster RTs), when the face is in the Near condition, as opposed to the Far condition. This effect is observable both in the Neutral and in the Joyful faces condition. Also, a main effect of the Face Emotion is observable: responses to tactile stimuli are facilitated in the Joyful, as opposed to the Neutral face condition. Asterisks indicate significant comparisons. Error bars represent the standard error of the mean (S.E.M.).

5.2.3 Experiment 2: Fearful faces

EXPERIMENT 2 will contrast the effect of neutral and fearful faces on the distribution of spatial attention in PPS. The hypothesis is that fearful and neutral faces, by prompting a differential distribution of spatial attention, would affect differently PPS representation, that was measured by a change in response times to tactile stimuli. As fearful faces intrude PPS, attention will be redistributed toward the periphery to promote the scanning of the environment in the search for the threat. It is expected to find faster responses when the faces, neutral or fearful, are in the near as opposed to far space (PPS effect). Furthermore, this effect is expected to be enhanced when the fearful face is presented with a ball appearing more in the periphery of the face with respect to when it appears closer to the face location. The peripheral near space is where the attentional modulation is expected to be stronger: the ball appearing that location is more likely to respect the criteria of spatiotemporal proximity necessary for multisensory integration.

5.2.3.1 Methods

Participants

Twenty-three healthy participants were recruited (12 females; mean age 27.61±4.36). None of the participants reported any history of neurological or psychiatric disorders, and all were naive to the purpose of the study. The experiment was conducted in accordance with the principles of the Declaration of Helsinki and approved by the Bioethics Committee of the University of Bologna. Each participant gave written informed consent before participating and after being informed about the procedure of the study. The sample size was determined via a power analysis conducted in G*Power 3.1 software (Faul et al., 2007); the modulation of spatial attention in PPS was expected to have a medium to large effect size (Torrence et al., 2017; Valdés-Conroy et al., 2014); the alpha was set at 0.05 and the power was set at 0.95. For a repeated measure within-factor analysis of variance (ANOVA) with no covariates, it was determined that a sample size of twenty-three would be enough to detect the effect.

Task and experimental procedure

Experimental stimuli, task and procedure were identical to EXPERIMENT 1 (see Paragraph 5.2.2.1 for a detailed description of the method), with the only difference that faces showed a neutral or a fearful expression (see Figure 4.1 A-C). The expression was manipulated ad hoc and validated in a preliminary study (see Chapter 4, Paragraph 4.2.2.3).

5.2.3.2 Results

Participants rate of omissions was low (M=1.35% SD=2.14). For this reason, the performance was analysed in terms of reaction times (RTs) only, as previously done in e.g., Canzoneri et al., 2012). Trials with RTs exceeding more than 2 standard deviations from the mean RT of each block were considered as outliers and excluded from the analyses (M=5.80% SD=3.12). For each participant, mean RTs were calculated for each condition and used for analysis.

A 2x2x2 RM ANOVA (Face Emotion: Neutral / Fearful; Space: Far / Near; Ball Position: Central / Peripheral) was conducted to test whether looming fearful, vs. neutral, faces induced a change in PPS representation (i.e. a difference in RTs to tactile stimulation) through a different distribution of spatial attention, probed by the ball appearing centrally or peripherally from the face.

Results showed a significant main effect of Face Emotion [F(1,22)=15.99; p<.01; η_p^2=0.42]; participants responded faster to Fearful than Neutral faces (Fearful faces: M=374.92 ms; SEM=0.89; Neutral faces: M=381.92 ms; SEM=0.88). There was also a significant main effect of Space [F(1,22)=69.60; p<0.01 ; η_p^2=0.76]; participants responded faster to faces in Near than Far space (Far space: M=395.33 ms; SEM=0.85; Near space: M=362.51 ms; SEM=0.87). There was no significant main effect of Ball Position [F(1,22)=0.24; p=0.62; η_p^2=0.01], Face Emotion by Space [F(1,22)=0.96; p=0.34; η_p^2=0.04] or Face Emotion by Ball Position [F(1,22)=2.20; p=0.15;

η_p^2=0.09] interaction. However, there was a significant Space by Ball Position [F (1,22) =7.66; p=0.01; η_p^2=0.26] interaction. In far space, participants responded faster to the central than peripheral ball (Peripheral: M=396.52 ms, SEM=16.67; Central: M=392.15 ms, SEM=16.49; p=0.03), while in near space, there was no difference in RTs between the central and peripheral ball (Peripheral: M=361.06 ms, SEM=16.56; Central: M=363.95 ms, SEM=17.31; p=0.13).

Crucially, there was a significant three-way Face Emotion by Space by Ball Position interaction [F(1,22)=4.45; p=0.04; η_p^2=0.17]. Newman-Keuls post-hoc comparisons revealed that in presence of neutral faces, there was no difference in RT between the central and peripheral ball either in far space (Central: M=396.84 ms, SEM=15.95 ms; Peripheral: M=400.53 ms; SEM=16.21 ms; p=0.17) or near space (central: M=364.15 ms, SEM=17.33 ms; peripheral: M=366.15 ms; SEM=17.32 ms; p=0.45). In presence of fearful faces in far space, RTs showed a trend to be faster with the central ball compared to the peripheral one, although not significant (Central: M=387.45 ms, SEM=17.17; Peripheral: M=392.51 ms, SEM=17.25; p=0.07). In contrast, when fearful faces appeared in near space, participants responded significantly faster to the peripheral compared to the central ball (Central: M=363.75 ms, SEM=17.39; Peripheral: M=355.97 ms, SEM=15.94; p<0.01).

Responses to tactile stimuli were facilitated when faces were near to, as opposed to far from, the participant (PPS effect). Moreover, fearful faces facilitate response to tactile stimuli compared to neutral faces. Importantly, in contrast to neutral faces, fearful faces responses to tactile stimuli were depending on their distance from the participant and the position of the ball. While in the far space, responses to tactile stimuli tended to be facilitated by the central rather than peripheral ball, in near space, responses to tactile stimuli were significantly facilitated by the peripheral rather than the central ball (see Figure 5.3).

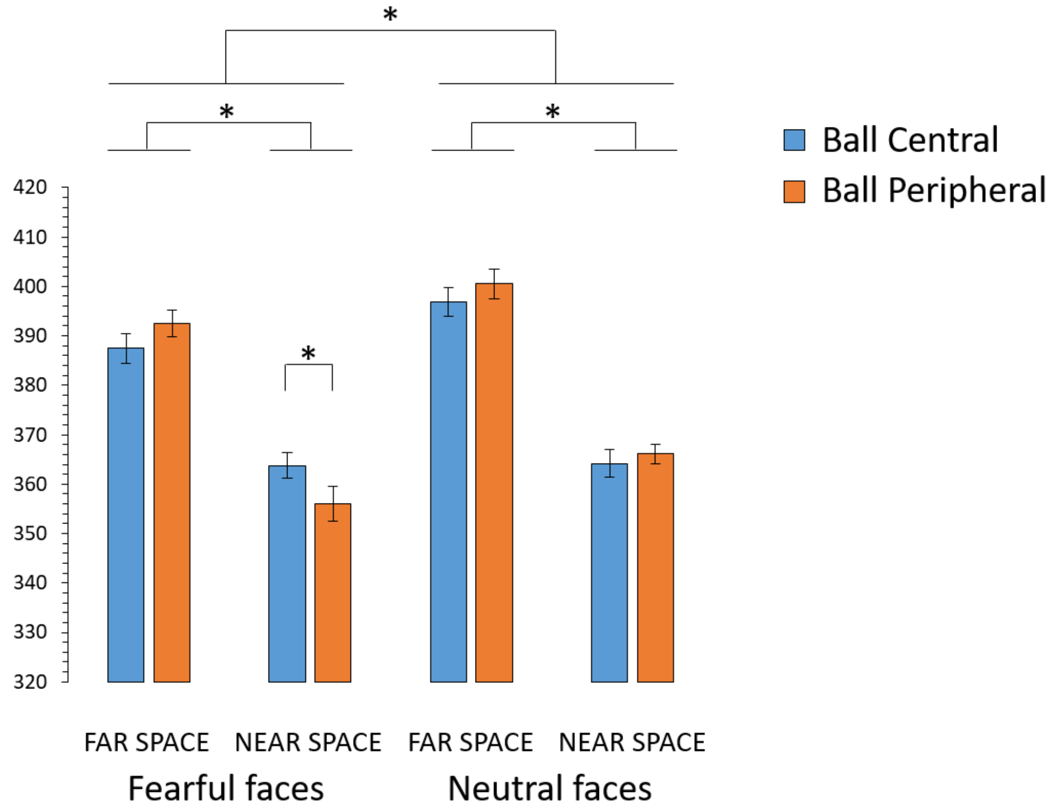


Figure 5.3. Results of Experiment 2. The bar graph shows the main effect of Distance. Responses to tactile stimuli are facilitated (faster RTs), when the face is in the Near condition, as opposed to the Far condition. This effect is observable both in the Neutral and in the Fearful faces condition. Also, a main effect of the Face Emotion is observable: responses to tactile stimuli are facilitated in the Fearful, as opposed to the Neutral face condition. Moreover, only when the face was fearful and in the near space, responses to tactile stimuli were facilitated in presence of the peripheral compared to the central ball. Asterisks indicate significant comparisons. Error bars represent the standard error of the mean (S.E.M.).

5.2.4 Discussion

Study 2a was proposed to investigate whether emotional expressions prompted a differential distribution of spatial attention in PPS. In the task adopted, healthy subjects responded to tactile stimuli delivered at the cheeks, while watching in virtual reality looming avatar faces, showing a neutral or an emotional expression: joyful (EXPERIMENT 1) or fearful (EXPERIMENT 2). The looming face could be presented in the space far from or near to the subject. To probe spatial attention, when the tactile stimulus was delivered, a ball (representing a static visual distractor) briefly appeared centrally or peripherally to the left or the right of the face's frontal plane.

In EXPERIMENT 1, the responses to tactile stimuli were faster when the faces appeared in the space near the subject than when they appear in the space far (PPS effect); also, a salience effect was found: tactile responses were faster when the face presented a joyful rather than a neutral expression; this effect was observed when the face was in the far rather than when the face was in the near space. Lastly, central, as opposed to peripheral, balls facilitated response to tactile stimuli, regardless of the emotional expression of the face or the distance of the face from the subject.

In EXPERIMENT 2, the responses to tactile stimuli were faster when the faces appeared in the space near the subject than when they appear in the space far (PPS effect). Also, responses to tactile stimuli appeared to be significantly facilitated when fearful faces were shown, compared to neutral faces. Crucially, fearful, but not neutral faces, modulated responses to tactile stimuli depending on their distance from the participant and the position of the ball. While in the far, responses to tactile stimuli tended to be facilitated by the central rather than the peripheral ball, in the near space, responses were significantly facilitated by the peripheral rather than the central ball.

Overall, in both experiments and irrespectively to the condition, participants were found to be faster in responding to tactile stimuli when delivered together with the face-ball compound presented in the near space, than in the far space. This effect was labelled as PPS effect, in line with the broad PPS literature (Serino, 2019); two stimuli of different modalities, tactile and visual, if in spatiotemporal proximity, can be integrated with an increase in responsiveness (Van der Stoep, Nijboer, et al., 2015). This gain in responsiveness is expected to be positively correlated with the proximity of the visual stimulus to the tactually stimulated body part (Làdavas, 2002).

At a difference with Study 1 and in contrast with previous studies (Serino, Noel, et al., 2015; Spaccasassi et al., 2019), in this paradigm, looming stimuli were not travelling in a constant portion of space; in these previous paradigms, the different spatial conditions were determined by the delay in which the tactile stimulation was delivered (i.e., earlier stimulation, the face is far from the subject; later stimulation, the face is closer to the subject). In this paradigm, the time of the tactile delivery from the beginning of the trial was always kept constant between the two different distance conditions (see Figure 5.1). Such manipulation allowed to control for the expectancy to receive the tactile stimulation as the delay between the appearance of the face and the delivery of the tactile stimulation increased (Kandula et al., 2015) while keeping constant the velocity of travelling.

Beside the PPS effect, also an effect of the salience was found. Response times to tactile stimuli were facilitated in the condition in which the face showed an emotional expression (joyful or fearful), rather than neutral. The effect of the stimulus salience can be attributed to a generalized increased reactivity to affective stimuli, and it was particularly evident when the face was in the farther position. Emotional faces are particularly salient stimuli, known to trigger a cascade of central and peripheral physiological processes associated with motor preparation (Liddell et al., 2004; Valk et al., 2015; Vuilleumier & Pourtois, 2007) which, compared to neutral, would have been affected the speeded motor responses. This evidence is in line with what found by previous studies implying a multimodal tactile detection task and stimuli varying in affective salience: negative arousing stimuli, but also positive (Spaccasassi et al., 2019), seem to increase their modulatory effect with the increase in distance from the body (Ferri et al., 2015; Spaccasassi et al., 2019). At shorter distances, the salience of the stimulus no longer affects tactile responses: every object near the body can be maximally relevant as a source of potential interaction (Bufacchi & Iannetti, 2018; Spaccasassi et al., 2019).

Importantly for the present study, in addition to the PPS and saliency effect, responses were further differentially modulated by the position of the ball with respect to the face, in interaction with the space of presentation, and the emotional condition. In EXPERIMENT 1, particularly, responses to tactile stimuli were faster when they were delivered when the ball was positioned centrally, closer to the face. This effect would suggest that attention may be focused on the immediate surrounding of the face, without being redirected. This is consistent with previous literature showing that joyful faces endogenously attract attention and hold it for a longer time than fearful faces (Torrence et al., 2017).

Crucially, when fearful faces were flanked by peripheral balls in the near space, responses to tactile stimuli were more facilitated than when the balls were presented centrally. This effect confirmed the main hypothesis of the present study: fearful faces in PPS are prompting a centrifugal redistribution of attention; the attention shifts from the face, to the space surrounding the face, to support the enhanced perceptual processing of any upcoming, threatening, event (Wieser & Keil, 2014). By manipulating the position of the ball in the space surrounding the face it was possible to capture indirectly, through the modulation of responses to tactile stimuli, the centrifugal effect of attention exerted by fearful faces when intruding the PPS. Even though faces were presented centrally, their effect was captured when combined with peripheral stimuli. Previous literature has shown that fearful faces, as particularly salient stimuli, do attract attention onto their location, modulating the response to subsequent stimuli; this effect, however, seems to be consistent only at shorter delays between the face and the appearance of a subsequent target (Holmes et al., 2005; Torrence et al., 2017): attention, once attracted by the face and as the time passes, seems disengaged from the face, possibly to promote the scanning of the environment. In these studies (Study 2a and 2b) time is not a variable of interest; as stated before, the delay between the appearance of the face and the tactile delivery is kept constant in all conditions; here, the redirection of attention by fearful faces has a spatial logic: it seems induced when the face looms in the proximity and modulate the subject’s readiness to respond to somatosensory stimuli on the subject’s body. Particularly urgent and relevant is the response to stimuli in the proximity of the body, where the imminence of threat is maximized. Threatening stimuli are perceived as more imminent and closer than non-threatening stimuli (Cole et al., 2013), and threat imminence is a decisive factor to elicit an attentional shift (Koster, Crombez, Van Damme, et al., 2004). Also, attentional shifts appear to be facilitated in the space near the subject, rather than farther in-depth (Chen et al., 2012).

The effect of redirection of attention found specifically in the near space, and not in the far, can be explained by considering the interaction between two factors. First, a shift of spatial attention may be more facilitated when a stimulus is near the body (Chen et al., 2012); second, if attention is diverted to the periphery by the fearful face, a near peripheral element, rather than a far one, is more likely to meet the spatiotemporal criteria for being integrated into the somatosensory processing of tactile stimuli. To note, this effect of redirection of attention observed here was found in the modulation of the response to tactile stimuli, and not as a purely visual phenomenon. In the interaction between spatial attention and multisensory integration, it is expressed the defensive function of PPS (de Vignemont & Iannetti, 2015; Graziano & Cooke, 2006; Lourenco et al., 2011; Sambo & Iannetti, 2013; Sambo et al., 2012).

The results of the present study seem in apparent contrast with what found in Study 1 when fearful faces were displayed (see Chapter 4). In the fearful face condition of Study 1, in fact, multisensory integration appeared to be reduced as the looming fearful face entered the space near the subject's body, compared with the neutral face condition in which multisensory integration increased as the neutral face entered the space near the participant. In the present Study 2a, responses in the fearful face condition presented a spatial effect as in the neutral condition: faster responses were found when the visual stimuli were projected in the near-space compared with the far. This apparent inconsistency, as the distance is concerned, can be explained by considering the features of the two experimental designs. In Study 2a, unlike in Study 1, another visual element (i.e., the ball) is presented beside the looming face, which appeared contextually with the tactile stimulation. The ball anchored attention, and modulated, multimodally, the processing of tactile stimuli.

