Fearful faces modulate spatial processing in peripersonal space: An ERP study

Published Version:

Ellena, G., Starita, F., Haggard, P., Romei, V., Làdavas, E. (2021). Fearful faces modulate spatial processing in peripersonal space: An ERP study. NEUROPSYCHOLOGIA, 156, 1-9 [10.1016/j.neuropsychologia.2021.107827].

Published:

DOI: http://doi.org/10.1016/j.neuropsychologia.2021.107827

Highlights

- In near space, tactile processing to centrally presented looming fearful faces is facilitated by the appearance of a peripherally presented visual probe, as compared to a centrally presented probe.
- This effect is accompanied by a reduction of the N1 mean amplitude elicited by the peripheral probe for fearful relative to neutral faces
- Thus, fearful faces intruding into PPS may increase expectation of a visual event occurring in the periphery.

Fearful faces modulate spatial processing in peripersonal space: an ERP study

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Abstract

Peripersonal space (PPS) represents the region of space surrounding the body. A pivotal function of PPS is to coordinate defensive responses to threat. We have previously shown that a centrally-presented, looming fearful face, signalling a potential threat in one's surroundings, **modulates spatial processing by** **promoting** a redirection of **sensory resources** away from the face towards the periphery, **where the threat may be expected** – but only when the face is presented in near, rather than far space. Here, we use electrophysiological measures to investigate the neural mechanism underlying this effect. Participants made simple responses to tactile stimuli delivered on the cheeks, while watching task-irrelevant neutral or fearful avatar faces, looming towards them either in near or far space. **Simultaneously with the tactile stimulation,** a ball with a checkerboard pattern (probe) appeared to the left or right of the avatar face. Crucially, this probe could either be close to **the** avatar face, and thus more *central* in the participant's vision, or further away from the avatar face, and thus more *peripheral* in the participant's vision. Electroencephalography was continuously recorded. Behavioural results confirmed **that** in near space only, **and for fearful relative to neutral faces**, tactile processing was facilitated by the peripheral compared to the central probe. **T**his **behavioural** effect was accompanied by a reduction of the **N1** mean amplitude **elicited by the peripheral probe** for fearful **relative** to neutral faces**. Moreover, the faster the participants responded to tactile stimuli with the peripheral probe, relative to the central, the smaller was their N1. Together these results, suggest that fearful faces intruding into PPS may increase expectation of a visual event occurring in the periphery.** This fear**-induced effect** would enhance the defensive function of PPS when it is most needed, i.e., when the source of threat is nearby, but its location remains unknown.

Keywords: peripersonal space; fearful faces; **N1**; multisensory integration; **space representation**

Introduction

In order to **successfully** interact with stimuli in the environment, humans and other animals need a representation of the body and of the space immediately surrounding it. This space is called peripersonal space (PPS). The representation of PPS is subserved by a cortical network that processes visual or auditory information occurring in the space immediately surrounding the body, as well as tactile information occurring on the body surface itself. Specific populations of multisensory neurons in the parietal and frontal areas respond both to tactile information on the body (arm, face or trunk) and visual or auditory stimuli occurring in PPS, i.e., close to the body. Thus, numerous studies in non-human primates (Avillac et al., 2005; Fogassi et al., 1996; Duhamel et al., 1997; Colby, Duhamel & Goldberg, 1993) and in humans (Brozzoli et al., 2014; Makin et al., 2007) have shown that multisensory cues, and specifically tactile cues, are processed by a specialized neural system representing PPS.

A pivotal function of PPS is to defend the body from harm. In monkeys, the electrical stimulation of multisensory neurons in the parietal and frontal regions induces defensive and avoidant motor responses (Cooke & Graziano, 2004; Graziano & Cooke, 2006; Graziano et al., 2002). Importantly, neurons in these multimodal regions are optimally tuned for the detection of dynamic visual stimuli and appear to be involved in predicting the impact of an object with the body (Cléry et al., 2017, 2018; Guipponi et al., 2013). Additionally, in humans, defensive responses increase as the vicinity of a potentially dangerous stimulus approaching the face increases (Bisio et al., 2017) and when the probability that the threatening stimulus impacts and harms the face (or the hand and the trunk) increases (Bufacchi & Iannetti, 2018). Moreover, rapidly approaching sounds, signalling potential threat, have been found to significantly enhance visual cortex excitability as they approach the participant (Romei et al., 2009, 2013), and to drive attentional resources in the direction of the sound source (Leo et al., 2011). In line with this, tactile response is facilitated when threatening pictures (for instance a snake or a knife) are presented in PPS rather than in far space (Poliakoff et al., 2007; Van Damme et al., 2009). Additionally, a stimulus, perceived as threatening, facilitates tactile processing at distances farther from the body as compared to a non-threatening stimulus (Taffou & Viaud-Delmon, 2014). Thus, PPS is not only modulated by the stimulus' proximity to the body but also by its speed and affective valence. These findings suggest the existence of a dynamic security space around the body with the aim of keeping us safe from any potential physical danger.

Fearful faces are **evolutionary relevant** stimuli, signalling a potential threat in one's surroundings. Interestingly, unlike angry faces or the threatening stimuli used in the studies described above, fearful facial expressions do not in themselves represent a direct threat to the body. Rather, they signal a potential upcoming danger in the environment, without specifying its nature or location (Hortensius et al., 2016). As such, fearful facial expressions might **induce the expectation of an impending threat away from the fearful face, in the surrounding environment** possibly to facilitate locating the actual source of the threat that has induced fear (Taylor & Whalen, 2014).

