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

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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 PPS: an ERP study.

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

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20 **Abstract**

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3 21 Peripersonal space (PPS) represents the region of space surrounding the body. A pivotal
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5 22 function of PPS is to coordinate defensive responses to threat. We have previously shown
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8 23 that a centrally-presented, looming fearful face, signalling a potential threat in one's
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10 24 surroundings, **modulates spatial processing by promoting** a redirection of **sensory**
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12 25 **resources** away from the face towards the periphery, **where the threat may be expected** –
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15 26 but only when the face is presented in near, rather than far space. Here, we use
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18 27 electrophysiological measures to investigate the neural mechanism underlying this effect.
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20 28 Participants made simple responses to tactile stimuli delivered on the cheeks, while watching
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23 29 task-irrelevant neutral or fearful avatar faces, looming towards them either in near or far
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25 30 space. **Simultaneously with the tactile stimulation,** a ball with a checkerboard pattern
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28 31 (probe) appeared to the left or right of the avatar face. Crucially, this probe could either be
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30 32 close to **the** avatar face, and thus more *central* in the participant's vision, or further away
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33 33 from the avatar face, and thus more *peripheral* in the participant's vision.
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35 34 Electroencephalography was continuously recorded. Behavioural results confirmed **that** in
36
37 35 near space only, **and for fearful relative to neutral faces,** tactile processing was facilitated
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40 36 by the peripheral compared to the central probe. **This behavioural** effect was accompanied
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42 37 by a reduction of the **N1** mean amplitude **elicited by the peripheral probe** for fearful
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45 38 **relative** to neutral faces. **Moreover, the faster the participants responded to tactile**
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47 39 **stimuli with the peripheral probe, relative to the central, the smaller was their N1.**
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50 40 **Together these results, suggest that fearful faces intruding into PPS may increase**
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52 41 **expectation of a visual event occurring in the periphery.** This fear-**induced effect** would
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54 42 enhance the defensive function of PPS when it is most needed, i.e., when the source of threat
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57 43 is nearby, but its location remains unknown.
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44 **Keywords:** peripersonal space; fearful faces; **N1**; multisensory integration; **space**

45 **representation**

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47 **Introduction**

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4 48 In order to **successfully** interact with stimuli in the environment, humans and other animals
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6 49 need a representation of the body and of the space immediately surrounding it. This space is
7
8 50 called peripersonal space (PPS). The representation of PPS is subserved by a cortical network
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11 51 that processes visual or auditory information occurring in the space immediately surrounding
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13 52 the body, as well as tactile information occurring on the body surface itself. Specific
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16 53 populations of multisensory neurons in the parietal and frontal areas respond both to tactile
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18 54 information on the body (arm, face or trunk) and visual or auditory stimuli occurring in PPS,
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21 55 i.e., close to the body. Thus, numerous studies in non-human primates (Avillac et al., 2005;
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23 56 Fogassi et al., 1996; Duhamel et al., 1997; Colby, Duhamel & Goldberg, 1993) and in
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25 57 humans (Brozzoli et al., 2014; Makin et al., 2007) have shown that multisensory cues, and
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28 58 specifically tactile cues, are processed by a specialized neural system representing PPS.

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31 59 A pivotal function of PPS is to defend the body from harm. In monkeys, the electrical
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34 60 stimulation of multisensory neurons in the parietal and frontal regions induces defensive and
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37 61 avoidant motor responses (Cooke & Graziano, 2004; Graziano & Cooke, 2006; Graziano et
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39 62 al., 2002). Importantly, neurons in these multimodal regions are optimally tuned for the
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42 63 detection of dynamic visual stimuli and appear to be involved in predicting the impact of an
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44 64 object with the body (Cléry et al., 2017, 2018; Guipponi et al., 2013). Additionally, in
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46 65 humans, defensive responses increase as the vicinity of a potentially dangerous stimulus
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49 66 approaching the face increases (Bisio et al., 2017) and when the probability that the
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52 67 threatening stimulus impacts and harms the face (or the hand and the trunk) increases
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54 68 (Bufacchi & Iannetti, 2018). Moreover, rapidly approaching sounds, signalling potential
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56 69 threat, have been found to significantly enhance visual cortex excitability as they approach
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58 70 the participant (Romei et al., 2009, 2013), and to drive attentional resources in the direction

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71 of the sound source (Leo et al., 2011). In line with this, tactile response is facilitated when
72 threatening pictures (for instance a snake or a knife) are presented in PPS rather than in far
73 space (Poliakoff et al., 2007; Van Damme et al., 2009). Additionally, a stimulus, perceived as
74 threatening, facilitates tactile processing at distances farther from the body as compared to a
75 non-threatening stimulus (Taffou & Viaud-Delmon, 2014). Thus, PPS is not only modulated
76 by the stimulus' proximity to the body but also by its speed and affective valence. These
77 findings suggest the existence of a dynamic security space around the body with the aim of
78 keeping us safe from any potential physical danger.

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

87 We recently investigated in a virtual reality environment whether such dynamic,
88 triggered by the presentation of different facial expressions, is modulated by the location of
89 the emotional faces in the near space, compared to far space (Ellena et al., 2020). Participants
90 performed a visuo-tactile integration task (akin to Pellencin et al., 2018; Serino et al., 2015)
91 by responding as fast as possible to tactile stimuli presented on the cheeks, while watching
92 task-irrelevant neutral, joyful or fearful avatar faces, looming in far or near space. This design
93 allowed us to assess changes in PPS representation operationalised as the gain in reaction
94 times in response to tactile stimuli depending on whether the stimulus was coupled with near