5.3. Study 2b: The spatial logic of fear is not valence-driven: Angry faces

5.3.1 Introduction

Emotional facial expressions, provide diverse information about others, including identity and several emotional and motivational aspects. Emotional facial expressions can be judged as positive (i.e., expressions of joy) or negative valenced (i.e., expressions of fear or anger), more or less arousing (i.e, a neutral or a very angry face). Importantly, other than these two dimensions, emotional faces are intrinsically identified by their emotional and motivational value; they may be informative about the state of the social or physical environment; for instance, they may communicate the intentions of others or the presence of a threat in the surrounding. Emotional expressions are thus salient stimuli that have been shown to interact with the defensive function of the multisensory PPS. The mechanism that mediates this interaction was hypothesized to involve modulation of spatial attention.

Study 2a tested whether joyful and fearful faces lead to a differential distribution of spatial attention, compared to neutral faces. Participants performed a tactile detection task of stimuli delivered at the cheeks, while simultaneously watching looming emotional faces, that could be presented in the space near or far from the subject, and flanked with a ball, very close to the emotional face or more peripheral. Responses to tactile stimuli were facilitated when the tactile stimulus co-occurred with the face near rather than far (PPS effect); more so, further facilitation was found depending on the position of the ball (central vs peripheral), assumed to reflect the portion of space where attention is more likely captured. When the looming face was close to the subject, responses to tactile stimuli were faster than when the looming face was far. Also, responses to tactile stimuli were faster in the presence of the central rather than the peripheral ball, suggesting that attention may be focused in the immediate surrounding of the face. However, when the faces were fearful and in the near space, response times to tactile stimuli were facilitated when the fearful face appeared together with the peripheral, rather than the central ball. The result was interpreted as a fear-evoked redirection of attention: as fearful face comes closer to the body, attention is redirected towards the periphery; the visual processing of the peripheral ball in the near-space is integrated into the somatosensory processing of the tactile stimulus. Emotional attention is, in this sense, enhancing the defensive function of PPS; in the eventuality of a nearby threat whose location has not yet been identified, attention privileges the portion of space where it is more likely to find a threat. The effect found in Study 2a with fearful faces seems to be attributed to the emotional and motivational value of the emotional expression that would communicate to the observer the presence of a threat in the surrounding, whose location is unknown. Nonetheless, an effect of arousal and of the negative valence of the emotion, in facilitating responses to tactile stimuli, when visual stimuli were in the near space, cannot be excluded. Fearful faces are in fact more negative and more arousing than joyful and neutral faces. In the present study, neutral faces are going to be contrasted with angry faces, that constitute another kind of negative emotional expression, comparable in intensity and arousal to fearful expression, but with different emotional content. Looming angry faces, although negative and highly arousing, would represent a direct threat to the individual. Spatial attention would be directed toward the looming angry face, which represents the threat per se, leaving any peripheral event unattended, to support the processing of events in the proximity of the face. Previous studies have described that static angry faces attract attention (Jenkins, 2017; Öhman et al., 2001; Sun et al., 2017) and hold it for longer period of time than fearful faces (Fox et al., 2002; Juncai et al., 2017).

By adopting a similar paradigm used in Study 2a, the present study will contrast the effect of neutral and angry faces on the distribution of spatial attention in PPS. The hypothesis is that both with angry and neutral faces in PPS, attention is focused on the approaching face (or space immediately surrounding it). Therefore, it is expected to find facilitation in the responses to tactile stimuli that depends on the distance of the face from the participant’s body: participants are expected to respond faster to the tactile stimulation when faces are in near, as opposed to far space (PPS effect). Also, since attention is expected to remain on the face, balls that appear close to it are expected to further facilitate the tactile responses, with respect to when they appear more in the periphery.

5.3.2 Methods

Participants

Twenty-three healthy participants were recruited (12 females; mean age 25±6.33). None of the participants reported any history of neurological or psychiatric disorders, and all were naive to the purpose of the study. The experiment was conducted in accordance with the principles of the Declaration of Helsinki and approved by the Bioethics Committee of the University of Bologna. Each participant gave written informed consent before participating and after being informed about the procedure of the study. The sample size was determined via a power analysis conducted in G*Power 3.1 software (Faul et al., 2007); the modulation of spatial attention in PPS was expected to have a medium to large effect size (Torrence et al., 2017; Valdés-Conroy et al., 2014); the alpha was set at 0.05 and the power was set at 0.95. For a repeated measure within-factor analysis of variance (ANOVA) with no covariates, it was determined that a sample size of twenty-three would be enough to detect the effect.

Task and experimental procedure

Experimental stimuli, task and procedure were identical to the ones adopted in Study 2a (see Paragraph 5.2.2.1 for a detailed description of the method), with the only difference that faces showed a neutral or an angry expression (see Figure 4.1 A-D). The expression was manipulated ad hoc and validated in a preliminary study (see Chapter 4, Paragraph 4.2.2.3).

5.3.3 Results

The rate of omissions was low (M=1.23% SD=1.3). For this reason, the performance was analysed in terms of reaction times (RTs) only, as previously done in e.g., Canzoneri, Magosso, & Serino (2012). Trials with RTs exceeding more than 2 standard deviations from the mean RT of each block were considered as outliers and excluded from the analyses (M=4.40%. SD=0.85). For each participant, mean RTs were calculated for each condition and used for analysis.

A 2x2x2 RM ANOVA (Face Emotion: Neutral / Angry; Space: Far / Near; Ball Position: Central / Peripheral) was conducted to test whether looming angry vs. neutral faces induced a change in PPS representation (i.e. a difference in RTs to tactile stimulation) through a different distribution of spatial attention, probed by the ball appearing centrally or peripherally from the face.

Results showed no significant main effect of Face Emotion [F(1,22)=1.33; p=0.26; η_p^2=0.06]. A significant main effect of Space [F(1,22)=83.33; p<0.01; η_p^2=0.79] was found; participants responded faster when tactile stimuli were delivered with faces in the Near than Far space (Near: M=340.28 ms; SEM=19.09; Far: M=371.52 ms; SEM=18.20). The main effect of Ball Position was not significant [F (1,22)=1.48; p=0.24; η_p^2=0.06]. No significant Face Emotion by Space interaction [F (1,22) =0.07; p=0.80; η_p^2<0.01] was found, nor a significant three-way Face Emotion by Space by Ball position interaction [F (1,22) =0.21; p=0.65; η_p^2<0.01]. Responses to tactile stimuli were facilitated when faces were near to, as opposed to far from, the participant (classic PPS effect). No effect of Face Emotion, nor interaction with the Ball position was found significant (see Figure 5.4).

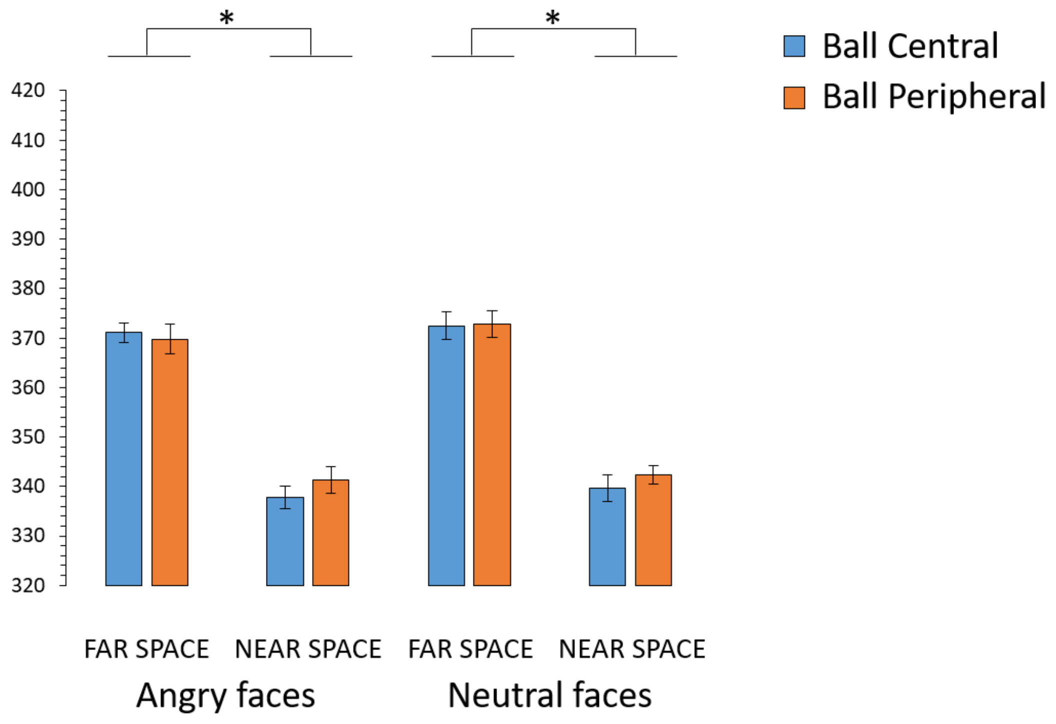


Figure 5.4. Results of Study 2b. The bar graph shows the main effect of Distance. Responses to tactile stimuli are facilitated (faster RTs), when the face is in the Near condition, as opposed to the Far condition. This effect is observable both in the Neutral and in the Angry faces condition. Asterisks indicate significant comparisons. Error bars represent the standard error of the mean (S.E.M.).

5.3.4 Discussion

Abundant empirical evidence has converged to suggest that emotional faces can strongly affect attentional mechanisms (Pourtois & Vuilleumier, 2006). Angry faces are particularly salient stimuli that represent a direct threat calling for attention to remain focused on the angry individual (Juncai et al., 2017; Sarlo & Munafò, 2010; Taylor & Whalen, 2014).

PPS is the multimodal sensorimotor interface around the body that mediates any interaction with the environment; it has specifically a defensive function and varies according to various factors including the affective salience of the stimulus. Study 2b aimed to investigate whether looming angry faces, contrasted to neutral, induce a change in PPS representation (i.e., a change in RTs to tactile stimulation), by promoting a different distribution of spatial attention, probed by a ball that could appear close to the face or more peripherally. Results showed that the responses to tactile stimuli were faster when the faces, with an angry or neutral expression, appeared in the space near the subject than when they appear in the space far. The facilitation of tactile responses associated with the space of presentation of the face is attributed to the multisensory integration of visual stimuli into the somatosensory processing of tactile stimuli on the body (PPS effect). Importantly no effect of the ball position was found. Responses to tactile stimuli were not further modulated by peripheral balls, nor when the face was looming in the far, nor in the near space of the subject, for both neutral and angry faces. This result can be taken as evidence that nor neutral nor angry faces would redirect spatial attention when looming in PPS. In this respect, this result was similar to what found with joyful faces in Study 2a and adds the evidence that both joyful and angry faces when intrudes PPS call for the attention to remain focused on the emotional face, without redirecting it. Unexpectedly, at a difference with the joyful faces in Study 2a, no advantage associated with the central ball was found; in fact, responses to tactile stimuli were similar when the face was presented with a central or a peripheral ball. The advantage of the central ball compared with the peripheral was previously taken as the hallmark of the attentional capture onto the face location and the immediate surrounding, at the expenses of the processing of events in the peripheral space. Nonetheless, this can still be interpreted as the fact that since the angry face is the threat, any event co-occurring with it, has very little importance for survival, even if it appears close to the face itself. The arousal generated by an angry face looming toward the subject would have had an important role in capturing attention, with no difference between the central and the peripheral balls. Angry faces, as salient threatening stimuli, are of particular relevance for survival and are shown to consistently capture attention (Fox et al., 2002; Holmes et al., 2009; Williams et al., 2005), with a harder disengagement from the angry face (Ambron et al., 2016; Fox et al., 2002; Juncai et al., 2017). These findings are in line with the results of the present study, which showed that the position of any other visual element, did not further modulate the tactile responses, that were only affected by the position of the face from the participant. Thus, with angry faces, it was not observed the redirection of attention found with fearful faces. Fearful and angry faces are both negatively valenced and similarly arousing stimuli (Hariri et al., 2002). As a further confirmation of this, is the result of the experimental stimuli validation (see Chapter 4, Paragraph 4.2.2.3), where angry faces did not obtain a differential intensity and arousal scores than fearful faces. Thus, the possibility that fearful expression produced a greater arousal response than angry faces is an unlikely explanation of the present findings. Previous literature would suggest a critical difference between the two expressions in the effect on attentional and memory processes. In a passive viewing task, Davis and colleagues (2011), showed that neutral words presented after fearful facial expressions were better remembered than those presented after the angry faces. Since fearful expressions are not informative about the source of the current threat, they induce the viewer to direct the attention to the context. On the other hand, angry faces, that embody a certain and a direct threat, might lead the observer to focus the attention on the angry individual, impairing the memorization of contextual neutral event. Consistently with this result, Taylor and Whalen (2014), showed that a fearful, but not an angry expression, diffuses attention to peripheral targets, in an attentional blink paradigm. In this paradigm, the ability to detect a subsequent peripheral target is increased by the presentation of a fearful face, but not by the presentation of an angry or a neutral face. Fearful and angry faces are both signalling an increase in the probability of encountering a threat, however, fearful faces are more context-dependent, their informative value is increased with the examination of contextual information, that may reveal the source of the threat for which the individual is fearful. As a consequence, it is expected that a fearful face should diffuse attention, eliciting a greater sensitivity to the surrounding context (Becker & Detweiler-Bedell, 2009; Phelps et al., 2006). The observer is then encouraged to learn about the environment and to gather information to disambiguate the threat.

To conclude, fearful and angry faces are at once, interesting, arousing and negatively valenced, so it would be expected that they would affect attention in the same way. However fearful faces produce a widening of attention not observed for angry faces; this is likely due to their different communicative value of providing different information about the social and physical environment.

5.4. Conclusions

Chapter 5 was dedicated to the presentation of studies that showed, at the behavioural level, that emotional faces in PPS differently modulated spatial attention. Faces are salient stimuli in the environment and are expected to attract attention. However, once invading PPS, only fearful faces, at the difference with neutral, joyful and angry faces seem to diffuse attention to the peripheral space. Study 2a tested the hypothesis that: first, joyful and neutral faces do not redistribute attention when they intrude PPS, and second, that fearful faces in PPS are associated with a redirection of attention from the face location to the periphery. To exclude any effect due to the negative valence of the emotional expression of fear, Study 2b contrasted neutral faces with another negative and arousing emotional expression, angry faces. The hypothesis tested was that angry faces do not redistribute attention when they intrude PPS. In both studies, in each emotional condition, it was found a PPS effect (i.e. faster responses to tactile stimuli when the face occurs in the space near the subject rather than far). Also, when the face was fearful and in the near space, responses to tactile stimuli were faster when presented together with a peripheral visual element (the ball), than when the same element was presented more centrally in the visual field (attentional effect). This attentional effect was not found for neutral and joyful facial expressions both in the far and in the near space. Importantly, the redirection of attention was not a generic reaction to threat, or attributable to the negative valence or the arousal level of the emotion expressed; at a difference for what found for fearful faces, angry faces did not trigger any redistribution of spatial attention when approaching the subject, similarly with neutral faces.

To conclude, fearful faces in PPS do not draw attention to the location of the face, at variance with other emotions, but to other locations where the threat may be located. The redirection of attention toward the periphery explains the facilitation of the responses to tactile target when another visual element (the ball) is presented exactly at the periphery. The spatial logic of fear is a complex multisensory event expressed by the somatosensory processing of tactile stimuli and visual processing of the face, mediated by spatial attention.

CHAPTER 6. Neural correlates of the Spatial Logic of Fear

6.1. Introduction

PPS defines an area of highest relevance for the protection of the body, where the presence of a threat is particularly imminent, and the preparation of an urgent defensive response is needed. A pivotal function of PPS is to defend the body against potential threats from the environment. Looming fearful faces, salient stimuli which signal the presence of a potential threat, at a difference with other emotions, elicit a differential pattern of multimodal interactions when presented in the space close to the subject (Study 1; Chapter 4). This PPS modulation can be attributed to the fact that an approaching fearful face, at variance with other emotions, elicits a shift of spatial attentional resources from the face to the surrounding of the face (Study 2a and 2b; Chapter 5). Fearful faces do not draw attention to their location, but to the peripheral space, where the threat may be located. The present chapter describes two studies aiming to investigate whether the attentional effect found at the behavioural level is reflected also in the electrophysiological response (EEG; Study 3) and in the skin conductance response (SCR; Study 4). Particularly, if it is true that a fearful face intruding the PPS elicits a diversion of the spatial focus of attention to the peripheral space leaving the face unattended, this effect should be reflected in the modulation of the neural signal associated with face processing (N170). Study 3 would address this question by adopting the same paradigm as in Study 2a and Study 2b while measuring EEG. The expectation is to find, for near looming fearful and neutral faces, a reduced evoked response in the condition in which attention may be exogenously captured by peripheral, rather than central, visual elements. This modulation of the signal would be particularly evident for fearful faces, which are expected to promote the shift of attention in the periphery. This grater recruiting of attentional resources in the space near the body would be adaptive to solve the ambiguous information provided by the fearful face: there is a potential threat somewhere here, but its location and source are unknown. The attentional scanning of the environment may be also sustained by the transient activation of the autonomous system, reflected with an increase of the SCR when a fearful face is looming in PPS. Study 4 will test this hypothesis by investigating whether looming fearful faces, at a difference with joyful and neutral, evoke an arousal response, which increases as the fearful faces are closer to the observer. These studies would complement behavioural findings and show that the attentional and the autonomic responses may enhance the defensive function of the multisensory PPS.