We recently investigated in a virtual reality environment whether such dynamic, triggered by the presentation of different facial expressions, is modulated by the location of the emotional faces in the near space, compared to far space (Ellena et al., 2020). Participants performed a visuo-tactile integration task (akin to Pellencin et al., 2018; Serino et al., 2015) by responding as fast as possible to tactile stimuli presented on the cheeks, while watching task-irrelevant neutral, joyful or fearful avatar faces, looming in far or near space. This design allowed us to assess changes in PPS representation operationalised as the gain in reaction times in response to tactile stimuli depending on whether the stimulus was coupled with near vs. far visual stimuli, which could express either fearful or neutral emotions. Importantly, in order to assess the **impact of** fearful faces **on visuo-spatial processing** a static, task-irrelevant, visual stimulus, a checkerboarded ball, thereafter, referred to as the **spatial** probe, appeared to the left or to the right of the face at the time of the tactile stimulation. Crucially, the probe could either be close to the face, and thus more *central* in the participant's vision, or further away from the face, and thus more *peripheral* in the participant's vision. With this paradigm, the spatial **distribution** of sensory **resources is** indirectly assessed through the amount of facilitation (faster reaction times) that visual stimuli have on processing tactile stimuli. We hypothesised that the probe would facilitate the response to tactile stimuli when it appears in a spatial location **where** it **is** **actually** **expected**. In particular, a fearful face **may** signal a **potential** threat **whose location is unknown and possibly** **expected elsewhere, away from the face. Consistent with this** **view, our previous** results (Ellena et al., 2020) showed that with neutral and joyful faces, simple reactions to tactile stimuli were facilitated in near rather than in far space (classic PPS proximity effect) and **with** **the** central rather than **the** peripheral **spatial** probe. However, when the face was fearful, tactile processing was modulated not only by the distance of the face from the participant but also by the position of the probe. Specifically, in near space only, tactile processing was additionally facilitated by the peripheral compared to the central probe. Thus, as fearful faces come closer to the body, they **facilitate spatial processing in the peripheral space.** **This in turn might** enhance the defensive function of PPS specifically when it is most needed, i.e., when the source of threat is nearby, but its location has not yet been identified.

The present study capitalizes on these results **by** investigating the electrophysiological mechanism underlying the effect of fearful faces on PPS. Specifically, here we assess the hypothesis of a differential modulation of electrophysiological response elicited by **peripheral as opposed to central probes** **as a function of the emotional context (**fearful vs. neutral faces) **and** position in PPS **in which they appear**. Of relevance in this respect is the **visual N1** ERP component, a negative deflection in electrical potential observed at temporo-occipital electrodes between 1**5**0 and 200 ms following presentation **of a visual stimulus (Luck, 2014), and considered to be a marker of visuospatial processing (Wascher et al., 2009). Interestingly, the N1 is modulated by exogenous as well as endogenous factors, and is sensitive to both the physical properties of the stimulus and to the nature of the interaction between the participant and the stimulus (Fabiani et al., 2009). For example, smaller amplitude of this component has been associated with predictable rather than unpredictable visual stimuli (Heilbron & Chait, 2018; Johnston et al., 2017; Robinson et al., 2020).**

Participants completed the same paradigm as in Ellena et al. (2020) described above, while electroencephalography was recorded. Note that in the present study we tested only fearful vs. neutral facial expressions. Different predictions can be made in relation to the facial expressions (neutral vs. fearful), the spatial positions of the probe (central vs. peripheral), and the spatial position of the looming face from the body (near vs. far). Behavioural results are expected to be analogous to those of Ellena et al. (2020) summarized above. As for EEG data, no significant modulation of the **N1** amplitude is expected for any condition in the far space. **In contrast, in near space, we expect the N1 evoked by the probe to be modulated by the emotional context provided by the facial expression (fear vs neutral) as a function of probe position (peripheral vs central). Given that a fearful face may increase expectation of a potential threat coming from the surrounding environment away from the face, N1 amplitude may be reduced with a peripheral as compared to central probe.**

Methods

Participants

Twenty-two healthy right-handed 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 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 prior to participating and after being informed about the procedure of the experiment. Using G*Power 3.1 software (G*Power; Faul et al., 2007), with an effect size of f = 0.25 (medium effect size), an alpha of 0.05 and a power ($1 – \beta$) of 0.9 for a repeated measure, 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).

Stimuli and materials

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. In order 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 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 (probe), appeared for 250 ms, either ≈1° (probe central) or ≈10° (probe peripheral) to the left or right of the face (left and right sides counterbalanced among trials; see Figure 1). The degree of eccentricity of the peripheral probe was 10°. This eccentricity produces a visual stimulus that, despite appearing in the periphery of the visual field, can influence processing of a centrally presented stimulus (Honda, 2005; Chen, 2008; Born & Kerzel, 2008; Findlay & Walker, 1999). Thus, at T1, touch coincides with perception of the probe 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 and colleagues (2015) corresponding to the same near and far distances as defined in Ellena and colleagues (2020). Also, given that the current study aimed to investigate the neural bases underlying the behavioural results of Ellena et al. (2020), we kept the structure of the task consistent across the two studies in order to maximize the reproducibility of the behavioural results. Given that participants respond with the right hand, we wanted to exclude an effect of spatial compatibility on response time. For example, we wanted to avoid spatial compatibility effects between the tactile stimulus and the response. Thus, a unilateral tactile stimulation might lead to a modulation in response times when delivered to the right (vs left) cheek for reasons of spatial compatibility rather than multisensory integration. Thus, here and in the original study, we decided to deliver a bilateral tactile stimulus to reduce this possibility.