95 vs. far visual stimuli, which could express either fearful or neutral emotions. Importantly, in
96 order to assess the **impact of** fearful faces **on visuo-spatial processing** a static, task-
97 irrelevant, visual stimulus, a checkerboarded ball, thereafter, referred to as the **spatial** probe,
98 appeared to the left or to the right of the face at the time of the tactile stimulation. Crucially,
99 the probe could either be close to the face, and thus more *central* in the participant's vision,
100 or further away from the face, and thus more *peripheral* in the participant's vision. With this
101 paradigm, the spatial **distribution** of sensory **resources is** indirectly assessed through the
102 amount of facilitation (faster reaction times) that visual stimuli have on processing tactile
103 stimuli. We hypothesised that the probe would facilitate the response to tactile stimuli when it
104 appears in a spatial location **where it is actually expected**. In particular, a fearful face **may**
105 signal a **potential** threat **whose location is unknown and possibly expected elsewhere,**
106 **away from the face. Consistent with this view, our previous** results (Ellena et al., 2020)
107 showed that with neutral and joyful faces, simple reactions to tactile stimuli were facilitated
108 in near rather than in far space (classic PPS proximity effect) and **with the** central rather than
109 **the** peripheral **spatial** probe. However, when the face was fearful, tactile processing was
110 modulated not only by the distance of the face from the participant but also by the position of
111 the probe. Specifically, in near space only, tactile processing was additionally facilitated by
112 the peripheral compared to the central probe. Thus, as fearful faces come closer to the body,
113 they **facilitate spatial processing in the peripheral space. This in turn might** enhance the
114 defensive function of PPS specifically when it is most needed, i.e., when the source of threat
115 is nearby, but its location has not yet been identified.

116 The present study capitalizes on these results **by** investigating the electrophysiological
117 mechanism underlying the effect of fearful faces on PPS. Specifically, here we assess the
118 hypothesis of a differential modulation of electrophysiological response elicited by
119 **peripheral as opposed to central probes as a function of the emotional context** (fearful

120 vs. neutral faces) **and** position in PPS **in which they appear**. Of relevance in this respect is
121 the **visual N1** ERP component, a negative deflection in electrical potential observed at
122 temporo-occipital electrodes between **150** and 200 ms following presentation **of a visual**
123 **stimulus (Luck, 2014), and considered to be a marker of visuospatial processing**
124 **(Wascher et al., 2009). Interestingly, the N1 is modulated by exogenous as well as**
125 **endogenous factors, and is sensitive to both the physical properties of the stimulus and**
126 **to the nature of the interaction between the participant and the stimulus (Fabiani et al.,**
127 **2009). For example, smaller amplitude of this component has been associated with**
128 **predictable rather than unpredictable visual stimuli (Heilbron & Chait, 2018; Johnston**
129 **et al., 2017; Robinson et al., 2020).**

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

143 Methods

144 **Participants**

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2 145 Twenty-two healthy right-handed participants with no history of neurological or psychiatric
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4 146 disorder were recruited (12 females; age: $M \pm SD = 27.68 \pm 4.3$ years). The experiment was
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7 147 conducted in accordance with the principles of the Declaration of Helsinki and approved by
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9 148 the Bioethics Committee of the University of Bologna. Each participant gave written
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11 149 informed consent prior to participating and after being informed about the procedure of the
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13 150 experiment. Using G*Power 3.1 software (G*Power; Faul et al., 2007), with an effect size of
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16 151 $f = 0.25$ (medium effect size), an alpha of 0.05 and a power ($1 - \beta$) of 0.9 for a repeated
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18 152 measure, within- factor analysis of variance (ANOVA) with no covariates, it was determined
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21 153 that an $N > 20$ would be needed to detect this effect. Thus, we recruited 22 participants,
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23 154 which is also consistent with sample sizes of studies measuring evoked potentials in
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26 155 peripersonal space paradigms (e.g., Sambo & Forster, 2009; Valdés-Conroy et al., 2014).

30 **Stimuli and materials**

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33 157 The experiment was implemented in ExpyVR (software freely available online at
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35 158 <http://lnc0.epfl.ch/expyvr>). The tactile stimuli were delivered on the cheeks bilaterally
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38 159 through a pair of vibrators (Precision MicroDrivers, shaftless vibration motors, model 312-
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40 160 101, 3V, 60 mA, 150 Hz, 5g). The motor had a surface area of 113 mm² and reached
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42 161 maximal rotation speed in 50 ms. This device was activated for 100 ms during tactile
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45 162 stimulation. In order to study the impact of different emotional conditions on PPS, faces with
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48 163 neutral vs. fearful expressions were presented either in the far or near the participant's space
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51 164 and looming at a constant speed towards the participant (see Figure 1). At the beginning of
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53 165 each trial (T0) an avatar face with a neutral or fearful expression appeared centrally on the
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55 166 visual field, either in the space near to (≈ 115 cm) or far from (≈ 220 cm) the participant, by
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58 167 relaying stereoscopically to the head-mounted display (HMD, Oculus Rift SDK, Oculus VR,

168 100° field of view, 60 Hz) worn by the participant. The face then moved toward the
169 participant on the sagittal plane for a total of 3000 ms until its final position (Near: ≈ 10 cm;
170 Far: ≈ 115 cm) where it remained still for 1000 ms (T2). Importantly, 2000 ms after the
171 beginning of the trial (T1), the tactile stimulation was delivered bilaterally, and,
172 simultaneously, a static checkerboarded ball (probe), appeared for 250 ms, either $\approx 1^\circ$ (probe
173 central) or $\approx 10^\circ$ (probe peripheral) to the left or right of the face (left and right sides
174 counterbalanced among trials; see Figure 1). The degree of eccentricity of the peripheral
175 probe was 10° . This eccentricity produces a visual stimulus that, despite appearing in the
176 periphery of the visual field, can influence processing of a centrally presented stimulus
177 (Honda, 2005; Chen, 2008; Born & Kerzel, 2008; Findlay & Walker, 1999). Thus, at T1,
178 touch coincides with perception of the probe and of the face, at different distances from the
179 participant (at ≈ 45 cm, in the near, and ≈ 150 cm in the far). The ITI was set at 2100 ms (\pm
180 100 of jitter). Distances of near and far spaces were calibrated as previously done in Serino
181 and colleagues (2015) corresponding to the same near and far distances as defined in Ellena
182 and colleagues (2020). Also, given that the current study aimed to investigate the neural bases
183 underlying the behavioural results of Ellena et al. (2020), we kept the structure of the task
184 consistent across the two studies in order to maximize the reproducibility of the behavioural
185 results. Given that participants respond with the right hand, we wanted to exclude an effect of
186 spatial compatibility on response time. For example, we wanted to avoid spatial compatibility
187 effects between the tactile stimulus and the response. Thus, a unilateral tactile stimulation
188 might lead to a modulation in response times when delivered to the right (vs left) cheek for
189 reasons of spatial compatibility rather than multisensory integration. Thus, here and in the
190 original study, we decided to deliver a bilateral tactile stimulus to reduce this possibility.