6.2. Study 3: Fearful faces modulate spatial attention in Peripersonal Space: an ERP study

6.2.1 Introduction

As a defensive margin around the body, PPS is the function that mediates the engagement into efficient actions, aimed at self-protection, whenever a salient and potentially harmful stimulus approaches the body (Fossataro et al., 2016; Sambo et al., 2012). Looming stimuli are particularly salient as may constitute a potential threat to the integrity of the body. Accordingly, they are likely to attract attention and influence the perceptual processing of another stimulus in a different modality (Bestmann et al., 2007; Leo et al., 2011; Merz et al., 2020; Romei et al., 2009, 2013; Thelen et al., 2012). Attention is not uniformly distributed across space. Previous research revealed that attention seems, instead, preferentially allocated to the space closer to the observer (Finlayson & Grove, 2015; Maringelli et al., 2001; Plewan & Rinkenauer, 2016, 2017). An enhanced amplitude of early visual evoked potential, i.e, P1/N1, which is considered the hallmark of enhanced spatial attention (Pourtois & Vuilleumier, 2006), was found for near, rather than far, attended stimuli (Kasai et al., 2003). This result was further confirmed by Valdés-Conroy and colleagues (2014). This near/far effect (enhanced attention for stimuli near the body versus stimuli far from the body stimuli) was reflected also in the somatosensory potentials (Sambo & Forster, 2009). Sambo and

Foster (2009) found that the spatial-correspondence of tactile stimuli, provided at the hand, and visual stimuli, appearing close to the stimulated hand, was enhancing amplitudes of potentials, recorded over and close to the somatosensory cortex and present as early as 100 ms, in comparison to the condition in which the visual stimulus was projected in the far or near to the non-stimulated hand. The near-space is also the space in which the shifts of attention in the frontal plane are more facilitated, i.e., between the left/right hemifield of the near-space, compared to when attention shifts in the far (Chen et al., 2012; Wang et al., 2016). Sambo and Foster (2009) found enhanced amplitudes of the somatosensory N140 when visual stimuli were delivered close to the tactually stimulated hand and the participants were instructed to attend the hand, compared to when the stimulated hand was not attended. However, when the visual and tactile stimuli were delivered in the near-space but presented in different hands, N140 amplitude did not differ if the tactually stimulated hand was attended or not. The authors speculated that the appearance of an opposite visual stimulus was acting as exogenous cues that drew the attention away from the side of tactile stimulation. This effect seemed to be present just in the near, and not in the far space, where potentials were overall higher if the tactile stimulus was attended rather than unattended. All together these findings are showing that the space near the body is where attention is preferentially oriented and that stimuli appearing in the proximity of the body are more likely to promote a shift of attention.

This attentional preference of the near-space is also enhanced by the affective salience of the stimulus (de Haan et al., 2016; Yiend, 2010) which appeared to modulate the estimation of the arrival time of looming stimuli going to impact the body (the time-to-collision judgments). Threatening stimuli are judged to a have shorter time-to-collision than neutral stimuli (Vagnoni et al., 2012) and, when presented close to the tactually stimulated hand, they facilitate tactile detection (Poliakoff et al., 2007; Van Damme et al., 2009). The allocation of attention to the affective properties of the stimuli (Carretié et al., 2004) was also reflected in the enhanced amplitude of the N1 and the occipital LPP (Valdés-Conroy et al., 2014) irrespectively of the space of presentation;

the parietal LPP amplitude, instead, showed a spatial effect, by being enhanced for near stimuli, compared to the far ones; this dissociation would support, according to the authors, the dorsal/ventral distinction (Valdés-Conroy et al., 2014). All these pieces of evidence are suggesting that both the valence and the distance would affect spatial attentive responses.

In a recent study, it was shown that looming fearful faces, very salient affective stimuli, prompt a shift of spatial attention from the face to the peripheral space when presented in the space near the subject (Ellena et al., 2020). This disengagement of attention may be adaptive to promote the attentional scanning of the environment, to search for the potential threat signalled by the fearful face. Importantly, this effect was observed as a multisensory event mediated by spatial attention. Indeed, it was found in the modulation of the speed of the motor response to tactile stimuli. Simple reaction times to tactile stimuli were facilitated when the tactile stimuli co-occurred with a fearful face looming in the near space and presented together with another peripheral visual element (peripheral ball), compared to when the face is presented with the same visual element, presented more centrally, close to the face (ball central). Since attention is assumed to be shifted from the fearful face to the periphery, any event appearing in the peripheral near space is integrated into the processing of tactile stimuli facilitating the motor response to them.

The present study aims to investigate whether this effect of redirection of attention may be also reflected in a modulation of the neural signal associated with face processing. Of relevance in this respect is the N170 ERP component, a negative deflection in electrical potential observed at temporo-occipital electrodes, peaking between 130 and 200 ms from the presentation of a face (Hinojosa et al., 2015; Rossion, 2014). This component appears to reflect the perceptual processing of low-level configurational features and high-level features, including facial expressions. N170 component has also been shown to be modulated by the degree of attention paid to the face, with larger negativities being associated with attended relative to unattended faces (Crist et al., 2008; Eimer, 2000; Holmes et al., 2003; Iidaka, 2014; Jacques & Rossion, 2006).

In this study, healthy participants were asked to complete a similar paradigm as in Ellena and colleagues (2020), and the electroencephalographic activity was recorded. In this study, only fearful and neutral faces were tested. It is hypothesized a differential modulation of the electrophysiological response evoked by the fearful face looming in the PPS and presented together with a peripheral visual element, compared to when it is presented with a visual element in more central positions. When a near fearful face is combined with a peripheral element, attention is expected to be disengaged from the face to favour the peripheral event, leaving the face unattended. This effect should correspond to the reduced amplitude of the evoked N170, compared to the condition where the face is presented with a central element, which should elicit larger amplitudes. The effect of the position of the ball (larger negative amplitudes with central than peripheral balls) is expected to be reduced with near-neutral faces, a condition in which the disengagement of spatial attention from the face to the periphery is expected to be less facilitated. Also, when the face is in the far space condition, no differential effect depending on the position of the ball is expected to be found.

6.2.2 Methods

Participants

Twenty-two healthy participants with no history of neurological or psychiatric disorder were recruited (12 females; age: M ± SD = 27.68 ± 4.3 years). The experiment was conducted following the principles of the Declaration of Helsinki and approved by the Bioethics Committee of the University of Bologna. Each participant gave written informed consent before participating and after being informed about the procedure of the experiment. Based on previous literature (Crist et al., 2008; Holmes et al., 2003; Li et al., 2016; Zhang et al., 2014), it was expected the modulation of the evoked N170 potential effect by spatial attention to have medium to large effect sizes (η_p^2 =0.12–0.34). Using G*Power 3.1 software (Faul et al., 2007), with an effect size of f= 0.25

(medium effect size), an alpha of 0.05 and a power (1 – β) of 0.9 for repeated measures, within-factor analysis of variance (ANOVA) with no covariates, it was determined that an N > 20 would be needed to detect this effect. Thus, we recruited 22 participants, which is also consistent with sample sizes of studies measuring evoked potentials in peripersonal space paradigms (e.g. Sambo & Forster, 2009; Valdés-Conroy et al., 2014).

Task and experimental procedure

Experimental design and paradigm were adopted from Study 2a (Paragraph 5.2.2.1) (Ellena et al., 2020). The experiment was implemented in ExpyVR (software freely available online at http://lnco.epfl.ch/expyvr). The tactile stimuli were delivered on the cheeks bilaterally through a pair of vibrators (Precision MicroDrivers, shaftless vibration motors, model 312-101, 3V, 60 mA, 150 Hz, 5g). The motor had a surface area of 113 mm2 and reached maximal rotation speed in 50 ms. This device was activated for 100 ms during tactile stimulation. To study the impact of different emotional conditions on PPS faces with neutral vs. fearful expressions were presented either in the far or near the participant's space and looming at a constant speed towards the participant (see Figure 5.1).

At the beginning of each trial (T0), an avatar face with a neutral or fearful expression appeared centrally on the visual field, either in the space near to (≈115 cm) or far from (≈220 cm) the participant, by relaying stereoscopically to the head-mounted display (HMD, Oculus Rift SDK, Oculus VR, 100° field of view, 60 Hz) worn by the participant. The face then moved toward the participant on the sagittal plane for a total of 3000 ms until its final position (Near: ≈10 cm; Far: ≈115 cm) where it remained still for 1000 ms (T2). Importantly, 2000 ms after the beginning of the trial (T1), the tactile stimulation was delivered bilaterally, and, simultaneously, a static checkerboarded ball, appeared for 250 ms, either ≈1° (Ball Central) or ≈10° (Ball Peripheral) to the left or right of the face (see Figure 5.1); left and right sides counterbalanced among trials. Thus, at T1, tactile vibration coincided with the perception of the ball and the avatar's face, at different distances from the participant (at ≈45 cm, in the near, and ≈150 cm in the far). The ITI was set at 2100 ms (+/- 100 of jitter).

There was a total of 320 experimental trials, evenly distributed among 8 experimental conditions (i.e. 40 trials per condition): Face Emotion: Neutral / Fearful; Space: Far / Near; Ball Position: Central / Peripheral. An additional 80 trials with no vibration and 20 trials with no ball presentation were introduced to decrease task predictability. Both central and peripheral balls could be presented either on the left or right side of the face. The entire experiment was split into 5 separate blocks of 84 trials each and conditions were randomly but equally distributed across blocks. The experimental session lasted approximately one hour, and participants could rest between blocks to prevent fatigue. After signing the consent form, participants seated on a comfortable chair, in a sound-attenuated room. Vibrators were then attached bilaterally on the cheeks with medical tape and electrophysiological activity was verified; EEG cap was fitted, and the virtual reality headset mounted on the head of the participant. Importantly, the bands of the VR montage were not in contact with the EEG electrodes selected for the analysis (P7, P07, P8, P08; see Figure 6.1). Before the task began, the lenses' focus was manually adjusted by each participant until a clear vision was reported. During the task, participants made simple speeded responses to the tactile stimulation by pressing a button placed on the table in front of the participant with their right hand.

Recording and Data Analysis

EEG signal was continuously recorded with Ag/AgCl electrodes (Fast n Easy Electrodes, Easycap, Herrsching, Germany) during task execution from 59 scalp sites (Fp1, AF3, AF7, F1, F3, F7, FC1, FC3, FC5, FT7, C1, C3, C5, T7, CP1, CP3, CP5, TP7, P1, P3, P5, P7, PO3, PO7, O1, Fp2, AF4, AF8, F2, F4, F8, FC2, FC4, FC6, FT8, C2, C4, C6, T8, CP2, CP4, CP6, TP8, P2, P4, P6, P8, PO4, PO8, O2, FPz, AFz, Fz, FCz, Cz, CPz, Pz, POz, Oz) and the left mastoid. The right mastoid was used as a reference, while the ground electrode was positioned on the right cheek. Vertical and horizontal EOG components were recorded from above and below the left eye, and from the outer canthus of both eyes. Signal impedance was maintained below 5 KΩ, which was checked at the end of every block. The electrooculogram (EOG) was recorded from above and below the left eye and from the outer canthi of both eyes. The EEG and EOG were recorded with a band-pass filter of 0.01–100 Hz and a slope of 12 dB/Oct, amplified by a BrainAmp DC amplifier (Brain Products, Gilching, Germany) and digitized at a sampling rate of 1000 Hz. The EEG data were pre-processed using EEGLAB toolbox, version 14.1.0 (Delorme and Makeig, 2004) and custom routines written in MATLAB R2016b (The MathWorks, Natick, MA). Data from all electrodes were re-referenced to the average of both mastoids and filtered with a high-band pass filter of 0.5 and low-band pass filter of 30 Hz. Continuous signals were segmented into epochs of 5000 ms, starting at 1000 ms preceding the face stimulus onset (T0) and for another 4000 ms until the offset of the face (T2). EEG activity was baseline-corrected throughout 200 ms preceding T0. Also, epochs with large artefacts contamination were identified and removed using two methods from the EEGLAB toolbox (Delorme et al., 2007): (1) an epoch was excluded whenever the voltage on an EEG channel exceeded 400 μV (this ensured that epochs with large EEG peaks were safely removed); (2) an epoch was excluded whenever the joint probability of a trial exceeded five standard deviations (this method ensured that epochs with improbable data were safely removed; mean excluded epochs: 5.98 %). The total number of epochs remaining after preprocessing was 92,02%. In each condition, the epochs left after preprocessing were: 91.02% in the Fear Far Central 91.48% in the Fear Far Peripheral, 91.7% in the Fear Near Central, 90.79% in the Fear Near Peripheral, 91.36% in the Neutral Far Central, 92.16% in the Neutral Far Peripheral, 92.95% in the Neutral Near Central and 94.66% in the Neutral Near Peripheral. Importantly, the number of remaining epochs did not differ between conditions in which the ball was central versus peripheral ($F(1,21)=0.48$; $p=0.49$). Moreover, residual artefacts (such as eye blinks or eye movements) were identified using an Independent Component Analysis (ICA) decomposition method (Makeig et al., 1997) and removed according to the ADJUST plugin application (Mognon & Buiatti, 2011).

Remaining epochs were divided into eight separate datasets, according to the stimulus condition. The N170 was evaluated as the activity of the left (P7, PO7) and right (P8, PO8) temporo-occipital recording sites (as in Jacques & Rossion, 2006; Kuefner et al., 2010). For each participant, the time closest to 170 ms (Gao et al., 2019), for which maximal negative deflection after T1 (the appearance of the ball and the delivery of the tactile stimulation) was observed, was used to anchor a relative sub-time-window of ±15 ms (Moore et al., 2014; Prieto et al., 2011). N170 component was quantified as the mean amplitude within this sub-time-window (Jacques et al., 2019). This method controlled for latency variance of N170 onset (Ganis et al., 2012), while preserving the mean amplitude measure's lower susceptibility to spurious peaks (Ito et al., 2014; Luck, 2014; Ott et al., 2011). N170 mean amplitudes were analysed with a 2x2x2 RM ANOVA (Emotion: Neutral / Fearful; Space: Far / Near; Ball Position: Central/ Peripheral, as within-participants factors). Post-hoc comparisons were carried out using the Newman–Keuls test.

Figure 6.1. Illustration of the EEG/VR montage. As it can be seen in the illustration, the bands of the VR montage were not in contact with the EEG electrodes, shown in red, selected for the analysis (P7; PO7; P8; PO8).

6.2.3 Results

Behavioural Results

Behavioural results (RTs to tactile stimuli) were expected to replicate what found in the previous study (Ellena et al., 2020). It is tested if the presence of a fearful face, relative to a neutral, had a differential impact on the motor response to tactile stimuli delivered on the participants' face. Tactile stimulation was always paired with the presentation of a ball that could appear next to or distal from the looming face. Importantly, to measure the potential impact of PPS on performance, this effect was measured as a function of the near (peripersonal) and far space (extrapersonal).

As the rate of omissions was low (M=1.25% SD=2.12), the performance was analysed in terms of reaction times (RTs) only, as in previous studies (e.g., Canzoneri, Magosso, & Serino, 2012). Trials with RTs exceeding more than 2.5 standard deviations from the mean RT of each block were considered outliers and excluded from the analyses (M=4.03%. SD=2.38). For each participant, mean RTs were calculated for each of the eight different conditions and used for analysis.

A 2x2x2 RM ANOVA (Face Emotion: Neutral vs. Fearful; Space: Far vs. Near; Ball Position: Central vs. Peripheral) was conducted to test whether looming fearful, vs. neutral faces, induced a change in PPS representation (i.e. a difference in RTs to tactile stimulation) through a different distribution of spatial attention, probed by the spatial ball appearing centrally (next to the face) or peripherally (far apart from the face).