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Visual stimuli validation

Note that all face stimuli (fearful 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 fearful or neutral expression.

In order to select the faces to be included in each experiment, 60 naive participants (30 females; mean age 29±10 SD) were instructed to rate 10 faces. Of those, 5 represented versions of fearful faces and the remaining 5, versions of neutral faces. Participants had to indicate which emotion was expressed by each presented face and subsequently rate on a 10-points Likert scale how strongly the emotion was expressed (0 = lowest intensity; 9, highest intensity). Also, they had to rate the arousal level generated by each stimulus, on a 10-point Likert scale (0= not at all arousing; 9= extremely arousing).

We selected a total of 2 fearful and 2 neutral facial expressions for which the highest percentage of participants correctly identified the facial emotion (mean hit rate for: fearful faces, 80%; neutral faces, 81%), which also showed the highest perceived intensity and the highest perceived arousing effect (Figure 2 shows an example of chosen stimuli).

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To check whether the mean ratings for intensity and arousal were significantly different between fearful and neutral faces, a 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 (1,59) =229.6; $p<0.01$; $\eta_p^2=0.79$]. Fearful expressions were judged as more intense than neutral ones (fearful faces: M=7.12; SEM=0.18; neutral faces: M=2.39; SEM=0.26). The analysis on arousal level showed that ratings were also different across emotions [F (1,59) =134.23; $p<0.01$; $\eta_p^2=0.69$]. Fearful expressions were judged as more arousing than neutral ones (fearful faces: M=5.08; SEM=0.30; neutral faces: M=2.39; SEM=0.20).

Task and procedure

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; Probe Position: central / peripheral. An additional 80 trials with no vibration and 20 trials with no probe presentation were introduced in order to decrease task predictability. Both central and peripheral probes 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 evenly 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 a 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 3). Before the task began, the lenses' focus was manually adjusted by each participant until 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.

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Recording and Data Analysis

The EEG was continuously recorded with Ag/AgCl electrodes (Fast n Easy Electrodes, Easycap, Herrsching, Germany) 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 electro-oculogram (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 over a period of 200 ms preceding T0. In addition, epochs with large artefacts contamination were identified and removed using two methods from the EEGLAB toolbox (Delorme & Makeig, 2004): (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 %). In each condition, the epochs left after pre-processing were **on average**: **36.41 (SEM=0.99;** 91.02%**)** in the Fear Far Central**, 36.59 (SEM=0.92;** 91.48%**)** in the Fear Far Peripheral, **36.68 (SEM=0.71;** 91.7%**)** in the Fear Near Central, **36.32 (SEM=0.7;** 90.79%**)** in the Fear Near Peripheral, **36.54 (SEM=0.9;** 91.36%**)** in the Neutral Far Central, **36.86 (SEM=0.99;** 92.16%**)** in the Neutral Far Peripheral, **37.18 (SEM=0.59;** 92.95%**)** in the Neutral Near Central and **37.86 (SEM=0.4;** 94.66%**)** in the Neutral Near Peripheral. Importantly, the number of remaining epochs did not differ between conditions in which the probe 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 (Delorme & Makeig, 2004) and removed according to the ADJUST plugin application (Mognon, Jovicich, Bruzzone & Buiatti, 2011).

Remaining epochs were divided into eight separate datasets, according to the stimulus condition. The **N1** was evaluated as the activity of the left (P7, PO7) and right (P8, PO8) temporo-occipital recording sites (**as in Wynn et al., 2015; Schindler et al., 2020; Robinson et al., 2018; Oribe et al., 2020**). For each participant, for which **the first** maximal negative deflection after T1 (the appearance of the probe and the delivery of the tactile stimulation) was observed, was used to anchor a relative sub-time-window of ±15 ms **(Jackson et al., 2008;** Prieto et al., 2011; Moore et al., 2014). **N1** component was quantified as the mean amplitude within this sub-time-window. This method controlled for latency variance of **N1** onset while preserving the mean amplitude measure’s lower susceptibility to spurious peaks (Luck, 2004; Ito, Gracco, & Ostry, 2014; Ott et al., 2011). **N1** mean amplitudes were analysed with a 2x2x2 RM ANOVA (Emotion: Neutral / Fearful; Space: Far / Near; Probe Position: Central/ peripheral as within-participants factors). Post-hoc comparisons were carried out using the Newman–Keuls test.

Results

Behavioural Results

We tested whether the presentation of a fearful face relative to a neutral face had a differential impact on the response to the participants own face's tactile stimulation. The tactile stimulation was always paired with the presentation of a visuo-spatial probe (represented by a static checkerboarded ball) next to or distal from the looming face. Moreover, in order to measure the potential impact of peripersonal space (PPS) on performance, this effect was measured as a function of the near (peripersonal) and far (extrapersonal) space. As the rate of omissions was low (M=1.25% SD=2.12), 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. We checked the skewness of the distribution of our RTs data as recommended by Field (2013) and found it to lie between 0 and 1 in all conditions. Additionally, when converting these values to z-scores we found they were all below 1.96, indicating that skewness was not significantly different from that of a normal distribution ($p>0.05$), except for the neutral faces in near space with the central probe, where skewness z-score=2.05 corresponding to $p=0.04$. Thus, given that the distributions of RTs were not significantly skewed except for one marginally significant condition, and that we had a within-subjects design with all conditions having the same sample size, we deemed parametric tests appropriate to analyse our data (Field, 2013).