191 ----- **Please insert Figure 1 about here** -----

192 **Visual stimuli validation**

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3 193 Note that all face stimuli (fearful and neutral) were created and validated together in a pre-
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6 194 experimental phase of the study. Face stimuli consisted of 3D avatar faces created with
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8 195 'Poser 10' (<http://my.smithmicro.com/poser-3d-animation-software.html>) that displayed a
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10 196 fearful or neutral expression.

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14 197 In order to select the faces to be included in each experiment, 60 naive participants
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16 198 (30 females; mean age 29±10 SD) were instructed to rate 10 faces. Of those, 5 represented
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19 199 versions of fearful faces and the remaining 5, versions of neutral faces. Participants had to
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21 200 indicate which emotion was expressed by each presented face and subsequently rate on a 10-
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24 201 points Likert scale how strongly the emotion was expressed (0 = lowest intensity; 9, highest
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26 202 intensity). Also, they had to rate the arousal level generated by each stimulus, on a 10-point
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29 203 Likert scale (0= not at all arousing; 9= extremely arousing).

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32 204 We selected a total of 2 fearful and 2 neutral facial expressions for which the highest
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34 205 percentage of participants correctly identified the facial emotion (mean hit rate for: fearful
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37 206 faces, 80%; neutral faces, 81%), which also showed the highest perceived intensity and the
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39 207 highest perceived arousing effect (Figure 2 shows an example of chosen stimuli).

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42 208 ----- **Please insert Figure 2 about here** -----
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46 209 To check whether the mean ratings for intensity and arousal were significantly
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49 210 different between fearful and neutral faces, a repeated measures ANOVA was conducted with
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51 211 mean intensity and mean arousal scores. The analysis on intensity level showed that ratings
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53 212 were different across emotions [$F(1,59) = 229.6; p < 0.01; \eta_p^2 = 0.79$]. Fearful expressions were
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56 213 judged as more intense than neutral ones (fearful faces: $M = 7.12; SEM = 0.18$; neutral faces:
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58 214 $M = 2.39; SEM = 0.26$). The analysis on arousal level showed that ratings were also different
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215 across emotions [$F(1,59) = 134.23$; $p < 0.01$; $\eta_p^2 = 0.69$]. Fearful expressions were judged as
216 more arousing than neutral ones (fearful faces: $M = 5.08$; $SEM = 0.30$; neutral faces: $M = 2.39$;
217 $SEM = 0.20$).

218 **Task and procedure**

219 There was a total of 320 experimental trials, evenly distributed among 8 experimental
220 conditions (i.e., 40 trials per condition): Face emotion: Neutral / Fearful; Space: Far / Near;
221 Probe Position: central / peripheral. An additional 80 trials with no vibration and 20 trials
222 with no probe presentation were introduced in order to decrease task predictability. Both
223 central and peripheral probes could be presented either on the left or right side of the face.
224 The entire experiment was split into 5 separate blocks of 84 trials each and conditions were
225 randomly but evenly distributed across blocks. The experimental session lasted
226 approximately one hour, and participants could rest between blocks to prevent fatigue. After
227 signing the consent form, participants seated on a comfortable chair, in a sound attenuated
228 room. Vibrators were then attached bilaterally on the cheeks with a medical tape and
229 electrophysiological activity was verified; EEG cap was fitted, and the virtual reality headset
230 mounted on the head of the participant. Importantly, the bands of the VR montage were not in
231 contact with the EEG electrodes selected for the analysis (P7, P07, P8, P08; see Figure 3).
232 Before the task began, the lenses' focus was manually adjusted by each participant until clear
233 vision was reported. During the task, participants made simple speeded responses to the
234 tactile stimulation by pressing a button placed on the table in front of the participant with
235 their right hand.

236 ----- **Please insert Figure 3 about here** -----

237 **Recording and Data Analysis**

238 The EEG was continuously recorded with Ag/AgCl electrodes (Fast n Easy Electrodes,
239 EasyCap, Herrsching, Germany) from 59 scalp sites (Fp1, AF3, AF7, F1, F3, F7, FC1, FC3,
240 FC5, FT7, C1, C3, C5, T7, CP1, CP3, CP5, TP7, P1, P3, P5, P7, PO3, PO7, O1, Fp2, AF4,
241 AF8, F2, F4, F8, FC2, FC4, FC6, FT8, C2, C4, C6, T8, CP2, CP4, CP6, TP8, P2, P4, P6, P8,
242 PO4, PO8, O2, FPz, AFz, Fz, FCz, Cz, CPz, Pz, POz, Oz) and the left mastoid. The right
243 mastoid was used as a reference, while the ground electrode was positioned on the right
244 cheek. Vertical and horizontal EOG components were recorded from above and below the
245 left eye, and from the outer canthus of both eyes. Signal impedance was maintained below 5
246 K Ω , which was checked at the end of every block. The electro-oculogram (EOG) was
247 recorded from above and below the left eye and from the outer canthi of both eyes. The EEG
248 and EOG were recorded with a band-pass filter of 0.01–100 Hz and a slope of 12 dB/oct,
249 amplified by a BrainAmp DC amplifier (Brain Products, Gilching, Germany) and digitized at
250 a sampling rate of 1000 Hz.