Results (see Figure 6.2) showed a significant main effect of Face Emotion [F(1,21)=16.32; p<0.01; η_p^2=0.44] with participants responding faster to Fearful relative to Neutral faces (Fearful faces: M=373.30 ms; SEM=17.29; Neutral faces: M=381.04 ms; SEM=16.79). There was also a significant main effect of Space [F(1,21)=87.44; p<0.01; η_p^2=0.81] with participants responding faster to faces in the Near relative to the Far space (Near space: M=359.90 ms; SEM=17.15; Far space: M=394.44 ms; SEM=17.08). There was no significant main effect of Ball Position [F(1,21)=0.97; p=0.34; η_p^2=0.04], nor Emotion by Space [F(1,21)=0.01; p=0.91; η_p^2<0.01] or Face

Emotion by Ball Position [F(1,21)=0.01; p=0.93; $\eta_p^2<0.01$] interaction. However, there was a significant Space by Ball Position [F(1,21)=4.26; p=0.05; $\eta_p^2=0.17$] interaction showing that the Ball position had a different impact on RTs. Crucially, the Space by Ball Position was best explained by the significant three-ways Face Emotion by Space by Ball Position interaction [F(1,21)=6.72; p=0.02; $\eta_p^2=0.24$] suggesting that the impact on the ball in the near and far space differently affected RTs for fearful and neutral face presentations. Specifically, Newman-Keuls post-hoc comparisons revealed that for neutral faces, RTs to the tactile stimuli were not affected by the spatial Ball position, either in the far (Neutral Far Central: M=397.09 ms, SEM=16.07; Neutral Far Peripheral: M=399.23 ms, SEM=16.07; p=0.33) or the near-space (Neutral Near Central: M=363.38 ms, SEM=17.50; Neutral Near Peripheral: M=364.37 ms, SEM=17.34; p=0.66). In contrast, when fearful faces were shown, Ball Position affected RTs to tactile stimuli differently for the far and the near-space: in the far space, RTs were faster for central relative to peripheral spatial Balls (Fear Far Central: M=386.83 ms, SEM=17.86; Fear Far Peripheral: M=394.52 ms, SEM=17.89; p<0.01); in the near space, instead, RTs were faster for peripheral relative to central spatial balls (Fear Near Central: M=358.45 ms, SEM=18.10; Fear Near Peripheral: M=353.38 ms, SEM=16.05; p=0.03). Finally, when examining the difference between fearful and neutral faces, we found that, in near space, tactile responses were faster to fearful than neutral faces, both with the central and peripheral balls (central ball: p=0.04; peripheral ball: p<0.01). In contrast, in far space, tactile responses were faster to fearful than neutral faces, for central balls only (p<0.01).

Additionally, the analysis was repeated including block (1 to 5) as a factor. This produced a significant main effect of block (p<0.01), with participants becoming faster as the task progresses. Nevertheless, and most importantly, we found no evidence of an interaction between blocks and emotion, suggesting that any effect on RTs due to task progression is independent of the emotion manipulation; all p≥0.34). Additionally, including ball side (sx, dx) as a factor revealed a main effect of side (p=0.01), with participants being faster to left than right stimuli. Nevertheless, there was no interaction between side and emotion (all $p \geq 0.09$), suggesting that any effect on RTs related to the side of ball appearance is independent of the emotional manipulation.

ERPs Results

As for EEG data, the peak negativity is expected to be larger when a fearful face, looming in the near space, is cued by a central than a peripheral ball. Attention, in the condition of a ball appearing in the periphery, is expected to be redirected towards the peripheral space and therefore away from the face. When a neutral face is looming in the near space, attention is not expected to be redirected towards the periphery, therefore the effect of the position of the ball on the peak negativity should be reduced. Finally, no significant modulation of the N170 amplitude is expected for any condition in the far space.

Results of the N170 component (see Figure 6.3) showed a significant main effect of the mean amplitude for the factor Ball Position [$F(1,21)=37.40$; $p<0.01$; $\eta_p^2=0.64$] showing more negative amplitudes for central relative to peripheral Balls (Central: M=-4.14 μV; SEM=0.64; Peripheral: M=-3.23 μV; SEM=0.64). Moreover, there was a significant interaction of Space by Ball Position [$F(1,21)=9.71$; $p<0.01$; $\eta_p^2=0.32$]. Crucially, the two-way interaction was best explained by a significant Emotion by Space by Ball Position interaction [$F(1,21) = 4.95$; $p=0.04$; $\eta_p^2=0.19$], suggesting that emotion of the face differently impacted N170 amplitude modulation as a function of spatial distance and ball position.

Specifically, Newman-Keuls post-hoc comparisons revealed that, when the face was in the far space, ball position did not modulate mean amplitude significantly, both for fearful (Fear Far Central: M=-3.9 μV, SEM=0.69; Fear Far Peripheral: M=-3.69 μV, SEM=0.71; p=0.63) and neutral faces (Neutral Far Central: M=-3.70 μV, SEM=0.66; Neutral Far Peripheral: M=-3.42 μV, SEM=0.64; p=0.44). Conversely, when the face was in the near space, ball position significantly modulated mean amplitude. Amplitude was more negative for central than for peripheral ball, both for fearful (Fear Near Central: M=-4.63 μV, SEM=0.71; Fear Near Peripheral: M=-2.58μV, SEM=0.69; p<0.01) and neutral faces (Neutral Near Central: M=-4.33 μV, SEM=0.64; Neutral Near Peripheral: M=-3.21 μV, SEM=0.64; p<0.01). Crucially, when the peripheral ball was presented in the near space, ERP amplitude was less negative for fearful (M=-2.58) than for neutral faces (M=-3.21) (p=0.01). No other main effects nor interactions were significant (all ps>0.08).

Correlation between behavioural and ERP responses

To further understand the relationship between our behavioural and electrophysiological results, two Pearson correlations were conducted on data for the fearful far and near conditions, where a difference in RTs was found between the central and peripheral balls. In order to facilitate data interpretability, a difference in RTs between the central and peripheral ball was first computed, as well as the difference in N170 mean amplitude between the peripheral and central ball. Thus, an RT difference greater than 0 indicates faster response to the peripheral relative to central ball. Also, an ERP difference greater than 0 indicates smaller N170 with the peripheral relative to central ball. Results showed a significant positive correlation between the difference in RTs and N170 amplitude both for the near and far conditions (near: r=0.46, n=22, p=0.03; far: r=0.67, n=22, p<0.01; see Figure 6.4). Thus, the faster participants responded to the peripheral relative to the central ball, the smaller was their N170.

Note, that although the relationship between ERP amplitude and RTs is found both for near and far spaces, visual inspection of Figure 6.4 shows a different distribution of individual participants' data. Specifically, in near space, the majority of participants responded faster to the peripheral (vs central) ball (RT difference > 0), and all but one participant had a smaller N170 when the ball was presented peripherally as opposed to centrally. This is reflected in the group mean (red dot) value, which falls in the upper right quadrant of the plot, indicating that both mean RT and ERP differences are positive. In contrast, in far space, the majority of participants responded more slowly to the peripheral than to the central ball (RT difference < 0). Also, about half of the group had a smaller N170 when presented with the peripheral (vs central) ball (ERP difference > 0), while the remaining half had the opposite pattern explaining the absence of significant differences in the post-hoc tests on ERPs for this condition. Again, this distribution of scores is reflected in the group mean (red dot) values, which falls in the upper left quadrant of the plot, indicating mean RT difference > 0 and mean ERP difference ~ 0.

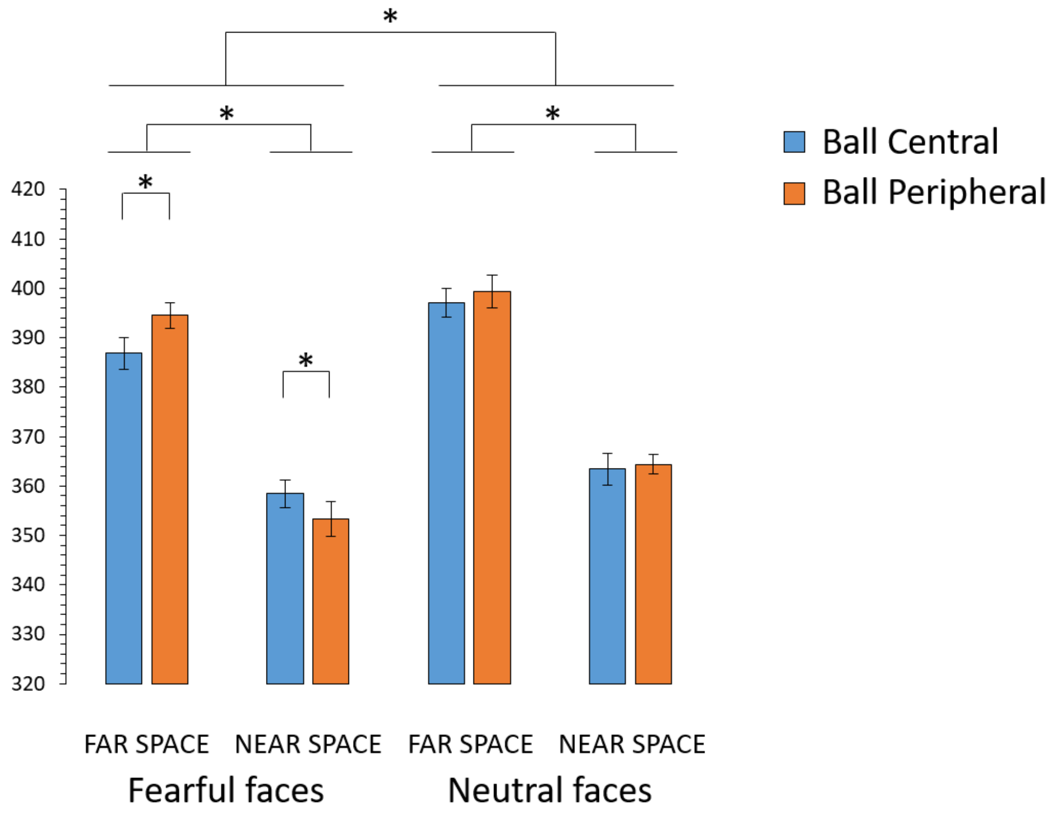


Figure 6.2. Behavioural results. The bar graph shows the main effect of Space. Responses to tactile stimuli are facilitated (faster RTs), when the face is in the Near condition, as opposed to the Far condition. This effect is observable both in the Neutral and in the Fearful faces condition. Also, a main effect of the Face Emotion is observable: responses to tactile stimuli are facilitated in the Fearful, as opposed to the Neutral face condition. Moreover, only when the face was fearful the Ball Position affected responses to tactile stimuli. In the Far condition responses to tactile stimuli were facilitated in presence of the central compared to the peripheral ball, while in the Near condition responses to tactile stimuli were facilitated in presence of the peripheral compared to the central

ball. Asterisks indicate significant comparisons. Error bars represent the standard error of the mean (S.E.M.).

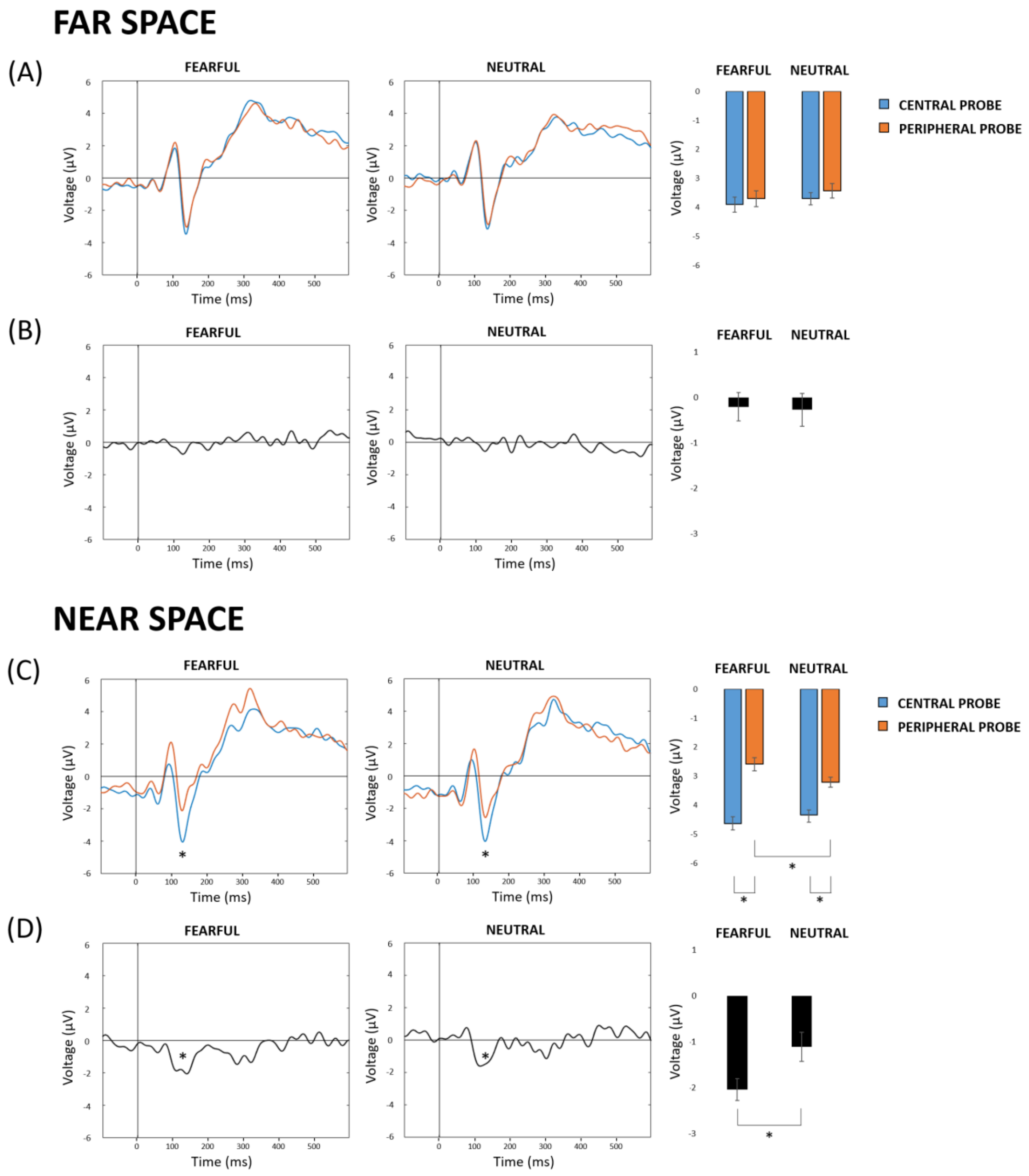


Figure 6.3. ERP results. Panel A and panel B represent ERPs results in the far space condition. In panel A, ERPs are plotted as a function of the ball position (central ball vs peripheral ball) in response to the emotion condition (fearful face vs neutral face). Bar plot on the rightmost part of

panel A depicts averaged values of the signal amplitude in the far space condition. Panel B depicts the ERP difference between the central and the peripheral ball condition in response to the emotion condition (fearful face vs neutral face). Bar plot in the rightmost part of panel B depicts the ball position effect calculated as the difference of the averaged values of the N170 amplitude between central and peripheral ball. Results in the far space condition showed that the ball position did not modulate amplitude negativity, both for fearful and neutral faces. Panel C and panel D represent ERPs results in the near space condition. In panel C, ERPs are plotted as a function of the ball position (central ball vs peripheral ball) in response to the emotion condition (fearful face vs neutral face). Bar plot on the rightmost part of panel C depicts averaged values of the signal amplitude in the near space condition. Panel D depicts the ERP difference between the central and the peripheral ball condition in response to the emotion condition (fearful face vs neutral face). Bar plot in the rightmost part of panel D depicts the ball position effect calculated as the difference of the averaged values of the N170 amplitude between central and peripheral ball. Results in the near space condition showed that when the face was in the near space, ball position did modulate amplitude negativity; amplitudes were more negative for central than for peripheral ball position, both for fearful and neutral faces. Crucially, the near space condition, a significant difference in the modulation of the signal amplitudes by the ball position was found between the fearful and the neutral faces: amplitudes in the peripheral ball condition, with fearful faces, were significantly less negative than in the peripheral ball condition with neutral faces. Asterisks indicate significant comparisons. Error bars represent the standard error of the mean.