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

Results (see Figure 4) showed a significant main effect of Emotion [F(1,21)=16.32; $p<0.001$; $\eta_p^2=0.44$] 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; $p<0.001$; $\eta_p^2=0.81$] 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 Probe Position [F(1,21)=0.97; p=0.34; $\eta_p^2=0.04$], nor Emotion by Space [F(1,21)=0.01; p=0.91; $\eta_p^2<0.01$] or Emotion by Probe Position [F(1,21)=0.01; p=0.93; $\eta_p^2<0.01$] interaction. However, there was a significant Space by Probe Position [F(1,21)=4.26; p=0.05; $\eta_p^2=0.17$] interaction showing that the probe position had a different impact on RTs. Crucially, the Space by Probe Position was best explained by the significant three-ways Emotion by Space by Probe Position interaction [F(1,21)=6.72; p=0.02; $\eta_p^2=0.24$] suggesting that the impact on the probe 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 probe 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 in 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, the spatial probe 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 probes (Fear Far Central: M=386.83 ms, SEM=17.86; Fear Far Peripheral: M=394.52 ms, SEM=17.89; p=0.002); in the near space, instead, RTs were faster for peripheral relative to central spatial probes (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 probes (central probe: $p=0.038$; peripheral probe: $p<0.001$). In contrast, in far space, tactile responses were faster to fearful than neutral faces, for central probes only ($p<0.001$).

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We also repeated the analysis including block (1 to 5) as a factor. This produced a significant main effect of block ($p<0.001$), 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 $p\geq0.344$). Additionally, including probe side (sx, dx) as a factor revealed a main effect of side ($p=0.014$), with participants being faster to left than right stimuli. Nevertheless, there was no interaction between side and emotion (all $p\geq0.09$), suggesting that any effect on RTs related the side of probe appearance is independent of the emotion manipulation.

ERP Results

Results of the <u>**N1**</u> component (Figure 5) showed a significant main effect of the mean amplitude for the factor Probe Position [$F(1,21)=37.40$; $p<0.01$; $\eta_p^2=0.64$] showing more negative amplitudes for central relative to peripheral probes (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 Probe 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 Probe Position interaction [$F(1,21)=4.95$; $p=0.04$; $\eta_p^2=0.19$], suggesting that Emotion differently impacted <u>**N1**</u> amplitude modulation as a function of spatial distance and probe position.

Specifically, Newman-Keuls post-hoc comparisons revealed that, when the face was in the far space, probe 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, probe position significantly modulated mean amplitude. Amplitude was **less** negative for **peripheral** than **central** probe, both for fearful (Fear Near Central: M=-4.63 µV, SEM=0.71; Fear Near Peripheral: M=-2.58 µV, 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 probe was presented in the near space, ERP amplitude was less negative for fearful (M=-2.58 µV) than neutral faces (M=-3.21 µV) (p=0.01). No other main effects nor interactions were significant (all ps>0.08).

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Correlation between behavioural and ERP responses

To further understand the relationship between our behavioural and electrophysiological results, we conducted two Pearson correlations on data for the fearful far and near conditions, where we found the difference in RTs between the central and peripheral probe. In order to facilitate data interpretability, we first computed the difference in RTs between the central and peripheral probe, as well as the difference in **N1** mean amplitude between the peripheral and central probe. Thus, an RT difference greater than 0 indicates faster response to the peripheral relative to central probe. Also, an ERP difference greater than 0 indicates smaller **N1** with the peripheral relative to central probe. Results showed a significant positive correlation between the difference in RTs and **N1** amplitude both for the near and far conditions (near: r=0.46, n=22, p=0.032; far: r=0.67, n=22, p<0.001; Figure 6). Thus, the faster participants responded to **the tactile stimulus with** the peripheral relative to the central probe, the smaller was their **N1**.

Note, that although the relationship between ERP amplitude and RTs is found both for near and far spaces, visual inspection of Figure 6 shows a different distribution of individual participants' data. Specifically, in near space, the majority of participants responded faster **with** the peripheral (vs central) probe (RT difference > 0), and all but one participant had a smaller **N1** when the probe 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 **with** the peripheral than the central probe (RT difference < 0). Also, about half of the group had a smaller **N1** when presented with the peripheral (vs central) probe (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.

---------------- Please insert Figure 6 about here --------------

Discussion

The aim of the present study was to investigate the neural **correlates** underlying **our** previously reported **modulation of spatial processing by** fearful faces **intruding into** PPS (Ellena et al., 2020). Thus, **electroencephalography was continuously recorded while** participants ma**d**e simple responses to tactile stimuli delivered on the cheeks, **during presentation of** task-irrelevant neutral or fearful avatar faces, looming towards them in far or near space. To probe spatial **processing**, a **checkerboarded** ball (**spatial** probe) appeared to the left or right of the avatar face, simultaneously with the tactile stimulation. Crucially, the probe could either be close to the avatar face, and thus more *central* in the participant's vision, or further away from the avatar face, and thus more *peripheral* in the participant's vision.