251 The EEG data were pre-processed using EEGLAB toolbox, version 14.1.0 (Delorme
252 and Makeig, 2004) and custom routines written in MATLAB R2016b (The MathWorks,
253 Natick, MA). Data from all electrodes were re-referenced to the average of both mastoids and
254 filtered with a high-band pass filter of 0.5 and low-band pass filter of 30 Hz. Continuous
255 signals were segmented into epochs of 5000 ms, starting at 1000 ms preceding the face
256 stimulus onset (T0) and for another 4000 ms until the offset of the face (T2). EEG activity
257 was baseline-corrected over a period of 200 ms preceding T0. In addition, epochs with large
258 artefacts contamination were identified and removed using two methods from the EEGLAB
259 toolbox (Delorme & Makeig, 2004): (1) an epoch was excluded whenever the voltage on an
260 EEG channel exceeded 400 μ V (this ensured that epochs with large EEG peaks were safely
261 removed); (2) an epoch was excluded whenever the joint probability of a trial exceeded five
262 standard deviations (this method ensured that epochs with improbable data were safely

263 removed; mean excluded epochs: 5.98 %). In each condition, the epochs left after pre-
264 processing were **on average: 36.41 (SEM=0.99; 91.02%)** in the Fear Far Central, **36.59**
265 **(SEM=0.92; 91.48%)** in the Fear Far Peripheral, **36.68 (SEM=0.71; 91.7%)** in the Fear Near
266 Central, **36.32 (SEM=0.7; 90.79%)** in the Fear Near Peripheral, **36.54 (SEM=0.9; 91.36%)**
267 in the Neutral Far Central, **36.86 (SEM=0.99; 92.16%)** in the Neutral Far Peripheral, **37.18**
268 **(SEM=0.59; 92.95%)** in the Neutral Near Central and **37.86 (SEM=0.4; 94.66%)** in the
269 Neutral Near Peripheral. Importantly, the number of remaining epochs did not differ between
270 conditions in which the probe was central versus peripheral ($F(1,21)=0.48$; $p=0.49$).
271 Moreover, residual artefacts (such as eye blinks or eye movements) were identified using an
272 Independent Component Analysis (ICA) decomposition method (Delorme & Makeig, 2004)
273 and removed according to the ADJUST plugin application (Mognon, Jovicich, Bruzzone &
274 Buiatti, 2011).

275 Remaining epochs were divided into eight separate datasets, according to the stimulus
276 condition. The **N1** was evaluated as the activity of the left (P7, PO7) and right (P8, PO8)
277 temporo-occipital recording sites (**as in Wynn et al., 2015; Schindler et al., 2020; Robinson**
278 **et al., 2018; Oribe et al., 2020**). For each participant, for which **the first** maximal negative
279 deflection after T1 (the appearance of the probe and the delivery of the tactile stimulation)
280 was observed, was used to anchor a relative sub-time-window of ± 15 ms (**Jackson et al.,**
281 **2008; Prieto et al., 2011; Moore et al., 2014**). **N1** component was quantified as the mean
282 amplitude within this sub-time-window. This method controlled for latency variance of **N1**
283 onset while preserving the mean amplitude measure's lower susceptibility to spurious peaks
284 (Luck, 2004; Ito, Gracco, & Ostry, 2014; Ott et al., 2011). **N1** mean amplitudes were
285 analysed with a 2x2x2 RM ANOVA (Emotion: Neutral / Fearful; Space: Far / Near; Probe
286 Position: Central/ peripheral as within-participants factors). Post-hoc comparisons were
287 carried out using the Newman-Keuls test.

288

Results

289 Behavioural Results

290 We tested whether the presentation of a fearful face relative to a neutral face had a
291 differential impact on the response to the participants own face's tactile stimulation. The
292 tactile stimulation was always paired with the presentation of a visuo-spatial probe
293 (represented by a static checkerboarded ball) next to or distal from the looming face.
294 Moreover, in order to measure the potential impact of peripersonal space (PPS) on
295 performance, this effect was measured as a function of the near (peripersonal) and far
296 (extrapersonal) space. As the rate of omissions was low ($M=1.25\%$ $SD=2.12$), performance
297 was analysed in terms of reaction times (RTs) only, as in previous studies (e.g., Canzoneri,
298 Magosso, & Serino, 2012). Trials with RTs exceeding more than 2.5 standard deviations
299 from the mean RT of each block were considered outliers and excluded from the analyses
300 ($M=4.03\%$ $SD=2.38$). For each participant, mean RTs were calculated for each of the eight
301 different conditions, and used for analysis. We checked the skewness of the distribution of
302 our RTs data as recommended by Field (2013) and found it to lie between 0 and 1 in all
303 conditions. Additionally, when converting these values to z-scores we found they were all
304 below 1.96, indicating that skewness was not significantly different from that of a normal
305 distribution ($p>0.05$), except for the neutral faces in near space with the central probe, where
306 skewness $z\text{-score}=2.05$ corresponding to $p=0.04$. Thus, given that the distributions of RTs
307 were not significantly skewed except for one marginally significant condition, and that we
308 had a within-subjects design with all conditions having the same sample size, we deemed
309 parametric tests appropriate to analyse our data (Field, 2013).

310 A 2x2x2 RM ANOVA (Emotion: Neutral vs. Fearful; Space: Far vs. Near; Probe
311 Position: Central vs. Peripheral) was conducted to test whether looming fearful, vs. neutral
312 faces, induced a change in PPS representation (i.e., difference in RTs to tactile stimulation)

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2 313 through a different distribution of spatial **resources**, probed by the spatial probe appearing
3 314 centrally (next to the face) or peripherally (far apart from the face).