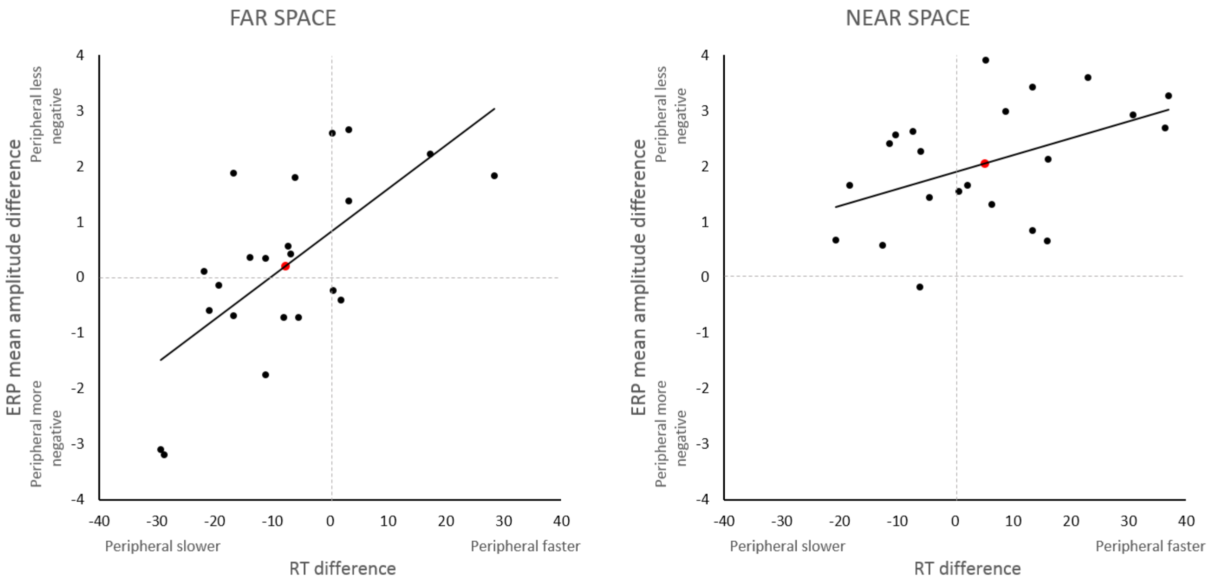


Figure 6.4. Correlation between the difference in RTs between the central and peripheral ball and the difference in N170 mean amplitude between the peripheral and central ball for fearful faces presented in far space (r=0.67, n=22, p<0.01) and in near space (r=0.46, n=22, p=0.03). The red dot indicates the mean of the group difference.

6.2.4 Discussion

In a previous study (Ellena et al., 2020) it was demonstrated that fearful faces, looming in the proximity of the subject, prompt a shift of spatial attention from the fearful face location to its surrounding. This effect was reflected in the differential modulation of the motor response to tactile stimuli when accompanied by the appearance of a central or a peripheral visual element, a ball. The facilitation of the motor response to tactile stimuli was assumed to be the outcome of a multisensory integration process of tactile and visual stimuli. Spatial attention, differentially directed by the fearful or neutral face, allowed the peripheral or the central ball to be integrated into the somatosensory processing of tactile stimuli.

The present study aimed to investigate the question of whether the redirection of spatial attention away from the fearful face is also reflected in the electrophysiological neural signal sensitive to face stimuli. To address this question healthy subjects were instructed to provide simple responses to tactile stimuli delivered at the cheeks, while task-irrelevant neutral or fearful faces were looming in the far or the near space of the subject. As in the previous study (Ellena et al., 2020), to capture spatial attention, a patterned ball was presented at the time of the tactile stimulation delivery. Importantly, the ball position could be relatively close to the face, on the left or the right side of the face, or relatively more displaced into peripheral positions on the frontal plane of the face, on the left or the right side of the face. Response times to tactile stimuli were collected and electrophysiological activity was recorded.

Behavioural results confirmed previous findings of Ellena and colleagues (Ellena et al., 2020). Faster responses to tactile stimuli were found when the face was presented in the near rather than in the space far from the subject (PPS effect). Also, faster responses to tactile stimuli were found when the face displayed a fearful rather than a neutral expression (salience effect). Crucially, the position of the ball affected responses to tactile stimuli in interaction with the face distance and the emotion displayed (attentional effect). More in details: when the face was neutral, tactile responses were not modulated by the position of the ball, nor when the neutral face was in the far nor the near space. When the face was fearful, the position of the ball influenced the tactile response times. In the far space, responses were facilitated when balls appeared centrally, close to the fearful face, suggesting that attention was engaged at face location. Crucially, in the near space, responses were facilitated when balls appeared peripherally, apart from the fearful face. The observed centrifugal effect of spatial attention, prompted by fearful faces, when looming in the proximity of the subject, would be functional to promote the scanning of the environment, to find the source of the threat signalled by the fearful face.

Electrophysiological results were in line with the expectations. The redirection of attention from the face to the peripheral space is indirectly reflected in the neural signal associated with the appearance of the ball-face compound. The position of the ball affected the N170 amplitude in interaction with the face distance and the emotion displayed. In the condition in which the face was looming far, the N170 amplitude did not differ when the ball appeared central, close to the face, or more peripheral; this result was found both when the face was neutral or fearful. On the contrary, when the face was looming in the space near the subject, the appearance of the ball had a modulation on the N170 amplitude. Larger negative amplitudes were observed when the ball appeared centrally, close to the face, rather than when the ball appeared in the periphery, distally from the face. This effect was observed both for fearful and for neutral faces. Importantly, while with central ball the evoked response did not differ according to the emotion of the face, with the peripheral ball the evoked response was significantly reduced for fearful than for neutral faces. Since a smaller amplitude of the N170 is associated with reduced attention to faces (Eimer, 2000; Holmes et al., 2003; Jacques & Rossion, 2006), the smaller amplitude of the N170, found in this condition, would suggest diminished attention on the fearful face, to favour the processing of events in the surrounding. Additionally, when correlating RTs (central - peripheral ball) with N170 mean amplitude (peripheral - central ball) for fearful faces, it was found that the faster the participants responded to the peripheral ball, relative to the central, the smaller was their N170. This further corroborates the interpretation that a reduction in N170 suggests a redirection of attention away from the centrally-presented face, and thus towards peripheral space.

Previous studies have pointed out the effects of attention on the neural signals reflecting face processing. The fusiform face area (FFA), neural area specialized in the processing of faces and localized in the fusiform gyrus, was found to be significantly modulated by the attentional level of the individual and by other contextual information (Iidaka, 2014; Vuilleumier et al., 2001). Vuilleumier, Armony, Driver, and Dolan (2001) presented to healthy participants a display with two faces and two houses positioned in the upper and lower part of the display, or the left/right part. The participants were, in turn, asked to focus their attention on the faces of the houses, while performing a matching task; brain activity was measured in an fMRI scan. They found that the right FFA was activated when participants were attending faces, and not when they were attending the houses (see also Furey et al., 2006). In a subsequent study, Holmes et al. (2003) adopted the same paradigm as in Vuilleumier et al. (2001) and measured the ERP response. It was found that the amplitude of the face-sensitive N170 component, which likely originates in the fusiform gyrus (Yovel, 2016), increased when faces were attended (vs unattended) and did not change according to the emotional facial expression. This result would suggest that spatial attention may affect the structural encoding of faces. At a difference with these studies (Furey et al., 2006; Holmes et al., 2003; Vuilleumier et al., 2001), which explicitly require the subject to pay attention to a certain location of space, in the present study, the fearful face is exogenously initiating the reorienting process of attention (Carretié, 2014). Attention is then again assumed to be exogenously captured by the appearance of the ball. Even though visual stimuli were task-irrelevant and attention oriented exogenously, modulation of the potential was still observed. Since attention is redirected towards the surrounding space of the fearful face, where the threat might be located, the fearful face itself is relatively less attended, and the N170 amplitude is, therefore, less negative.

These electrophysiological results would complement the behavioural ones in supporting the redirection hypothesis by fearful faces in PPS (Ellena et al., 2020). Previous literature has shown that although fearful faces would rapidly capture spatial attention (Brosch et al., 2011; Cisler & Koster, 2010; Vogt et al., 2008), this capture seems to be fleeting as the time passes (Holmes et al., 2005; Torrence et al., 2017). Fearful faces are rapidly processed, but then attention seems to oscillate in avoidance of the face (Becker & Detweiler-Bedell, 2009). This dynamic deployment of attention, from early capture to successive redirection, may function to locate the actual source of threat (Berggren & Derakshan, 2013; Taylor & Whalen, 2014). Other emotions instead, such as joyful faces (Fox et al., 2002; Torrence et al., 2017) or angry faces (Juncai et al., 2017), appear to hold attention for longer, without redirecting it (Davis et al., 2011). For this reason, the effect found, seem to be attributed to the specific communicative signal of the fearful face, thus not attributable to other emotions, which were not tested in the present study. Nonetheless, at the behavioural level, when joyful and angry faces were tested with the same paradigm (Ellena et al., 2020; Study 2a and Study 2b), no evidence of redirection of attention in PPS was reported.

Lastly, as observed in the previous study (Ellena et al., 2020; Study 2a), the redirection of attention by fearful faces has a spatial logic, reflected both in the behavioural and electrophysiological results. Fearful faces looming in the near-space signal potential imminent threats, for which the urgency of preparing a defensive response is higher. Also, the space close to the subject is where attention seems to be preferentially deployed (Finlayson & Grove, 2015; Maringelli et al., 2001; Plewan & Rinkenauer, 2016, 2017) and where attentional shifts are facilitated (Chen et al., 2012; Wang et al., 2016).

6.3. Study 4: The spatial effect of fearful faces in the autonomic response

6.3.1 Introduction

Several pieces of evidence are showing that the progressive vicinity of the stimulus to the body is correlated with an increase of the neural and behavioural responses to those stimuli (Bufacchi & Iannetti, 2018; Cléry, Guipponi, Wardak, et al., 2015; Van der Stoep, Nijboer, et al., 2015). This proximity effect is mediated by the multimodal sensory-motor PPS mechanisms, which aim to create or avoiding contact with a stimulus approaching the body (Bufacchi & Iannetti, 2018). Importantly, the proximity is not the only factor that modulates those responses. For instance, information about the stimulus' movement, such as direction (Colby et al., 1993) and speed (Fogassi et al., 1996; Noel, Blanke, Magosso, et al., 2018) have been shown to resize PPS. The affective salience of the stimulus is another relevant factor that influences PPS representation. Several pieces of evidence are showing that the proximity effect is enhanced when a stimulus is considered as potential harm for the subject; for example, the sound of an approaching barking dog elicits earlier and faster tactile motor responses in cynophobic individuals. In this situation, the affective salience and the proximity of the stimulus appear to be in interaction. The affective salience modulates the proximity rules of multisensory integration and the proximity of a threatening stimulus may modulate its salience. To read adequately threat signal in the environment one needs to prioritize the processing of certain features or locations in the environment by a shift of the attentional focus. To support this function, neural circuities including cortical and subcortical structures in connection with the autonomous system are involved (Wood et al., 2014). Previous studies are showing that the emotional capture of attention in response to affective stimuli is associated with a higher arousing value of the stimulus (Bradley et al., 2003; Schimmack, 2005; Schupp et al., 2006, 2004) and a higher autonomic response (Cuthbert et al., 2000; Pastor et al., 2007). A prominent structure in the emotion-related processes is the amygdala (Öhman, 2005), whose activation was found as particularly relevant in the initiation of the autonomic response to a threatening situation (Gläscher & Adolphs, 2003; Gore et al., 2002; Laine et al., 2009). Skin conductance response (SCR) (Wang et al., 2018) which can be considered as an indicator of the transient activation of the autonomic nervous system in response to a stimulus, was found to be modulated not only by the mere presence of a threatening stimulus but also by its perceived imminence. For instance, it was demonstrated that the increasing size of an affective picture, that makes it appear closer, elicits an increased SCR (Codispoti & De Cesarei, 2007), which is possibly in support for the activation of the strategic motivational system which enhances attention allocation. Fearful facial expressions, particularly salient stimuli that signal not a direct but an environmental threat, have been shown to particularly activate the amygdala (Adolphs et al., 1994; Anderson et al., 2013; Britton et al., 2008; Hariri et al., 2002; Steiner et al., 2018; Whalen et al., 2001) and to elicit robust SCR (Fusar-Poli, Landi et al., 2009; Hariri et al., 2002; Tsikandilakis & Chapman, 2018; Williams et al., 2004). It can be hypothesized that these correlated activations might be in support of the adaptive reaction to fearful faces, that is to engage the subject in an attentional investigation of the environment in search of the threat. In this respect, the distance of the fearful face from the observer might constitute an important factor in evoking this adaptive reaction. The present study aims to investigate whether approaching fearful faces would modulate the evoked autonomic response according to their distance from the observer. Also, the effect of joyful faces, more positive and less arousing stimuli, is examined. The prediction is to find an increase in SCR as fearful faces become closer to the subject, while no increase with proximity is expected for joyful faces. In this study, healthy subjects perform a tactile detection task, where they were asked to respond to tactile stimuli delivered at the checks while watching task-irrelevant fearful, joyful and neutral faces, approaching them from the very far to near space in an immersive virtual environment. The administration of neutral faces is of importance to control for the effect of stimulus movement parameters, such as size and speed, known to influence the effect of proximity. Previous evidence, investigating the effect of emotional faces in space on the autonomic response (Cartaud et al., 2018), was showing that an angry face, also when presented at perceptual threshold (Cartaud et al., 2020), elicits a stronger physiological activation than joyful or neutral faces, only if presented within a reaching distance (at 65 cm), but not outside the reaching distance (at 250) (Cartaud et al., 2018).

In contrast with these works (Cartaud et al., 2020, 2018), which conceived the PPS as an in-or-space which evokes a discrete response, in the present task PPS is modelled as a sequence of graded receptive fields (Bufacchi & Iannetti, 2018) eliciting a gradual rather than a discrete response. For this reason, the present design allowed to test three different spatial distances (Ultra-Far, Far, Near) to test the gradual modulations of SCR as a function of these distances. Moreover, in contrast with Cartaud and colleagues (2018), which explicitly asked the participant to consider the spatial positions of the emotional avatar, by expressing a reachability judgment, in this task space is evaluated implicitly, since participants were only asked to respond to the tactile vibration. Importantly here, to quantify the emotional modulation of the autonomic response in PPS, the SCR elicited by fearful and joyful faces in the different spatial conditions, is subtracted to the response elicited by neutral faces. This computation is also necessary to control for the confounding stimulus movement parameters, such as speed and size.

6.3.2 Methods

Participants

Twenty-seven healthy participants with no history of neurological or psychiatric disorders were recruited (17 females; mean age ± SD = 25 ± 2.5 years). This study was performed in line with the principles of the Declaration of Helsinki. Approval was granted by the Bioethics Committee of the University of Bologna (Date 8-8-2019 /No. 178302). All participants gave informed written consent to participate after being informed about the experiment. The sample size was determined via a power analysis conducted in G*Power 3.1 software (Faul et al., 2007); the modulation of the arousal response in PPS was expected to have a medium to large effect size (Cartaud et al., 2018; Rossetti et al., 2015); the alpha was set at 0.05 and the power was set at 0.95. For a repeated measure within-factor analysis of variance (ANOVA) with no covariates, it was determined that a sample size of twenty-seven would be enough to detect the effect.

Task and experimental procedure

The experiment was implemented in ExpyVR software (a framework for designing and running experiments in virtual reality, available online at https://lnco.epfl.ch/) and run on a Windows PC (XPS 8930, Dell, Round Rock, Texas, USA). The tactile stimuli consisted of vibrations delivered bilaterally to the participants' cheeks by a pair of shaftless vibration motors (Precision MicroDrives, model 312-101, 3 V, 60 mA, 150 Hz, 5 g). Each motor had a surface area of 113 mm2 and reached maximal rotation speed in 50 ms. The devices were activated for 100 ms during tactile stimulation. The visual stimuli were avatar faces showing a fearful, joyful or a neutral expression and were presented by relaying to the head-mounted display (HMD, Oculus Rift SDK, Oculus VR, 100° field of view, 60 Hz). The stereoscopic vision was obtained by projecting the stimulus in a slightly different angle to the left and right eye (for more details see https://developer.oculus.com/design/bp-vision/). The angular size, which is the size of the image that an object produces on the retina of the observer, was not corrected, thus, far faces were perceived as smaller than closer faces. The avatar emotional facial expressions were manipulated ad hoc to render the desired features with Poser software (vers. 10; Smith Micro Software, Aliso Viejo, California, USA). Stimuli implemented in the study were chosen through a validation procedure (see Chapter 4, Paragraph 4.2.2.3).