Behavioural results confirmed previous findings of Ellena et al. (2020), by showing faster responses in the near relative to far space (classical PPS effect), and for fearful than neutral faces (salience effect). Importantly, the spatial probe had a differential effect on RTs depending on the combination of emotional facial expression and its position in space (**spatial** effect). While in the neutral faces condition responses were not modulated by the spatial probe position, in the fearful face condition the spatial position of the probe had an effect on behavioural responses. Additionally, this effect depended on whether the face was in far or in near space. In far space, responses were facilitated for central spatial probes. In contrast, in near space, peripheral probes speeded up RTs. This result can be interpreted as an effect of **the emotional context whereby fearful faces facilitate peripheral spatial processing**, possibly in order to promote scanning the environment for the threat signalled by the fearful face. Importantly, this happens only once the face intrudes into the PPS. The behavioural result supporting this inference is a net advantage in RTs for the near fearful face when paired with peripheral probes. Indeed, RTs in this condition were lower than in any other condition in our design. Additionally, this inference is further corroborated by faster responses with fearful faces (vs neutral) in near space. This result appears to rule out the possibility that the difference between RTs in the fear near peripheral vs central conditions results from a slowdown in the central probe condition, as opposed to a response facilitation in the peripheral probe condition. Thus, in sum, in near space only, fearful face**s** facilitate the response to tactile **stimuli**, when a task-irrelevant visual probe is simultaneously presented **in a peripheral location**.

This **modulation of spatial processing through the** redirection of **visual** **resources** from the central face towards peripheral space is then indirectly reflected into the electrophysiological response evoked by the probe event. **Emotional faces** differentially impacted the amplitude of the probe-evoked **N1** as a function of spatial distance and probe position. When the looming face was in far space, probe position did not modulate **N1** mean amplitudes, both for fearful and neutral faces. In contrast, when the face was in the near space, probe position did modulate the **N1** amplitude; mean amplitudes were **less** negative for **the peripheral** than **the** **central** probe position, both for fearful and neutral faces. Crucially, **however,** in presence of peripheral probes, **N1** amplitude was significantly reduced for fearful faces as compared to neutral faces. Since a smaller amplitude of this component **has been** associated with **greater stimulus predictability both in the visual and auditory domains** (Heilbron & Chait, 2018; Johnston et al., 2017; Robinson et al., 2020), the lower amplitude in our peripheral probe condition suggests that **fearful faces looming in near space may increase expectation for events occurring in the periphery, possibly to facilitate response to threat**. **Indeed, a fearful face presented centrally may be interpreted as implying a threat at *another*, more peripheral location. This idea was also supported** when correlating RTs (central - peripheral probes) with **N1** mean amplitude (peripheral - central probes) for fearful faces. **Indeed,** the faster the participants responded to **tactile stimuli with** the peripheral probe, relative to the central, the smaller was their **N1.**

The results of the present study suggest that PPS representation arises from the interaction between different cognitive systems, which contribute to determine its functionality. In particular, they support the hypothesis of a functional connection between the neural structures dedicated to processing affective stimuli and those representing PPS, corroborating the defensive function of PPS (Graziano & Cooke, 2006). In this regard, the amygdala plays an important role in evaluating stimulus salience and shows greater activation when a stimulus is presented in ambiguous and uncertain environmental circumstances, such as in the presence of ambiguous threat (Adams & Kleck, 2003). Additionally, the amygdala is a core structure for perception and recognition of emotional facial expressions (Adolphs et al., 2005) and is believed to play a major role in orienting **sensory resources** towards threat-related stimuli (Cisler & Koster, 2010; Peck et al., 2013; Vuilleumier, 2005), integrating not only emotional, but also spatial information. In line with this, fearful faces, unlike other negative expressions such as anger, signal an environmental threat whose source and location are unknown (Fanselow & Pennington, 2018) and, as such, can be conceived as a salient but ambiguous or incomplete stimulus (Hortensius et al., 2016). After fearful face presentation, enhanced amygdala-mediated vigilance and arousal may facilitate scanning of the environment and dealing with the uncertainty of the upcoming danger. An indirect demonstration of such a connection comes from the work of Åsh and colleagues (2014) and Faul et al. (2020**)**: conditioned threats were more resistant to extinction processes when they invaded PPS than when they were distant. De Borst and colleagues (2018) provided further support to this result, finding that the activity in emotion-related structures (amygdala, ACC, insula) was more synchronized across participants when the threat was nearby. Moreover, when the threat was perceived as directed towards oneself, activity in regions of PPS network 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. All these findings suggest that the amygdala and emotion related structures contribute to PPS representation, in particular in the context of stimuli perceived as salient by the individual (Belkaid et al., 2015).

Furthermore, PPS has been conceived as a sensory-motor interface for body protection (Graziano & Cooke, 2006). In this regard, threatening scenarios (as opposed to joyful or neutral scenarios) and fearful faces (as opposed to joyful or neutral faces) have been found to induce a selective early increase in motor corticospinal excitability (Borgomaneri et al., 2014; Schutter et al., 2008). These results show that the emotional system and the motor system are closely related and that such stimuli act as cues that rapidly prepare the organism for action critical to survival (Anderson & Phelps, 2001). Given the sensory-motor functions of PPS, a fearful face would enhance the defensive function of PPS specifically when it is most needed, i.e., when the source of threat is nearby, and at a location that has not yet been identified. Thus, the functionality of PPS seems to rely on the interaction between an affect/threat and a sensorimotor responding system. How such interactions take place is probably the key current open question in the field of PPS research. Tailored neuroimaging studies, focusing on functional connectivity between different neural structures will increase our knowledge about PPS.