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5 315 Results (see Figure 4) showed a significant main effect of Emotion [$F(1,21)=16.32$;
6 $p<0.001$; $\eta_p^2=0.44$] with participants responding faster to Fearful relative to Neutral faces
7 316 (Fearful faces: $M=373.30$ ms; $SEM=17.29$; Neutral faces: $M=381.04$ ms; $SEM=16.79$).

8 317
9 318 There was also a significant main effect of Space [$F(1,21)=87.44$; $p<0.001$; $\eta_p^2=0.81$] with
10 319 participants responding faster to faces in the Near relative to the Far space (Near space:
11 320 $M=359.90$ ms; $SEM=17.15$; Far space: $M=394.44$ ms; $SEM=17.08$). There was no significant

12 321 main effect of Probe Position [$F(1,21)=0.97$; $p=0.34$; $\eta_p^2=0.04$], nor Emotion by Space

13 322 [$F(1,21)=0.01$; $p=0.91$; $\eta_p^2<0.01$] or Emotion by Probe Position [$F(1,21)=0.01$; $p=0.93$;

14 323 $\eta_p^2<0.01$] interaction. However, there was a significant Space by Probe Position

15 324 [$F(1,21)=4.26$; $p=0.05$; $\eta_p^2=0.17$] interaction showing that the probe position had a different

16 325 impact on RTs. Crucially, the Space by Probe Position was best explained by the significant

17 326 three-ways Emotion by Space by Probe Position interaction [$F(1,21)=6.72$; $p=0.02$; $\eta_p^2=0.24$]

18 327 suggesting that the impact on the probe in the near and far space differently affected RTs for

19 328 fearful and neutral face presentations. Specifically, Newman-Keuls post-hoc comparisons

20 329 revealed that for neutral faces, RTs to the tactile stimuli were not affected by the spatial probe

21 330 position, either in the far (Neutral Far Central: $M=397.09$ ms, $SEM=16.07$; Neutral Far

22 331 Peripheral: $M=399.23$ ms, $SEM=16.07$; $p=0.33$) or in the near space (Neutral Near Central:

23 332 $M=363.38$ ms, $SEM=17.50$; Neutral Near Peripheral: $M=364.37$ ms, $SEM=17.34$; $p=0.66$). In

24 333 contrast, when fearful faces were shown, the spatial probe position affected RTs to tactile

25 334 stimuli differently for the far and the near space: in the far space, RTs were faster for central

26 335 relative to peripheral spatial probes (Fear Far Central: $M=386.83$ ms, $SEM=17.86$; Fear Far

27 336 Peripheral: $M=394.52$ ms, $SEM=17.89$; $p=0.002$); in the near space, instead, RTs were faster

28 337 for peripheral relative to central spatial probes (Fear Near Central: $M=358.45$ ms,

338 SEM=18.10; Fear Near Peripheral: M=353.38 ms, SEM=16.05; p=0.03). Finally, when
339 examining the difference between fearful and neutral faces, we found that, in near space,
340 tactile responses were faster to fearful than neutral faces, both with the central and peripheral
341 probes (central probe: p=0.038; peripheral probe: p<0.001). In contrast, in far space, tactile
342 responses were faster to fearful than neutral faces, for central probes only (p<0.001).

343 ----- Please insert Figure 4 about here -----

344 We also repeated the analysis including block (1 to 5) as a factor. This produced a
345 significant main effect of block (p<0.001), with participants becoming faster as the task
346 progresses. Nevertheless, and most importantly, we found no evidence of an interaction
347 between blocks and emotion, suggesting that any effect on RTs due to task progression is
348 independent of the emotion manipulation; all p≥0.344). Additionally, including probe side
349 (sx, dx) as a factor revealed a main effect of side (p=0.014), with participants being faster to
350 left than right stimuli. Nevertheless, there was no interaction between side and emotion (all
351 p≥0.09), suggesting that any effect on RTs related the side of probe appearance is
352 independent of the emotion manipulation.

353 ERP Results

354 Results of the **N1** component (Figure 5) showed a significant main effect of the mean
355 amplitude for the factor Probe Position [F(1,21)=37.40; p<0.01; $\eta_p^2=0.64$] showing more
356 negative amplitudes for central relative to peripheral probes (Central: M=-4.14 μ V;
357 SEM=0.64; Peripheral: M=-3.23 μ V; SEM=0.64). Moreover, there was a significant
358 interaction of Space by Probe Position [F(1,21)=9.71; p<0.01; $\eta_p^2=0.32$]. Crucially, the two-
359 way interaction was best explained by a significant Emotion by Space by Probe Position
360 interaction [F (1,21)=4.95; p=0.04; $\eta_p^2=0.19$], suggesting that Emotion differently impacted
361 **N1** amplitude modulation as a function of spatial distance and probe position.

362 Specifically, Newman-Keuls post-hoc comparisons revealed that, when the face was
363 in the far space, probe position did not modulate mean amplitude significantly, both for
364 fearful (Fear Far Central: $M=-3.9 \mu\text{V}$, $\text{SEM}=0.69$; Fear Far Peripheral: $M=-3.69 \mu\text{V}$,
365 $\text{SEM}=0.71$; $p=0.63$) and neutral faces (Neutral Far Central: $M=-3.70 \mu\text{V}$, $\text{SEM}=0.66$; Neutral
366 Far Peripheral: $M=-3.42 \mu\text{V}$, $\text{SEM}=0.64$; $p=0.44$). Conversely, when the face was in the near
367 space, probe position significantly modulated mean amplitude. Amplitude was **less** negative
368 for **peripheral** than **central** probe, both for fearful (Fear Near Central: $M=-4.63 \mu\text{V}$,
369 $\text{SEM}=0.71$; Fear Near Peripheral: $M=-2.58 \mu\text{V}$, $\text{SEM}=0.69$; $p<0.01$) and neutral faces
370 (Neutral Near Central: $M=-4.33 \mu\text{V}$, $\text{SEM}=0.64$; Neutral Near Peripheral: $M=-3.21 \mu\text{V}$,
371 $\text{SEM}=0.64$; $p<0.01$). Crucially, when the peripheral probe was presented in the near space,
372 ERP amplitude was less negative for fearful ($M=-2.58 \mu\text{V}$) than neutral faces ($M=-3.21 \mu\text{V}$)
373 ($p=0.01$). No other main effects nor interactions were significant (all $ps>0.08$).