At A0 (see Figure 6.5), at the beginning of each trial, a black fixation dot appeared centrally in the participant’s visual field, on a grey background, for 500 ms, at an apparent distance of 400 cm from the participant. At T0, an avatar face with a neutral, fearful or joyful expression appeared centrally in the visual field, in one of three different positions: Near space (~ 70 cm away), Far space (~ 210 cm away) or Ultra far space (~ 350 cm away) from the participant (see Figure 6.6). Faces moved toward the participant on the sagittal plane for a total of 3000 ms. The endpoint of the looming face was always fixed near the participant (~ 10 cm away), where the face remained still for 1000 ms before stimulus offset. Therefore, stimuli in each condition covered different lengths of space in the same amount of time, resulting in different travelling speeds: 20 cm/s, 66.7 cm/s and 113.3 cm/s, for the Near, Far and Ultra-Far conditions, respectively. At T1, 1500 ms after the presentation of the face, the tactile stimulus was delivered. Thus, touch coincided with the perception of the face at different distances from the participant (40 cm in the Near condition, 110 cm in the Far condition and 180 cm in the Ultra-far condition). Lastly, at T2, at the face offset, the fixation dot reappeared, at the previous location, for 500 ms. Note that, in the 15% of trials, the colour of the fixation dot changed from black to red at T2. Participants were asked to detect the colour change and signal it to the experimenter. The change in fixation dot colour always happened at the end of the trial (T2) when the face disappeared. The inter-trial interval (ITI) was a grey empty environment, with a variable duration ranging from 11 to 14 s (± 1 s of jitter). This design allowed us to exclude a potential confounding effect of temporal expectation on tactile facilitation since the tactile stimulation was always delivered with the same delay after the appearance of the face in each spatial condition. When a moving object approaches the body, it does not only trigger the multisensory PPS neurons that influence tactile processing but also the impending contact with the approaching object creates an expectation of an upcoming tactile event that influences the response time to the tactile stimuli. Also, the expectation increases as time elapses and it approached the body (Kandula et al., 2017). There was a total of 27 trials, evenly distributed among the 9 experimental conditions defined by facial expression (Neutral/Fearful/Joyful) and spatial position (Ultrafar/Far/Near; i.e., 3 trials per condition). Trial order was randomized. The choice of not including unimodal conditions served to keep the number of trial repetition low, due to the rapid habituation of the SCR response (Bradley et al., 1993; Codispoti et al., 2006; Codispoti & De Cesarei, 2007).

After signing the consent form, participants sat on a comfortable chair in a sound-attenuated room. Vibrators were then attached bilaterally on the cheeks with medical tape, and a virtual reality headset was mounted onto the head of the participant. Before the task began, the lens focus of the Oculus VR was manually adjusted by each participant until a clear vision was reported and the SCR activity recording was verified. During the task, participants made speeded simple responses to the tactile stimulation by pressing a button placed on the table in front of them with their right hand.

At the end of the experimental phase, participants were invited to fill out a form in which they were asked to recognize the emotions represented in VR and to rate their intensity and arousal levels with two separate 10-point Likert scales. For intensity, the anchors were 0 (mild-neutral) to 9 (very intense), and, for arousal, they were 0 (not exciting at all-relaxing) to 9 (highly arousing-exciting). Moreover, participants were invited to rate the pleasantness of their general experience in the VR environment with a 10-point Likert scale that ranged from 0 (not pleasant at all) to 9 (very pleasant).

SCR recording and data processing

SCR was recorded with a Biopac MP-150 (BIOPAC Systems, Inc., Goleta, California, USA) at a 200-Hz sampling rate, and collected with AcqKnowledge 3.9 software (BIOPAC Systems) for offline analysis. SCR was acquired with two Ag/AgCl electrodes (TSD203; BIOPAC Systems) filled with isotonic hypo-saturated conductant gel and attached to the distal phalanges of the second and third fingers of the participant’s non-dominant hand. A Biopac EDA100C (BIOPAC Systems) was used to measure SCR (gain switch set to 5 μS/V, low pass to 35 Hz, high pass to DC). SCR data were analyzed offline using MATLAB (Version R2018b; The MathWorks, Inc., Natick, Massachusetts, USA), and all statistical analyses were performed with STATISTICA (StatSoft, v. 13.0, Round Rock, Texas, USA). Each trial (see Figure 6.7 as an example of single SCR traces) was extracted from the entire SCR signal and, to reduce inter-individual variability, a baseline correction was applied using the mean value of the signal 1000 ms before each stimulus presentation as a baseline (Alpers et al., 2011; Banks et al., 2012; Shiban et al., 2015). Then, for each baseline-corrected trial, the peak-to-peak value was calculated as the amplitude during the 500–4500 ms time window after emotional face onset. The minimum response criterion was 0.02 μS, and smaller responses were encoded as zero. Raw SCR scores were square root-transformed to normalize the data distribution (Boucsein et al., 2012; Schiller et al., 2008).

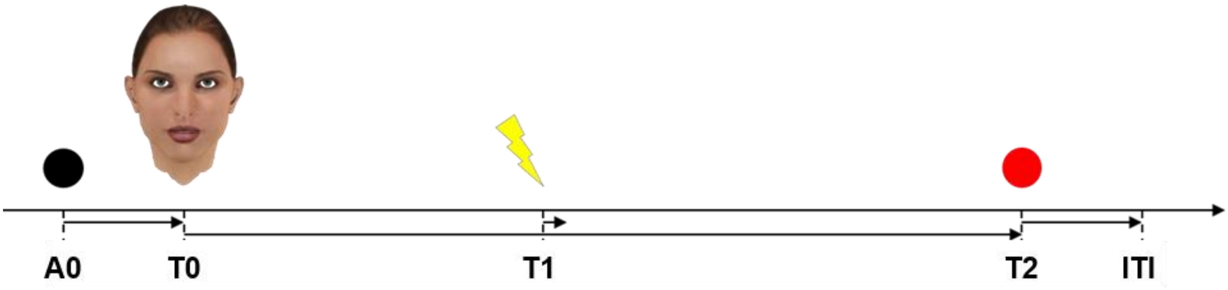


Figure 6.5. Experimental timeline. At A0, the fixation dot (black) appeared for 500 ms. At T0, the face moved for 3000 ms toward a location near the participant, where it remained still for 1000 ms (T2). At T1, tactile stimulation was delivered. At T2, the face disappeared and the fixation dot (black/red) re-appeared for 500 ms. The ITI was set at 11-14 s.

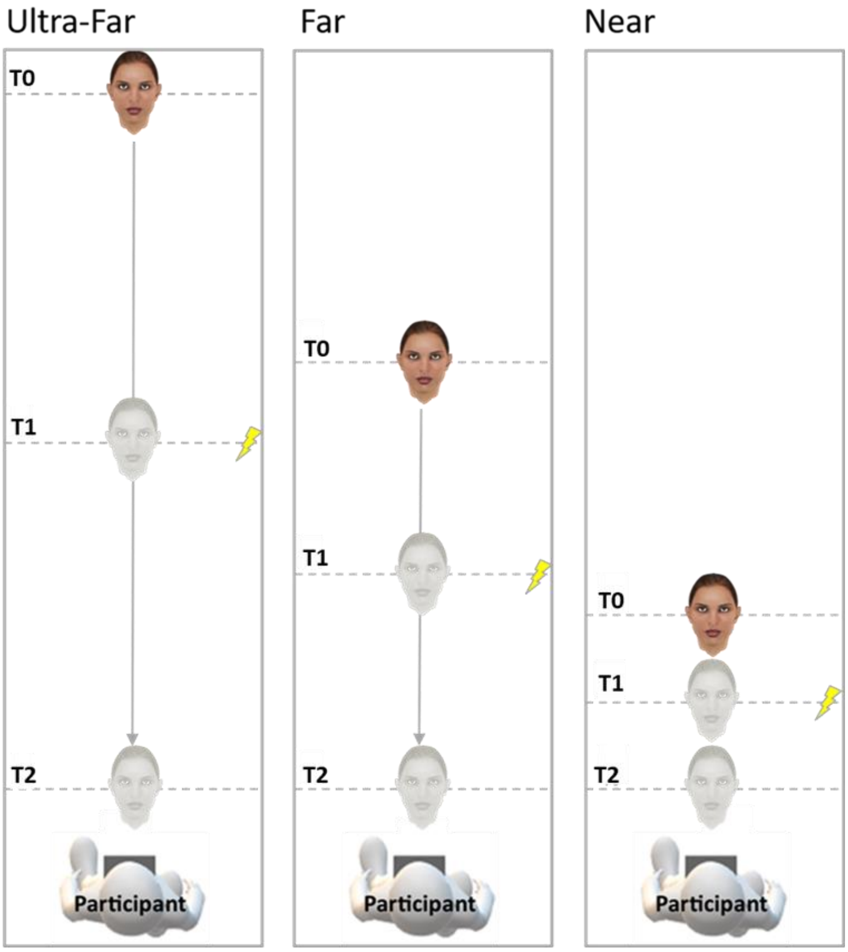


Figure 6.6. Spatial conditions. In each spatial condition, the endpoint was fixed at a location near the participant (10 cm), while the starting point differed, resulting in a distance from the participant of approximatively 350 cm in the Ultra-far condition, 210 cm in the Far condition and 70 cm in the Near condition. At T1, when tactile stimulation was delivered, the face appeared to be 180 cm away in the Ultra-far condition, 110 cm away in the Far condition and 40 cm away in the Near condition. The face was always displayed for 4000 ms (from T0 to T2).

6.3.3 Results

Concerning the psychophysiological data, the assumption of a normal distribution of data was verified, and mixed-design ANOVAs were used to investigate the modulations of arousal (SCR) during the experimental task. Post hoc analyses were conducted with Bonferroni corrections, and the significance threshold was set at $p < 0.05$. The effect size was calculated as partial eta-squared

(η_p^2). Three participants, considered SCR non-responders, were excluded from the analysis due to the minimal level of recorded responses (Boucsein et al., 2012). To quantify the mere effect of the emotion (fear, joy, neutral) at each distance, an index (ΔSCR) was created by subtracting the mean value of the phasic response to neutral faces from the phasic responses to the fearful and joyful expressions, for each distance (Ultra-far, Far, Near). Thus, ΔSCR allowed us to control for possible effects of both the stimulus speed and size. Indeed, it is important to highlight that the looming faces started at different distances from the participant, but the endpoint was always the same. This means that the stimuli covered different distances in the same amount of time, resulting in different travel speeds, as well as faces presented at different distances appearing in different sizes. A repeated-measures ANOVA was performed to investigate the effect of the Face Emotion (two levels: ΔSCR Fear, ΔSCR Joy), the effect of the Space (three levels: Ultra-far, Far, Near) and their interaction. There was neither a main effect of the Face Emotion (F (1,26) = 1.25; p = 0.27; η_p^2= 0.05), nor of the Space (F(2,52) = 2.63; p = 0.08; η_p^2= 0.09). Crucially, a Face Emotion*Space interaction was found (F(2,52) = 6.76; p < 0.01; η_p^2= 0.21). Bonferroni-corrected post hoc comparisons revealed that, for the joyful faces condition, there was no difference between the Ultra-far, Far and Near conditions (ΔSCR Joy Ultra-far: M = 0.00; SEM = 0.03; ΔSCR Joy Far: M = 0.03; SEM = 0.02; ΔSCR Joy Near: M = 0.01; SEM = 0.02; all p = 1). In the fearful faces condition, instead, values in the Ultra-far condition were significantly lower than values in the Far and Near conditions (ΔSCR Fear Ultra-far: M = – 0.04; SEM = 0.03; ΔSCR Fear Far: M = 0.04; SEM = 0.03; ΔSCR Fear Near: M = 0.09; SEM = 0.03; all p < 0.02). ΔSCR Fear in the Far condition did not differ from ΔSCR Fear in the Near condition (p = 0.49). Importantly, ΔSCR Fear was higher than ΔSCR Joy in the Near condition (p = 0.01; see Figure 6.8). Finally, we also analyzed the latencies of the peaks, computed as the period between the stimulus onset (T1; the appearance of the face) and the SCR maximal peak elicited by the visuotactile compound. Largest deflections of the SCR signal, except for one subject in one condition, were always following the time of the touching delivery (T2; 1500 ms), at latencies that were around 4130 ms on average (SEM = 60). As a sanity check, analysis on the SCR peaks was rerun with the exclusion of the mentioned subject, and similar results were obtained. Moreover, we checked whether the latencies of the peaks were modulated by our experimental conditions (Face Emotion and Space). Results from the repeated measures ANOVA confirmed that latencies were not modulated by the main effect Face Emotion (F (2,52) = 0.67; p = 0.51; η_p^2= 0.03), nor by the main effect of Space (F (2,52) = 0.80; p = 0.45; η_p^2= 0.03), nor by their interaction (F (4,104) = 1.03; p = 0.39; η_p^2= 0.04). Concerning the behavioural data, all participants detected 100% of the attentional dots and were also accurate at detecting the tactile stimulus, as the rate of the omissions was low (< 1%). Due to the limited number of trials per conditions (n = 3), response times to tactile stimuli were not analyzed. Concerning the final rating results, the totality of the subjects correctly reported the identity of the emotional faces (mean hit rate of 100%). Intensity and arousal levels, rated at the end of the experimental session, were analyzed separately. A repeated-measures ANOVA was used to evaluate differences in the intensity ratings of the stimuli. Results showed a main effect of Face Emotion (F (2,52) = 17.95; p < 0.01; Fear: M = 7.40; SEM = 0.27; Joy: M = 4.85; SEM = 0.44; Neutral: M = 4.26; SEM = 0.51). Bonferroni-corrected post hoc comparisons revealed that fearful faces were rated as more intense than joyful and neutral faces (all p < 0.01). Another repeated-measures ANOVA was used to evaluate differences in the arousal ratings of the stimuli. Results showed a main effect of Face Emotion (F (2,52) = 6.91; p <0.01 Fear: M = 5.44; SEM = 0.27; Joy: M = 5.11; SEM = 0.35; Neutral: M = 4.44; SEM = 0.37). Bonferroni-corrected post hoc comparisons revealed that fearful faces were rated as more arousing than neutral faces (p < 0.01) but not significantly different from joyful faces (p = 0.06). Finally, participants rated their general experience in VR as mildly pleasant (M = 6.66; SEM = 0.42).

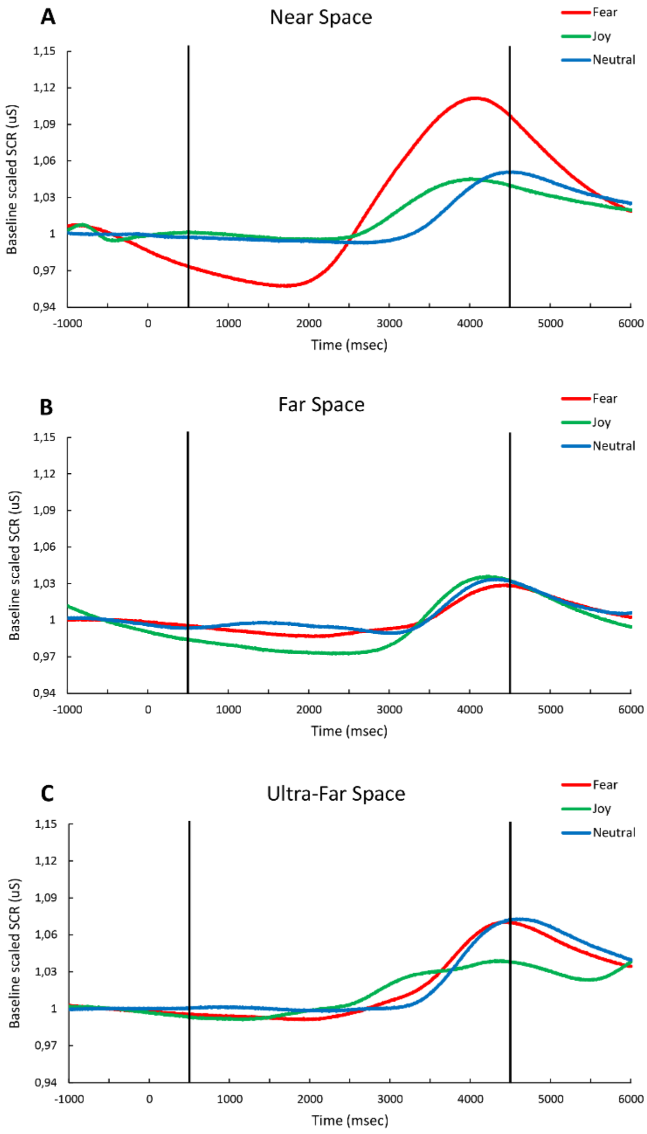


Figure 6.7. Plots showing an example of single-trial SCR from a single participant. Each panel reports the plot of three trials, one per each emotion condition, in the Near space (upper panel A), in the Far space (middle panel B) and the Ultra-Far space condition (lower panel C). Lines intercepting the x-axis are delimiting the time-window chosen for the analysis (500 ms -4500 ms after T0, the onset of the looming face).