The present study did not include the presentation of other negative emotional facial expressions, so we cannot exclude that the reported effect is not elicited by other emotional expressions. However, in our previous report (Ellena et al., 2020) we did not find any behavioural evidence for this **spatial processing** effect in response to joyful faces. A fearful face indicates a possible threat at some location other than the location of the face itself. In contrast, other negative emotions, such as anger, are directly threatening in themselves. Forthcoming evidence from our laboratory suggests that looming angry faces do not produce any **differential effect on tactile processing by the position of the probe.**

To conclude, both behavioural and electrophysiological results support the **modulation of spatial processing** by fearful faces in PPS. Behavioural data show a net advantage in RTs **with** the near fearful face paired with peripheral probes, leading to the fastest RTs among the other conditions. This **effect** is then indirectly reflected into the electrophysiological response evoked by the probe. Since **an event is expected** in the space **peripheral to the fearful face** where the threat might be located, the **N1** amplitude is less negative **at the appearance of the peripheral as compared to the central** **probe**. Finally, both the ERP and behavioural effects follow the spatial-proximity rule since all the effects of interaction of emotional face by probe position are exclusively visible for the near, but not the far space.

Disclosures

Funding: This work was supported by grants from the Ministero Istruzione Università e Ricerca [PRIN. Protocol: PRIN2015 NA455] to Elisabetta Làdavas. V.R. is supported by the Bial Foundation (204/18).

Conflict of Interest: The authors declare that they have no conflict of interest.

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Figures

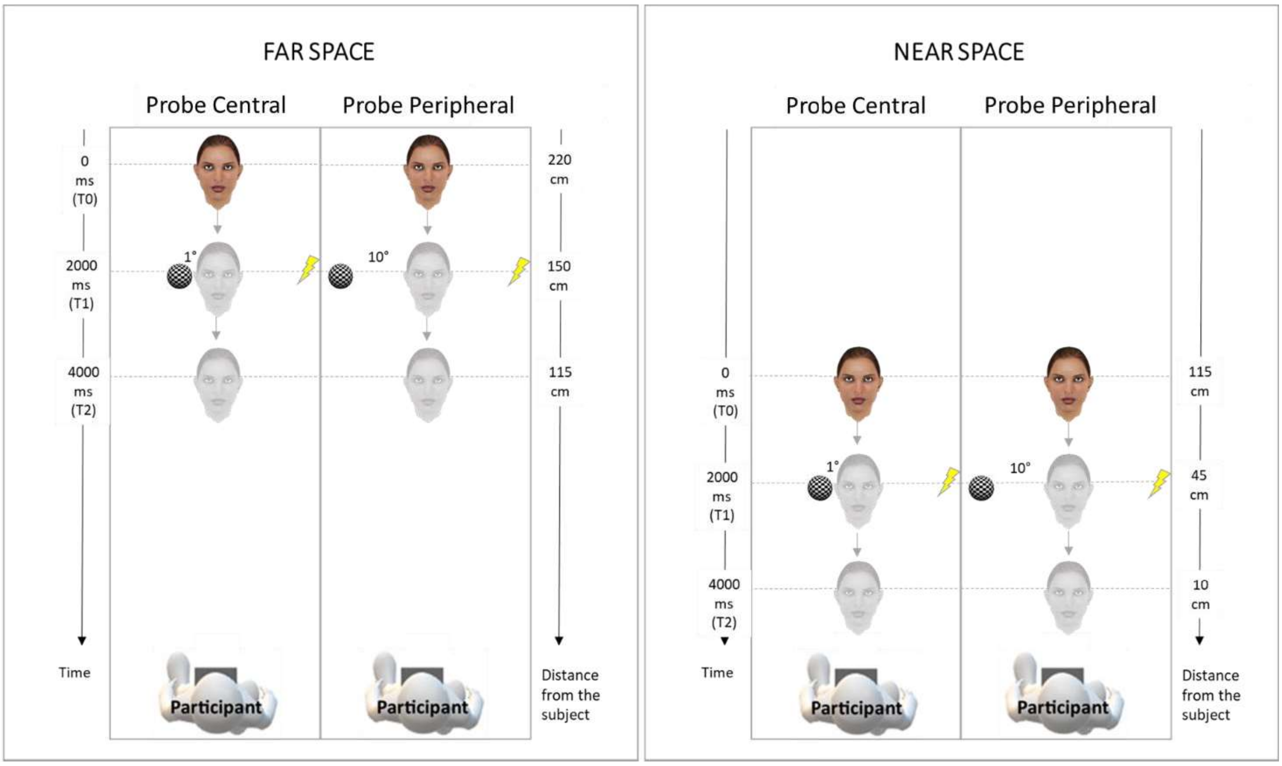

Figure 1. Experimental paradigm. Looming faces appeared at T0 in far (left panel) or near space (right panel) relative to the participant's position and moved towards the participant at a constant speed until T2. At T1, bilateral tactile stimuli were delivered to the participant's cheeks simultaneously to the appearance of a checkerboarded ball (probe), which was flashed centrally or peripherally from the face frontal plane for 250 ms.

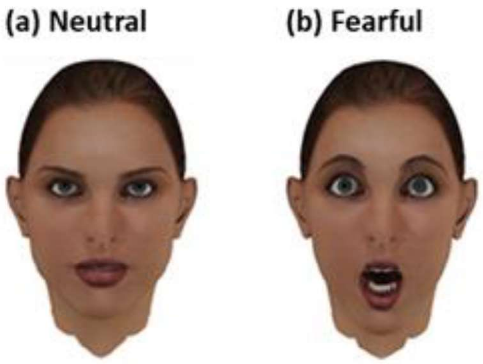

Figure 2. Exemplars of neutral (a) and fearful (b) face stimuli.

Figure 3. Illustration of the EEG/VR montage. As it can be seen in the illustration, the VR montage did not interfere with the EEG recording on the target electrodes shown in red (P7; PO7; P8; PO8).