374 ----- Please insert Figure 5 about here -----

375 **Correlation between behavioural and ERP responses**

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

386 faster participants responded to **the tactile stimulus with** the peripheral relative to the central
387 probe, the smaller was their **N1**.

388 Note, that although the relationship between ERP amplitude and RTs is found both for
389 near and far spaces, visual inspection of Figure 6 shows a different distribution of individual
390 participants' data. Specifically, in near space, the majority of participants responded faster
391 **with** the peripheral (vs central) probe (RT difference > 0), and all but one participant had a
392 smaller **N1** when the probe was presented peripherally as opposed to centrally. This is
393 reflected in the group mean (red dot) value, which falls in the upper right quadrant of the plot,
394 indicating that both mean RT and ERP differences are positive. In contrast, in far space, the
395 majority of participants responded more slowly **with** the peripheral than the central probe
396 (RT difference < 0). Also, about half of the group had a smaller **N1** when presented with the
397 peripheral (vs central) probe (ERP difference > 0), while the remaining half had the opposite
398 pattern explaining the absence of significant differences in the post-hoc tests on ERPs for this
399 condition. Again, this distribution of scores is reflected in the group mean (red dot) values,
400 which falls in the upper left quadrant of the plot, indicating mean RT difference > 0 and mean
401 ERP difference ~ 0 .

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

403 Discussion

404
405 The aim of the present study was to investigate the neural **correlates** underlying **our**
406 previously reported **modulation of spatial processing by** fearful faces **intruding into** PPS
407 (Ellena et al., 2020). Thus, **electroencephalography was continuously recorded while**
408 participants made simple responses to tactile stimuli delivered on the cheeks, **during**
409 **presentation of** task-irrelevant neutral or fearful avatar faces, looming towards them in far or

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410 near space. To probe spatial **processing**, a **checkerboarded** ball (**spatial** probe) appeared to
411 the left or right of the avatar face, simultaneously with the tactile stimulation. Crucially, the
412 probe could either be close to the avatar face, and thus more *central* in the participant's
413 vision, or further away from the avatar face, and thus more *peripheral* in the participant's
414 vision.

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

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434 response to tactile stimuli, when a task-irrelevant visual probe is simultaneously presented in
435 a peripheral location.

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

455 The results of the present study suggest that PPS representation arises from the
456 interaction between different cognitive systems, which contribute to determine its
457 functionality. In particular, they support the hypothesis of a functional connection between
458 the neural structures dedicated to processing affective stimuli and those representing PPS,

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459 corroborating the defensive function of PPS (Graziano & Cooke, 2006). In this regard, the
460 amygdala plays an important role in evaluating stimulus salience and shows greater activation
461 when a stimulus is presented in ambiguous and uncertain environmental circumstances, such
462 as in the presence of ambiguous threat (Adams & Kleck, 2003). Additionally, the amygdala is
463 a core structure for perception and recognition of emotional facial expressions (Adolphs et
464 al., 2005) and is believed to play a major role in orienting sensory resources towards threat-
465 related stimuli (Cisler & Koster, 2010; Peck et al., 2013; Vuilleumier, 2005), integrating not
466 only emotional, but also spatial information. In line with this, fearful faces, unlike other
467 negative expressions such as anger, signal an environmental threat whose source and location
468 are unknown (Fanselow & Pennington, 2018) and, as such, can be conceived as a salient but
469 ambiguous or incomplete stimulus (Hortensius et al., 2016). After fearful face presentation,
470 enhanced amygdala-mediated vigilance and arousal may facilitate scanning of the
471 environment and dealing with the uncertainty of the upcoming danger. An indirect
472 demonstration of such a connection comes from the work of Åsh and colleagues (2014) and
473 Faul et al. (2020): conditioned threats were more resistant to extinction processes when they
474 invaded PPS than when they were distant. De Borst and colleagues (2018) provided further
475 support to this result, finding that the activity in emotion-related structures (amygdala, ACC,
476 insula) was more synchronized across participants when the threat was nearby. Moreover,
477 when the threat was perceived as directed towards oneself, activity in regions of PPS network
478 was enhanced and direct neural connections were found from the left intraparietal sulcus
479 (considered a key area of the PPS network; Grivaz, Blanke & Serino, 2017) to the right
480 anterior cingulate cortex, and from that structure to the right amygdala and the left anterior
481 cingulate cortex. All these findings suggest that the amygdala and emotion related structures
482 contribute to PPS representation, in particular in the context of stimuli perceived as salient by
483 the individual (Belkaid et al., 2015).

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

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

506 To conclude, both behavioural and electrophysiological results support the
507 **modulation of spatial processing** by fearful faces in PPS. Behavioural data show a net

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508 advantage in RTs **with** the near fearful face paired with peripheral probes, leading to the
509 fastest RTs among the other conditions. This **effect** is then indirectly reflected into the
510 electrophysiological response evoked by the probe. Since **an event is expected** in the space
511 **peripheral to the fearful face** where the threat might be located, the **N1** amplitude is less
512 negative **at the appearance of the peripheral as compared to the central probe**. Finally,
513 both the ERP and behavioural effects follow the spatial-proximity rule since all the effects of
514 interaction of emotional face by probe position are exclusively visible for the near, but not the
515 far space.