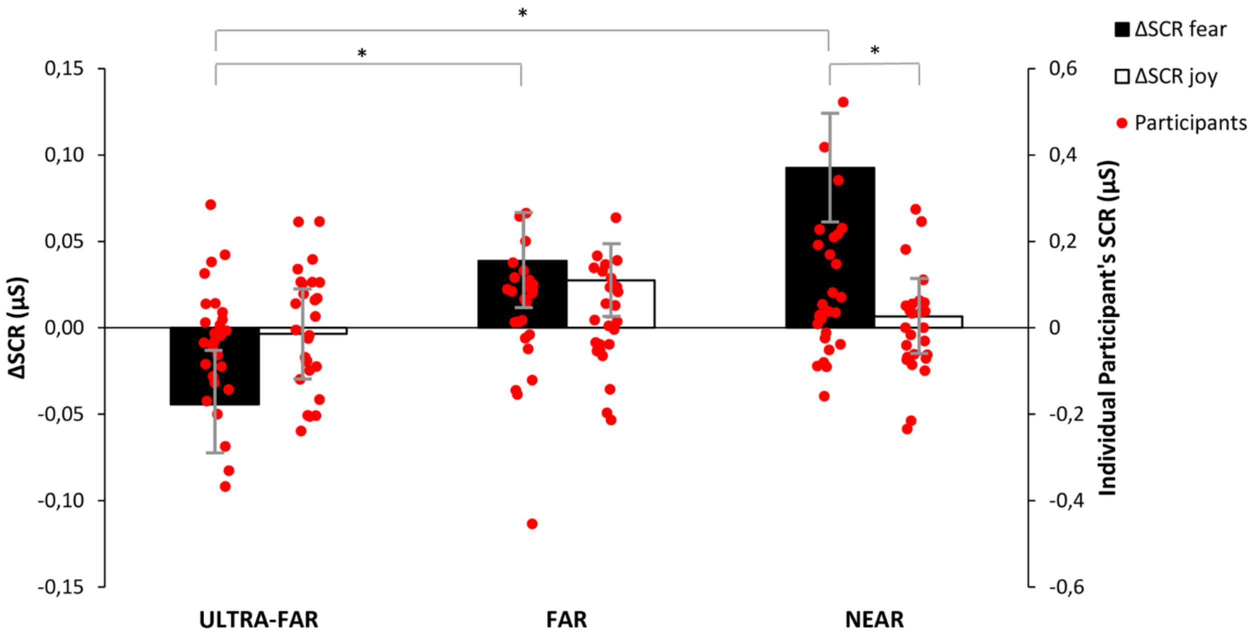


Figure 6.8. Bar graph showing the experimental results. In particular, the graph shows the interaction between Emotion and Space. In the joyful faces condition, ΔSCR did not differ between spatial conditions, whereas ΔSCR for the fearful faces was significantly modulated by spatial distance. Asterisks indicate significant comparisons. Error bars represent the standard error of the mean. Overlaid dots show the individual subjects' data per each condition.

6.3.4 Discussion

The question that this study tries to address is whether approaching facial expressions of fear, at a difference with facial expressions of joy, would differently modulate the evoked autonomic response as a function of the face distance from the subject. It is predicted a modulatory effect of the autonomic response over distance only for fearful faces, very salient cue of the presence of a potential threat in the environment. No modulatory effect over distance is expected for joyful faces. To address this question, healthy participants are asked to respond to tactile stimuli delivered at the cheeks, while fearful, joyful or neutral faces appeared to approach them from three different distances (Ultra-Far, Far, Near). The tactile stimulus delivery always occurred within the same latency, from the appearance of the face, to control for the expectancy, known to be a confounding factor in classical PPS paradigm (Kandula et al., 2017). Since faces started to move from different positions, the delivery of the tactile stimulus coincided with the perception of faces, at different distances from the participants. The effect of the emotion over the different distance conditions was quantified by comparing the evoked response to the emotional faces (fearful and joyful) net of the response evoked by the neutral faces. This method allows also to take control of the possible confounding factors known to affect PPS (Fogassi et al., 1996; Noel, Blanke, Magosso, et al., 2018), such as the different speeds of travelling, or the size of the stimulus (closer faces were also bigger than the farther ones).

Results were in line with the hypotheses: approaching fearful faces and not joyful, elicited a gradual increase in SCR magnitude as the face become closer to the observer. The lowest response was recorded when the fearful face was looming in the farthest portion of space at the time of the tactile stimulation (~180 cm from the subject). This response significantly increased in the condition in which the fearful face was looming in a nearer portion of space at the time of the tactile stimulation (~ 110 cm from the subject). The greater response was recorded when the fearful face was looming in the nearest portion of space at the time of the tactile stimulation (~40 cm from the subject). In this nearest distance condition, the relative enhancement evoked by fearful faces was higher than the one evoked by joyful faces. The relative evoked response by joyful faces was not modulated by the distance of the face. This study indicates that the proximity of a fearful face, and not a joyful one, influences the SCR, an indication of the transient activation of the autonomous response, which increased gradually as the fearful face was looming closer to the subjects.

Several studies are showing that emotional faces trigger a cascade of central and peripheral physiological processes which are associated with action preparation (i.e., Liddell et al., 2004; Valk et al., 2015; Vuilleumier & Pourtois, 2007). Joyful faces would motivate an approach bias, while fearful faces, a response of avoidance. Nonetheless, a rapid response would be expected to be adaptive mainly in the case of a threatening situation, such as the one signalled by the fearful face. Fearful facial expressions are signals of the potential threat and they appear to rapidly prepare the individual for action (Anderson & Phelps, 2001) as shown by the fact that they increase the corticospinal motor tract excitability compared to happy and neutral faces (Schutter et al., 2008); on the other side, joyful faces more positive and signalling an intention to approach, are less likely to induce a rapid action preparation associated with the fight-flight response (Borgomaneri et al., 2014; Schutter et al., 2008). This fight-flight response is mediated by circuits involving the amygdala, which plays an important role in evaluating stimulus salience and generating a physiological response such as SCR. Pieces of evidence are showing that amygdala is particularly activated when a stimulus is presented in ambiguous circumstances (Blasi et al., 2011; Mushtaq et al., 2011; Whalen, 1998; Whalen et al., 2001) or when it presents an intrinsic ambiguity, such as a fearful face. A fearful face would signal the presence of a potential threat in the environment. A straight fearful gaze poses a certain ambiguity regarding the source of the threat, while on the other hand, a fearful averted gaze might offer information regarding where the threat might be located. Indeed, the amygdala was found to be more responsive to fearful faces with straight than averted gaze (Adams et al., 2003). Consistently, fearful faces with straight gaze are perceived as less intense and less quickly and accurately recognized than fearful faces with averted gaze (Adams & Kleck, 2005; Benton, 2010). The enhanced amygdala-mediated vigilance would be necessary to scan the environment and to resolve the uncertainty of the upcoming danger. In the present study, gaze direction was not manipulated and all faces were presented with a straight gaze. The gradual increase in SCR, as fearful faces approached the participant, may be correlated with a greater amount of attentional resources required to search for the threat source. This result would support previous findings (Alpers et al., 2011; Fusar-Poli, Landi, et al., 2009) by showing that fearful facial expressions are salient stimuli that elicit activation of the autonomous response. Moreover, it adds that this activation gradually increases as the face is perceived closer to the subject. The result of the present study further confirms the defensive definition of PPS. The salience of the fearful face here emerges in interaction with the proximity of the body, and it is maximal when the face starts to approach in the very proximity of the subject, where the threat might be inescapable and the need for defence is most pressing.

It cannot be excluded that the valence of the emotional face itself, which determines the pleasantness or unpleasantness of the stimulus (Kensinger et al., 2006), may have played a role in determining the result. Fearful faces, by carrying important information about a potential threatening circumstance, are not only more salient stimuli than joyful faces but have also more negative valence. This aspect needs to be investigated by future studies.

Lastly, it cannot be excluded, that comparable results may be observed if SCR, in response to approaching emotional faces, was measured by adopting other paradigms, such as the reaching space or the interpersonal space (Cartaud et al., 2018), which operationalize other definitions of space around the body. These constructs, which were shown to dissociate behaviorally and at the neural level from the multimodal PPS considered here (see Chapter 2), are normally assessed with the explicit processing of space, by direct cognitive estimations of the space, which is not of interest for the present study.

6.4. Conclusions

Fearful faces in PPS do not draw attention to the location of the face, at variance with other emotions, but to other locations where the threat may be located. Chapter 6 aimed to investigate the physiological correlates of the attentional mechanisms, by both looking at the attentional effect on emotional faces in PPS expressed by its electrophysiological correlate (Study 3), but also by asking whether this effect in PPS would be supported by a differential increase of the autonomic response (Study 4). Electrophysiological results of Study 3 were consistent with the centrifugal attentional effect in response to near fearful, relative to neutral, faces. The particularly reduced amplitude of the face-sensitive N170, observed when fearful faces were flanked with visual elements positioned in more peripheral locations, was interpreted as the hallmark of reduced attention on the near fearful face, to favour the processing of the peripheral surrounding of the face, where the threat may be located. Fearful faces pose an intrinsic ambiguity to the observer, as they signal a potential threat. Unless other additional pieces of information are provided, the subject is asked to resolve that ambiguity by deploying a higher amount of attentional resources, where threat imminence would be maximal: the space near the body. This defensive reaction corresponded to an increase of the defensive autonomous activation, which was measured in Study 4. The results of the SCR, which was recorded during the presentation of emotional faces looming from three different distances, were showing that the SCR to fearful faces, but not the response to joyful or neutral, was modulated by the apparent distance of the fearful face from the participant’s body.

CHAPTER 7: General Discussion

7.1 Introduction

The present chapter will initially present an overview of the PPS mechanisms and its modulations, which founded, theoretically, the questions addressed in the present thesis project. Also, in the first paragraph, studies' methods and main results are summarized. Results from the different studies are then discussed together, and organized around the three main effects that were found: the effect of the proximity of the stimulus (the *PPS effect*), the effect of the affective content of the stimulus, and the specific attentional effect found with fearful faces. Lastly, final remarks will delineate how the results of the present studies may contribute to extending the current literature on the affective modulation of PPS.

7.2 General discussion

7.2.1 Overview of the studies' results

PPS is the representation of the space surrounding the body (Rizzolatti et al., 1997), and it is coded in a specific population of multimodal neurons, found mainly in frontoparietal areas, such as the inferior and superior parietal lobule, the intraparietal sulcus, the primary somatosensory areas, and the ventral and dorsal premotor cortices. PPS extent can be defined as the portion of space in which multisensory information between somatosensory and visual or auditory stimuli has a higher probability of being integrated (Graziano & Cooke, 2006; Làdavas, 1998; Serino, 2019). The amount of multisensory response enhancement is determined by the degree of spatiotemporal proximity between the visual or the auditory stimulus and the tactile stimulus. The integration of the visual or auditory into the processing of the tactile stimulus is observable by the amount of facilitation of the motor response to tactile stimuli (i.e., faster responses to multimodal stimuli than to the tactile stimulus alone). Apart from proximity, other low-level factors have been shown to modulate visuo-tactile or audio-tactile integration: i.e., the direction of the stimulus, its speed of travelling or its size. Also, higher-level factors, such as the affective salience of the stimulus, would modulate PPS (e.g. harmful objects, threatening animals, negatively valenced sounds) (de Haan et al., 2016; Ferri et al., 2015; Lloyd et al., 2006; Spaccasassi et al., 2019; Taffou & Viaud-Delmon, 2014; Vagnoni et al., 2012). All these dynamic changes suggest that PPS has an adaptive role as a protective safety barrier to incoming threats (Bufacchi, 2017; Cooke et al., 2003; de Vignemont & Iannetti, 2015).

This thesis project aims to investigate how the multisensory PPS would be affected by the exposure to emotional faces, a particularly salient cue in our environment. In a series of studies, it is investigated how the different emotional expressions, that differ in their valence, arousal level and communicative value, may differentially modulate PPS, and which are the mechanisms involved. In each study described, although with some variations, the effect of emotional faces on the multisensory PPS is assessed by a modified version of a well-validated multimodal interaction task (Canzoneri et al., 2012; Pellencin et al., 2018; Serino, Noel, et al., 2015), in which healthy subjects are asked to detect a vibrotactile stimulus delivered bilaterally at the cheeks, while watching, in a virtual reality environment, avatar’s faces, expressing different emotional expressions, such as joyful, angry, fearful and neutral. Faces appeared on a grey background, always looming toward the subject, from the distant space until its proximity. Study 1 aimed to observe the effect of emotional faces on the multisensory PPS. Faces were always looming from the distant space until the proximity of the subject. Tactile stimuli could be delivered with five different delays from the appearance of the face which could be perceived at five different positions when the tactile stimulus was delivered. In the neutral, joyful and angry faces conditions, the multisensory facilitation of RTs was gradually affected by the proximity of the looming face: participants became faster in responding to visuo-tactile stimuli as the face approached. A differential pattern was found with fearful faces: in this condition, the multisensory facilitation remained constant across the different spatial positions, resulting significantly lower in the closest position of the face compared with the neutral condition. Fearful faces, signalling the presence of a potential environmental threat, trigger a multisensory facilitation effect that, contrarily to other emotional faces, does not depend on the distance of the face from the subject, possibly reflecting the role of emotional attentional processes in detecting sources of the threat in the environment. When a fearful face enters the PPS, attention may no longer be on the face location but redirected to the peripheral space, where there might be a potential source of danger. Instead, with the other facial expressions, attention might be located on the looming face. Study 2a directly tested the hypothesis that fearful, at a difference with the other emotional faces, differently distributed spatial attention when presented in PPS. Subjects were performing a tactile detection task while watching task-irrelevant looming emotional faces: neutral and joyful (Experiment 1), neutral and fearful (Experiment 2). At a difference with Study 1, in which faces were looming across the same distance points and the tactile stimulus was delivered at different temporal delays, here faces were looming from two different distance points and the time of the tactile stimulation was kept constant in each of the two distance conditions (Far space; Near space). Also, at the time of the tactile stimulus delivery, another visual element was introduced: a static ball could briefly appear close to the looming face or more distally, in the subject's frontal plane. In each emotional condition tested, it was found a PPS effect: faster tactile motor responses when near condition than in the far. Further, only when fearful faces were looming in the near space, tactile motor responses were faster with peripheral than with central balls (attentional effect). Only when a fearful face was looming in the space near the subject, a redirection of attention from the face to the peripheral space was prompted. This effect would explain the facilitation of the responses to tactile targets when a ball is presented at the periphery. This fear attentional effect was not found for neutral and joyful faces both in the far and in the near space. Study 2b provided evidence that nor neutral nor angry faces, looming in the space near the subject, would redirect spatial attention. In this respect, the result observed was similar with what found with joyful faces in Study 2a and added evidence that both joyful and angry faces, when entering PPS, call for the attention to remain focused on the emotional face, without redirecting it. Study 3 aimed to study whether this mechanism of redirection of attention observed behaviourally was reflected in the electrophysiological signal associated with face processing. The same paradigm adopted in Study 2a and 2b was adopted and the electrophysiological signal was recorded. In this study, only neutral and fearful faces were tested. Electrophysiological results showed that the redirection of attention was accompanied by a reduction of the N170 mean amplitude for fearful compared to neutral faces, consistent with a shift of attention away from the centrally presented face towards the peripheral ball. Study 4 was designed to investigate whether the redirection of attention could also be supported by an increase of the physiological arousal in the space near to the body. Subjects performed a tactile detection task, while neutral joyful and fearful faces were looming from three distances. In each distance condition, the time of the tactile delivery was kept constant and the face was always looming until the proximity of the subject. Skin conductance response (SCR) was measured. The physiological signal evoked by each emotional condition was subtracted from the signal evoked by the neutral condition, to compute the contribution of the emotional component in the evoked physiological signal, net of the mere presentation of the face and to control for the possible confounding factors such as size and different speeds. The results revealed that the SCR to fearful faces, but not joyful or neutral faces, was modulated by the apparent distance from the participant's body, maximal in the near and reduced in the far. The proximity of the fearful face provided a cue to the presence of a threat in the environment and elicited a robust and urgent organization of defensive responses.