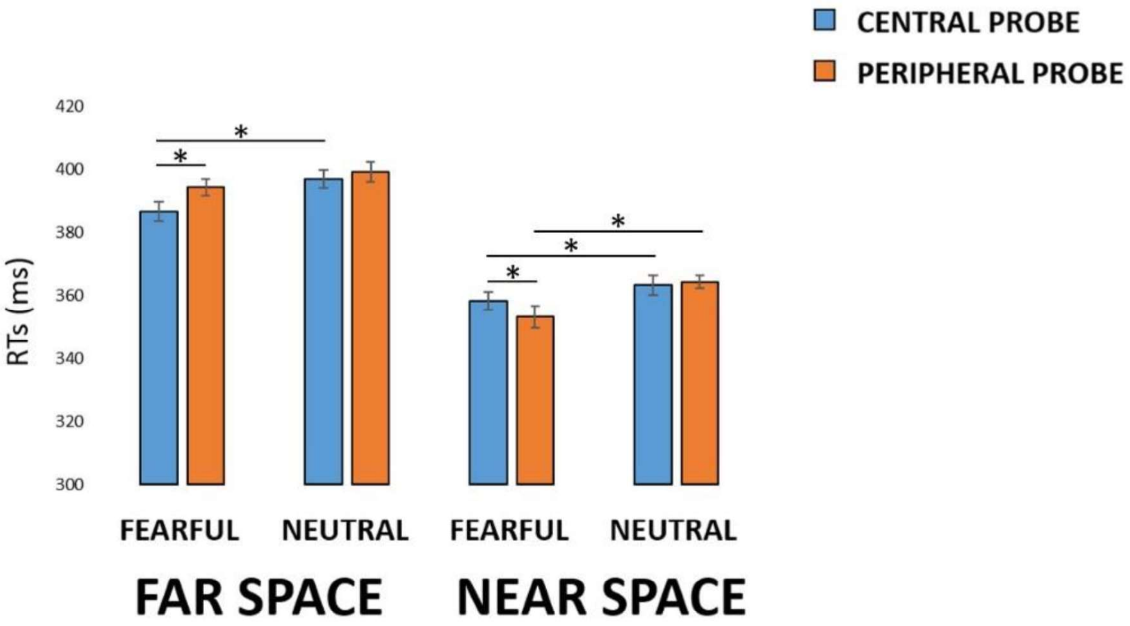

Figure 4. Behavioral results. Bar plots showing the emotion x space x probe position interaction. Asterisks show that in far space participants responded faster with fearful than neutral stimuli with the central probe and responded faster with the central than peripheral probe with fearful faces. In contrast, in near space, participants responded faster with fearful

than neutral stimuli both with the central and peripheral probes, and, crucially, they responded faster with the peripheral than the central probe with fearful faces. Error bars represent SEM corrected for within-subjects design (Morey, 2008).