516

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4
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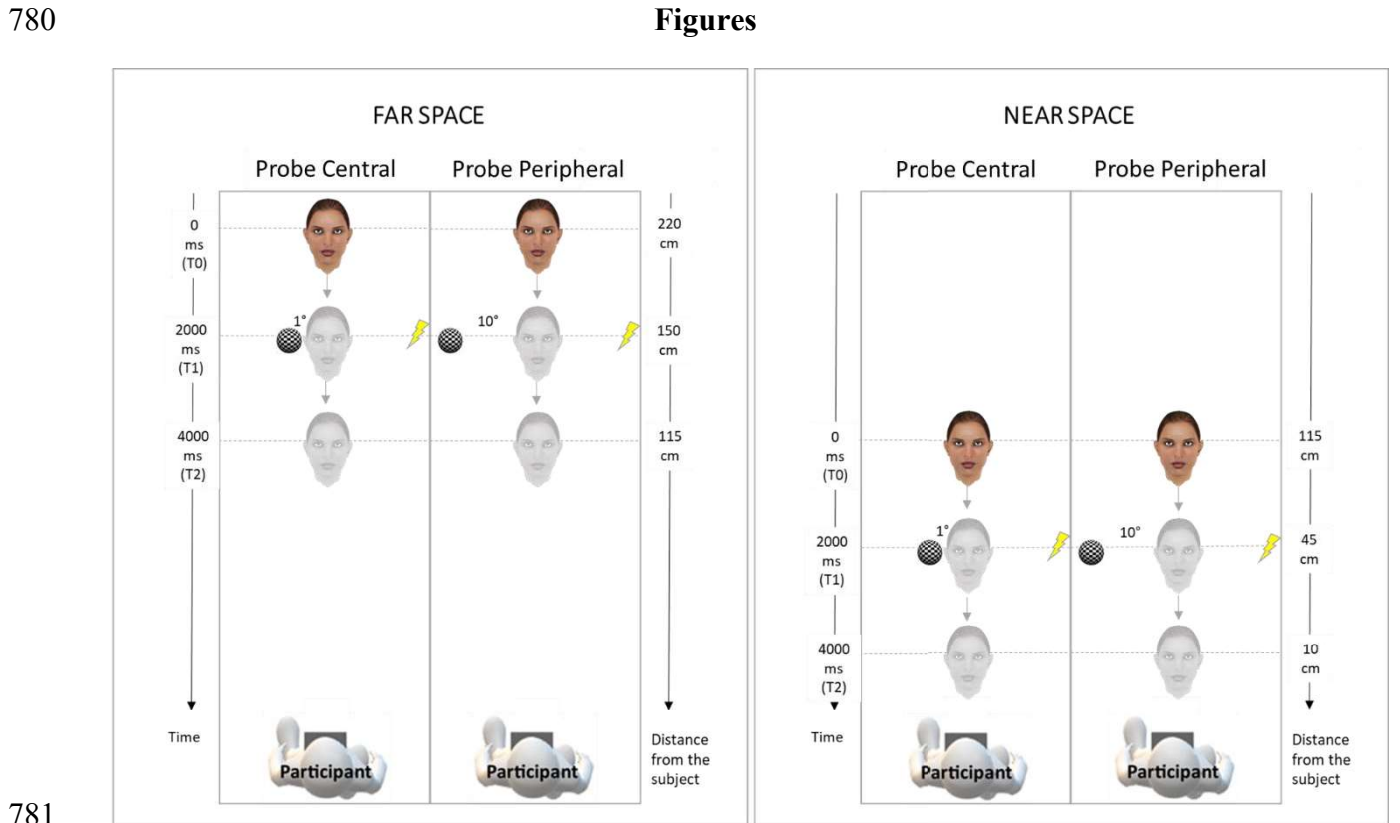
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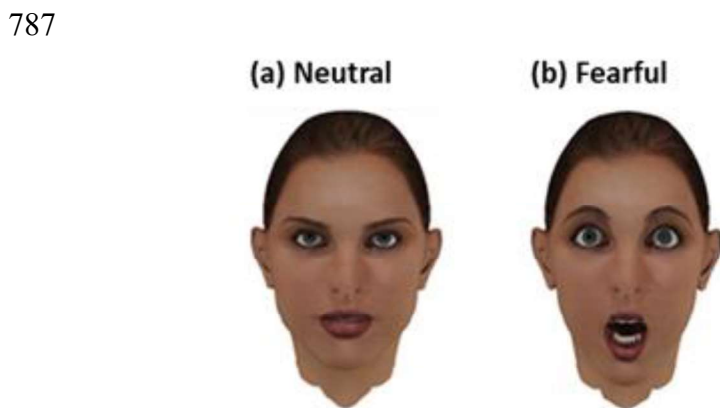
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782 **Figure 1.** Experimental paradigm. Looming faces appeared at T0 in far (left panel) or near
 783 space (right panel) relative to the participant's position and moved towards the participant at
 784 a constant speed until T2. At T1, bilateral tactile stimuli were delivered to the participant's
 785 cheeks simultaneously to the appearance of a checkerboarded ball (probe), which was flashed
 786 centrally or peripherally from the face frontal plane for 250 ms.