7.2.2 The peripersonal space effect

One first main result of these studies, particularly in Study 1, 2a, 2b and 3, was that participants were faster to respond to tactile stimuli at their cheeks, when those were delivered simultaneously to the presentation of visual stimuli, the faces, looming in the space closer to the participants' body, compared to farther positions. This PPS effect is in line with the broad literature on PPS (Canzoneri et al., 2012; di Pellegrino & Làdavas, 2015; Holmes & Spence, 2004; Macaluso & Maravita, 2010; Pellencin et al., 2018; Serino, Noel, et al., 2015) and has been attributed to the process of multisensory integration of a tactile and a visual stimulus; this process of integration was maximal when the visual face was closer the site of the tactile stimulation. This distance-dependent multisensory facilitation would reflect the fundamental property of the multisensory neurons, that were described in the frontoparietal networks associated with the PPS coding (Brozzoli, Makin, et al., 2011; di Pellegrino & Làdavas, 2015; Serino, 2019). Those neurons were found to be sensitive to the spatio-temporal dynamics of objects in the environment (Colby et al., 1998; Fogassi et al., 1996). Spatiotemporal proximity constitutes one of the factors which would determine whether two stimuli, in this case, tactile stimuli on the body and visual or auditory information from external events, are going to be attributed to the same source, and thus, jointly processed (Noel, Samad et al., 2018). The information from this joint processing is directly transferred into the motor system, supporting the gain in responsiveness to tactile stimuli. Previous studies provided electrophysiological evidence of this motor signature of the PPS (Finisguerra et al., 2015; Makin et al., 2009; Serino et al., 2009). Serino, Annella and Avenanti (2009) found an enhanced activity of the corticospinal motor representation of the hand, immediately after (<80 ms) a static auditory stimulus was presented close to the subject's hand, rather than far. This result was confirmed by Finisguerra and colleagues (Finisguerra et al., 2015) which provided evidence of an enhanced hand muscle motor evoked potentials, when a single pulse TMS was delivered and dynamic sounds approached the space near the hand. Bufacchi and Iannetti (2018) have recently defined PPS as a series of response "fields" describing the magnitude of a certain response to a stimulus in space. The speeding up of the motor responses to stimuli, appearing close to the body, would be an index of how much a given action, or a set of actions, are relevant to create or avoiding contact of the external object with the body. Among others, the proximity of the visual stimulus to the body is one important factor which determines the action relevance and the magnitude of the response (Bufacchi & Iannetti, 2018).

Notably, the facilitation of the responses appeared to be gradual. It was found, not only when two spatial positions, a near-space (45 cm from the subject's body) and a far space (150 cm from the subject's body) (Study 2a, 2b, 3), were sampled, but importantly, it appeared to be progressively affected by the proximity of the approaching, joyful, angry or neutral face when five distances were sampled (45, 80, 115, 150, 185 cm from the subject's body; Study 1). This evidence would sustain a conceptualization of PPS, as a series of graded response fields (Bufacchi & Iannetti, 2018), rather than a sharp delimited spatial boundary of response. This model would meet also electrophysiological monkey's literature which described the graded response of the PPS neurons when a stimulus was approaching the tactually stimulated body part of the animal (Colby et al., 1993). To note, at a difference with Study 1 which sampled a more continuous portion of space, in Study 2 a, 2b, and 3, only two spatial conditions were tested. Nonetheless, this methodological choice did not negate a conceptualization of PPS as a continuum of responses.

7.2.3 When fear is near: the effect of the affective content of the stimulus

A second main result of these studies was that, other than the effect of the face distance at the time of the tactile stimulation (*PPS effect*), the affectively relevant content of the emotional expression of the looming face affected the behavioural and the physiological responses. Enhanced defensive responses were elicited when the fearful face was closer rather than far from the observer. A growing amount of studies are describing that the defensive responses are different if the threat is signalled in the proximity of the body compared with the distant space (Åhs et al., 2014; de Borst & de Gelder, 2018; Löw et al., 2015; Marchant et al., 2009; Mobbs et al., 2015, 2020, 2007): proximal threats are likely more harmful than far threats, and consequently they may elicit more intense defensive responses. Fearful and angry faces, by both signalling a high probability of encountering a threat, are quite likely to elicit an increase of the defensive responses as they approach the observer. However looming fearful faces, along with their increased imminence (Fanselow & Lester, 1988; Fanselow, 2018) are more context-dependent than angry faces. Their informative value is heightened with the examination of contextual information, as demonstrated by the elicited greater sensitivity to the surrounding context (Becker & Detweiler-Bedell, 2009; Phelps et al., 2006; Taylor & Whalen, 2014). The appearance of a fearful face would initially be detected and processed; but while it approaches the subject, it might elicit an increased attentivity to the context to gather information from the environment. The closer is the fearful face, the more the threat is imminent and the need to prepare an adequate, complex, defensive response is urgent. To select the most optimal response (Gladwin et al., 2016), enhanced perceptual and attentional processes (Erickson et al., 2003; Lang et al., 2000) are necessary. The individual is likely to pass through an attentive state, similar to what described by Roelofs (2017), in which the immediate action is prevented to enable the subject to scan the environment in preparation for a successive active response, that can be creating or avoiding the contact with the upcoming threat. Therefore, as the looming fearful face approaches the subject, an enhanced attentive scanning of the environment is prioritized, and its position would likely not determine the readiness of a motor response to a tactile target. Results from Study 1 seem to go in the direction of this hypothesis. Contrarily to what found with joyful, angry and neutral expressions, in which the position of the looming face determined the preparedness to respond to tactile stimuli, with fearful facial expression, the participants' responses to touch did not speed up any further, as the face approached the body. The fearful face may have prompted a general increase of attentivity to the environment, at the expenses of the attention onto the looming fearful face's location which would be more fleeting. For this reason, with looming fearful faces, responses to tactile targets were less dependent upon the distance of the approaching face. Notably, the effect found for fearful faces does not seem to reflect a generic response to negative stimuli, as it was not observed for angry faces, but it is related to the capability of the facial expression of fear to warn of potential dangers. This signal would require more complex defensive responses, such as an increased attentivity to the surrounding space which may also be supported by an increased arousal response. In this respect, Study 4 demonstrated that a fearful face gradually modulated the evoked physiological arousal response as the fearful face was perceived closer to the individual, at a difference with joyful faces in which its response was constant in space and significantly lower than the one evoked by fearful faces when it appeared in the proximity of the subject. This increasing of the physiological arousal response was found to be modulated not only by the mere presence of a threatening ambiguous stimulus but also by its perceived imminence (i.e., when the face was looming closer to the subject). Studies have shown that the imminence of the threat would affect brain activity differently than far and non-imminent threats (Marchant et al., 2009; Mobbs et al., 2007; Wendt et al., 2017). Particularly, an increase of skin conductance response, which is a proxy of the arousal reaction, was reported as the imminence of the threat was increasing (Combe & Fujii, 2011; Löw et al., 2008; Wendt et al., 2017). Åsh and colleagues (2014) demonstrated that conditioned threatening humans, approaching the participant in virtual reality, were more resistant to extinction processes when the threatening character was closer to the participant than when it was distant. Further, this condition corresponded with a more synchronized activity across participants in the emotion-related structures (amygdala, ACC, insula), as demonstrated by De Borst and colleagues (2018). These authors also found that when the first-person perspective was induced, and consequently the threat was perceived as directed towards oneself, the activity of PPS network areas was enhanced, and direct neural connections were found from the left intraparietal sulcus (considered a key area of the PPS network; Grivaz, Blanke & Serino, 2017) to the right anterior cingulate cortex, and from that structure to the right amygdala and the left anterior cingulate cortex. Besides, the amygdala has also been shown to be particularly activated by the ambiguity of the stimulus, such as by fearful faces with a straight gaze, rather than averted toward a specific location (Adams & Kleck, 2005; Benton, 2010). An enhanced amygdala activation would support the attentive scanning of the environment to resolve the uncertainty and the ambiguity of the upcoming danger, signalled by the fearful face. To conclude, the behavioural and the physiological results from Study 1 and 4, provided a piece of evidence that the affective content of a fearful face (Alpers et al., 2011; Fusar-Poli, Landi, et al., 2009) is maximally effective when the face approached the very proximity of the subject, where the potential threat might be inescapable, and the need for defence is most pressing.

7.2.4 The spatial logic of fear

The third main result of these studies was defined as the attentional effect of fearful faces, that was mainly reported in Study 2a and Study 3. In contrast to what found with neutral, joyful, and angry faces, when faces displayed a fearful expression, responses to tactile stimuli were modulated not only depending on their distance from the participant, but also according to the position of another visual element, a static ball. In the near space, but not in the far, responses to tactile stimuli were facilitated when the ball appeared more peripherally, compared to when it appeared closer to the face. This result would also complement the effect described in Study 1. The reduced multisensory integration found when fearful faces were entering the space near the body (Study 1), was attributed to an enhanced attentivity to the surrounding space of the face; when another visual stimulus, i.e., the ball, was introduced (Study 2a), it captured the attention, particularly when appearing in the surrounding peripheral space. The appearance of a contextual element would complement the communicative value of fearful faces, which signal an upcoming threat from the environment. The co-occurrence of the fearful face and the peripheral ball, in the near space, produced not only the capture of the attention by the ball, which is visible in the fastening of the responses to tactile stimuli (compared to when the ball is central) but, also, the complementary effect of attentional disengagement from the face. This last effect was visible in a reduction of the face-sensitive N170 component evoked by the face-peripheral ball compound (compared to when the ball is central). The diminished attention to the face itself, in this phase, would be essential to favour the processing of any upcoming event in the surrounding.

Notably, this effect was not attributed to the negative valence or arousing level of the fearful face. Angry faces, similarly negative and arousing stimuli as fearful faces, were not different from neutral when tested in Study 2b: when angry or neutral faces were looming in the space near the subject, responses to tactile stimuli were not modulated by the position of the ball; this effect was taken as the evidence that looming angry faces, similarly to neutral, attract attention that remains on the face as it approaches. This interpretation would also explain results from Study 1, in which angry faces, like neutral, showed gradual facilitation of the tactile responses as the face approached the subject. Pieces of evidence pointed out that fearful and angry emotional expressions differently affect the attention and memory processing of contextual elements (Davis et al., 2011; Taylor & Whalen, 2014). This differential effect has to be attributed to their different communicative values, which provide different information about the social and physical environment. Angry faces are a direct threat. Fearful faces, instead, are associated with potential threats. To solve the intrinsic ambiguity of the stimulus of fear, fast and efficient processing of contextual information is adaptively prompted by an increase of attention to the surrounding. Results from Study 1, Study 2a and 2b confirm that angry and fearful faces exert different effects when tested in the multimodal spatial task. Looming fearful faces produced a widening of attention which was not observed for the angry faces.

Importantly, this effect of redirection of attention found with fearful faces both in the modulation of the response to tactile stimuli and in the face-sensitive ERP component presented a spatial logic. It was found only when the face was looming in the space near the body and not in the far. As argued above, fearful faces, looming in the near, signal a potential imminent threat, for which the urgency of preparing a defensive response is higher (Koster, Crombez, Van Damme, et al., 2004; Löw et al., 2015; Marchant et al., 2009). Also, the space closer to the subject is where attention seems to be preferentially deployed (Finlayson & Grove, 2015; Maringelli et al., 2001; Plewan & Rinkenauer, 2016, 2017) and where attentional shifts are facilitated (Chen et al., 2012; Wang et al., 2016). Also, the near-space is the condition in which the stimulus would be more respecting the spatiotemporal criteria of multisensory integration: the ball and the tactile stimulation are presented simultaneously and the near peripheral ball is more likely to be jointly processed with the tactile stimulus, rather than the far peripheral ball. Indeed, the attentional effect evoked by fearful faces, observed here, is not described as a purely visual attentional phenomenon. Although shifts of visual-spatial attention are not directly measured, the different configurations of visual stimuli (face flanked with ball central versus ball peripheral) allowed to create different conditions to probe, indirectly, where the focus of spatial attention was, to more effectively determining the readiness in the response to tactile stimuli. Spatial attention may have interacted with the strength of the visuotactile integration in determining the sensorimotor response.

To conclude, these results confirmed the hypothesized attentional dynamic triggered by the presentation of the fearful face, which showed a distinctive centrifugal spatial pattern, compared to the other emotional expressions. The emotional attention mechanisms (Vuilleumier, 2005) would not only mediate the initial capture by the face but also the reflexive tendency to disengage from the face to favour the surrounding, producing an attentional bias toward the peripheral space of the face. When a fearful face rapidly approaches the space near the subject's body, attention would be fleeting and biased toward the surrounding of the face. Attention is likely to be easily disengaged from the face, by any events in this surrounding space; such upcoming events (i.e., the appearance of the peripheral ball) would capture attention. This bias may set an area of relevance in which the multisensory processing is enhanced (De Meo et al., 2015; Talsma, 2015; Talsma et al., 2010; Tang et al., 2016).

7.2.5 Limitations and future research

The first limitation concerns the difficulty in determining the exact contribution of the multisensory stimulation compared to the unimodal stimulation. In Study 2, the attentional dynamic, triggered by the presentation of the fearful face, is expressed by a multisensory phenomenon (i.e., the modulation of the response to tactile stimuli by the different visual conditions); nonetheless, due to the lack of unisensory conditions, the independent contribution of the visual and the tactile stimulation cannot be assessed. Similarly, and connected to this point, the electrophysiological response measured in Study 3, and the electrodermal activity in Study 4, are induced by the multisensory compound stimulus which includes the tactile stimulus and the visual stimulus (looming face in Study 3 and 4, and the ball in Study 3). Yet, it cannot be determined which would have been the contribution of the visual stimulation alone if the tactile stimulus would not have been presented or set as a target. To conclude, the lack of unisensory control conditions, to evaluate the multisensory effect's magnitude, presents the first and important limitation of the present research.

A second point concerns the interpretation of the results. Fearful faces convey broad signalling of threat in the environment that widens attention. If the interpretation of the present results is correct, the effects found with fearful faces are due to the spatial ambiguity conveyed by a fearful forward/straight gaze. Therefore, providing a spatial cue of exogenous orienting, i.e., a fearful face with adverted gaze, would reduce the threat's spatial ambiguity. If fearful faces had the gaze averted towards the position of the visual ball, the predicted results would differ from the ones obtained when the fearful face had a straight gaze. To conclude, the manipulation of the gaze would be important to confirm the present experimental hypothesis.

7.3 Conclusions and Final Remarks

In sum, the present thesis project showed that fearful faces elicit differential behavioural responses in PPS when compared with other emotions; this effect is not ascribed to the valence of the stimulus but to the fearful face itself (Study 1). This PPS modulation can be attributed to the fact that an approaching fearful face, at variance with other emotions, elicits a shift of spatial attention from the face to the peripheral space (Study 2a and 2b). This effect is reflected also at the physiological level both in the ERP (Study 3) and in the arousal response (SCR) (Study 4). The redirection of attention toward the peripheral space, prompted by the fearful face, would support the prompt reaction to any upcoming threat from the environment. This results would extend the present literature in two main directions.

First, the present results reveal a fundamental property of fearful faces that would fulfil their adaptive function precisely in the situation of maximal imminence, that is when looming near the subject’s body. The highlighted effect of attentional diffusion would also be seminal in distinguishing the effect exerted by fearful faces from that of other threats, first among all, angry faces. Angry faces were often ontologically merged with fearful faces, as equivalent examples of negatively valenced, and threat-related, stimuli (Hariri et al., 2002).

Second, the result of the present study well fits a recent conceptualization of PPS proposed by Bufacchi and Iannetti (2018) and may constitute empirical evidence to support this model. Bufacchi and Iannetti (2018) have defined PPS as a series of graded response fields which reflects how much a certain action is relevant to the aim of avoiding or creating the contact of objects with the body. This reconceptualization of a graded PPS (Bufacchi & Iannetti, 2018), departs from the oversimplification of PPS as an in or out bubble and allows a richer description of the response properties related to PPS. In the present studies, it was demonstrated that distance-dependent multisensory facilitation showed a response that was not binary but graded with the reduction of stimulus distance from the body. Further, following the reconceptualization proposed by the authors (Bufacchi & Iannetti, 2018), the neural populations of the frontoparietal networks would transform the visual inputs into the representation of a set of potential actions. Importantly, according to this model, the relevance of possible actions would not only depend upon the position of the objects or other agents, but also upon which are the actions available in that precise situation; i.e., actions dependent on proximity to the body are more relevant given the aim of contact with an object, but contextual factors may change the relevance of those actions. The present results showed that the proximity of a stimulus is not the only factor in determining the action relevance in creating or avoiding contact with an object, but also the nature of the stimulus (i.e. a face expressing fear). The perception of a fearful face, rapidly approaching the space near the body, may generate different response fields reflecting the relevance of actions to defend the body from harms. In this case, those fields may describe the maximal relevance of action in the surrounding space of the face; in other words, since the threat is likely to be elsewhere, an action toward the fearful face itself, might not be relevant in defending the body. Therefore, it can be concluded that the graded field of action-relevance, is determined by both the proximity of the stimulus and its affective content. This implies the participation of other brain functions such as the limbic processing of emotions, the frontoparietal attentional networks, the autonomic regulation of the arousal response. These systems interact with the contact-prediction function which defines the multisensory PPS to support an adequate defensive response.

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