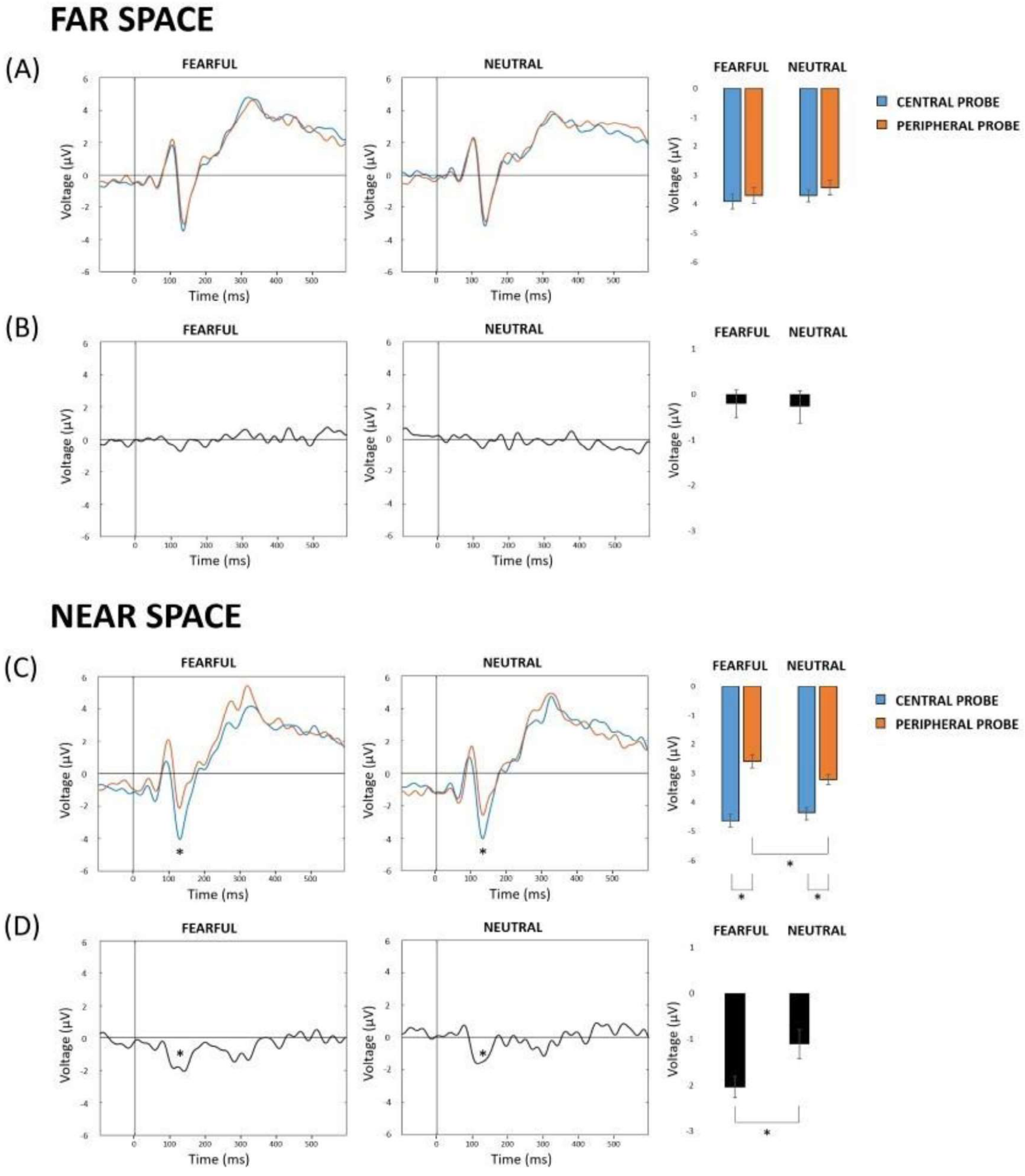

Figure 5. ERP results. Panel A and panel B represent ERPs results in the far space condition. In panel A, ERPs are plotted as a function of the probe position (central probe vs peripheral probe) in response to the emotion condition (fearful face vs neutral face). Bar plot on the rightmost part of panel A depicts averaged values of the **N1** amplitude in the far space

condition. Panel B depicts the ERP difference between the central and the peripheral probe condition in response to the emotion condition (fearful face vs neutral face). Bar plot in the rightmost part of panel B depicts the probe position effect calculated as the difference of the averaged values of the **N1** amplitude between central and peripheral probe. Panel C and panel D represent ERPs results in the near space condition. In panel C, ERPs are plotted as a function of the probe position (central probe vs peripheral probe) 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 N1 amplitude in the near space condition. Panel D depicts the ERP difference between the central and the peripheral probe condition in response to the emotion condition (fearful face vs neutral face). Bar plot in the rightmost part of panel D depicts the probe position effect calculated as the difference of the averaged values of the **N1** amplitude between central and peripheral probe. Asterisks indicate significant comparisons. Error bars represent SEM corrected for within-subjects design (Morey, 2008).

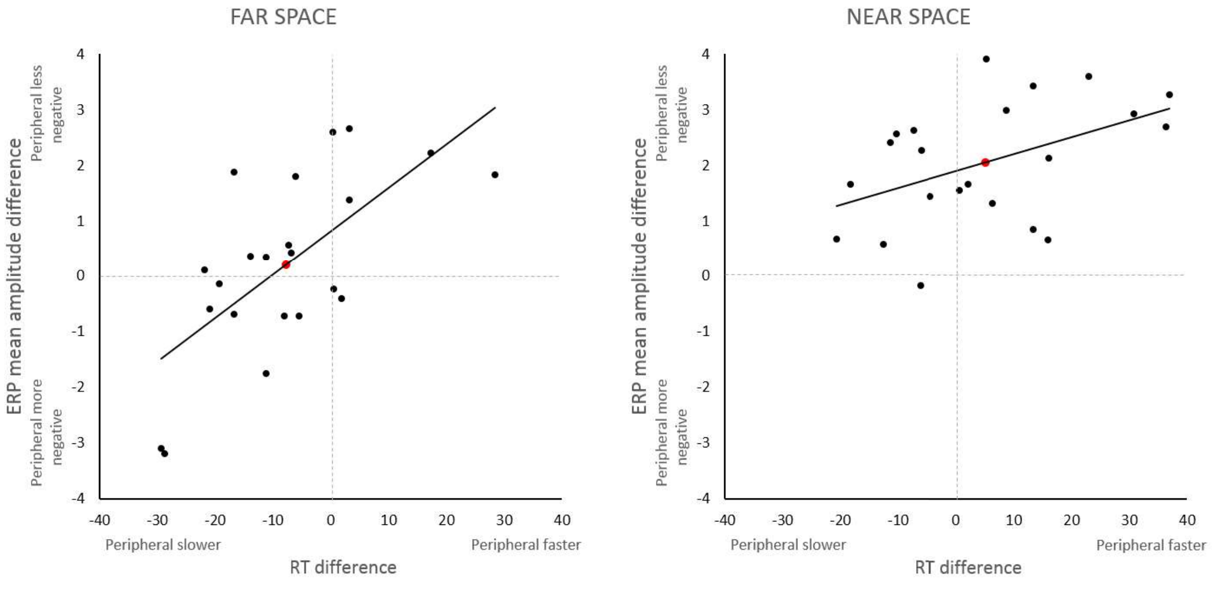

Figure 6. Correlation between the difference in RTs between the central and peripheral probe, and the difference in N1 mean amplitude between the peripheral and central probe for fearful faces presented in far space (r=0.67, n=22, p<0.001) and in near space (r=0.46, n=22, p=0.032). The red dot indicates mean of the group difference.

Credit author statement

Giulia Ellena: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Writing - Original Draft, Visualization. **Francesca Starita:** Conceptualization, Methodology, Formal analysis, Writing - Review & Editing, Visualization. **Patrick Haggard:** Conceptualization, Methodology, Writing - Review & Editing, Supervision. **Vincenzo Romei:** Conceptualization, Methodology, Resources, Writing - Review & Editing, Supervision. **Elisabetta Làdavas:** Conceptualization, Methodology, Resources, Writing - Review & Editing, Supervision