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

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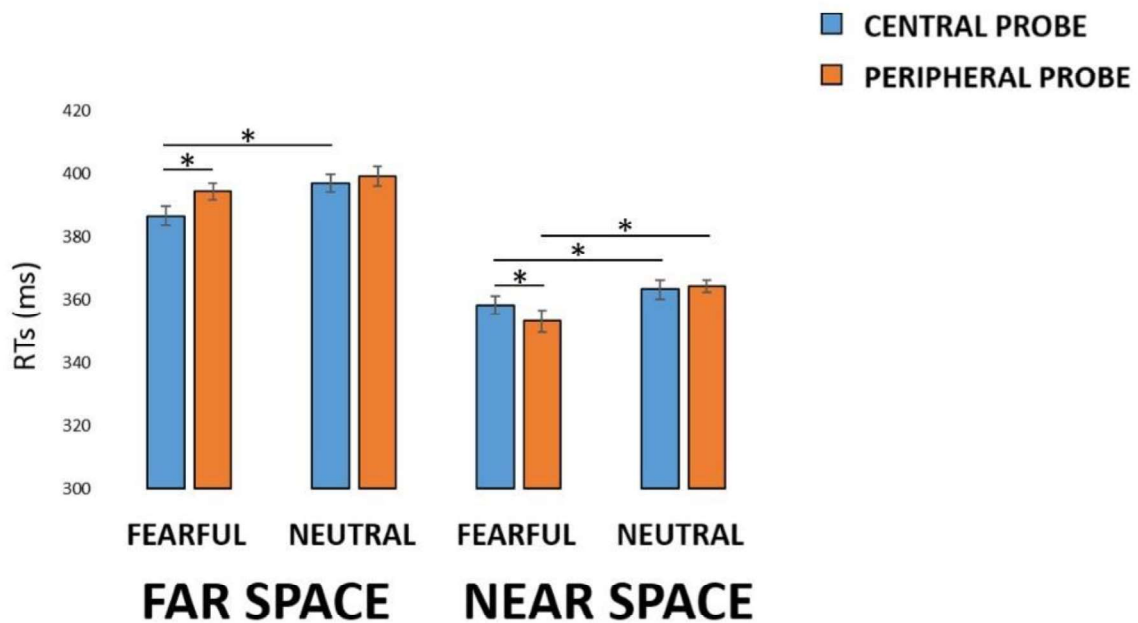
Figure 3. Illustration of the EEG/VR montage. As it can be seen in the illustration, the VR

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montage did not interfere with the EEG recording on the target electrodes shown in red (P7;

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PO7; P8; PO8).



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Figure 4. Behavioral results. Bar plots showing the emotion x space x probe position

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interaction. Asterisks show that in far space participants responded faster with fearful than

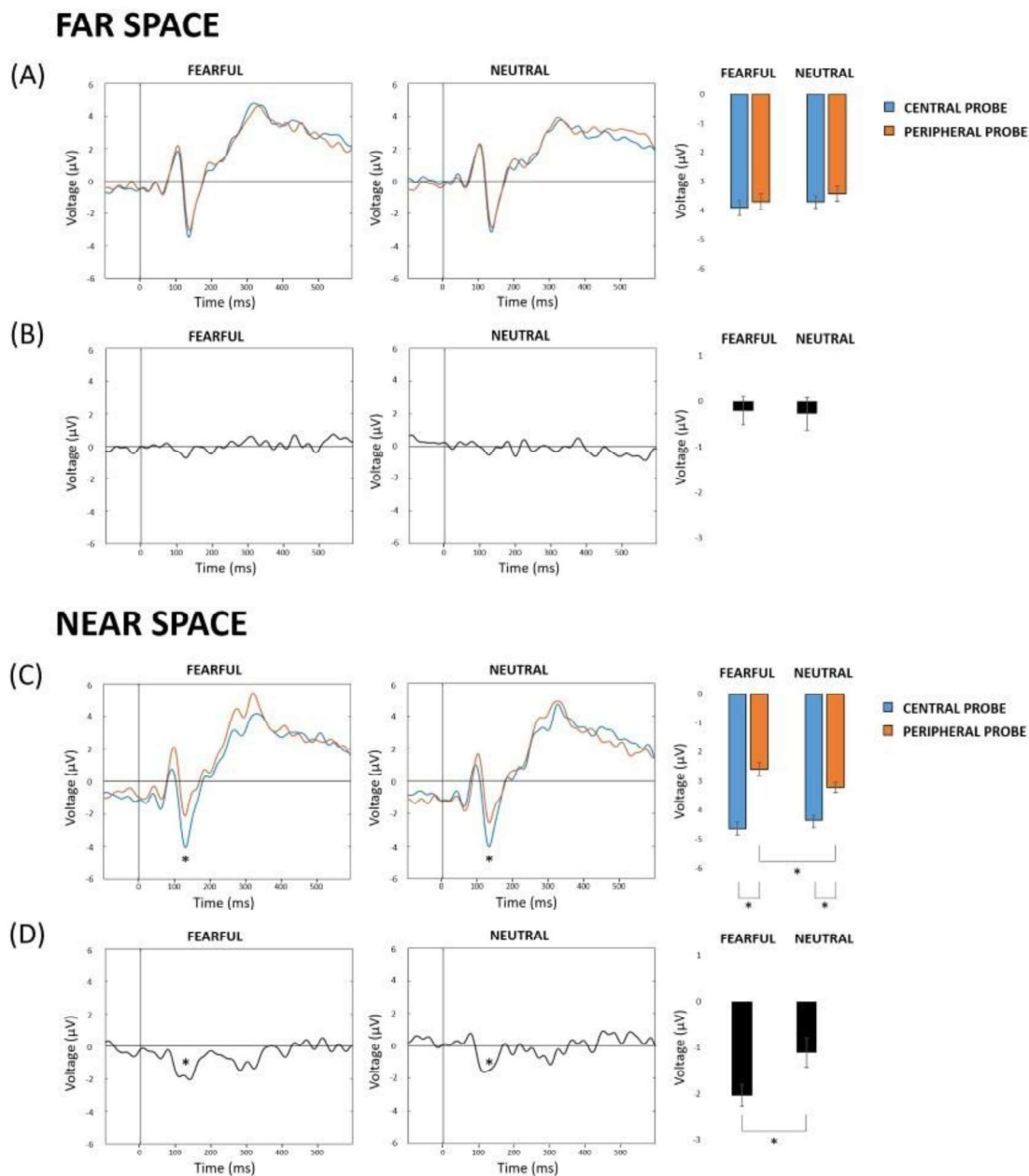
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neutral stimuli with the central probe and responded faster with the central than peripheral

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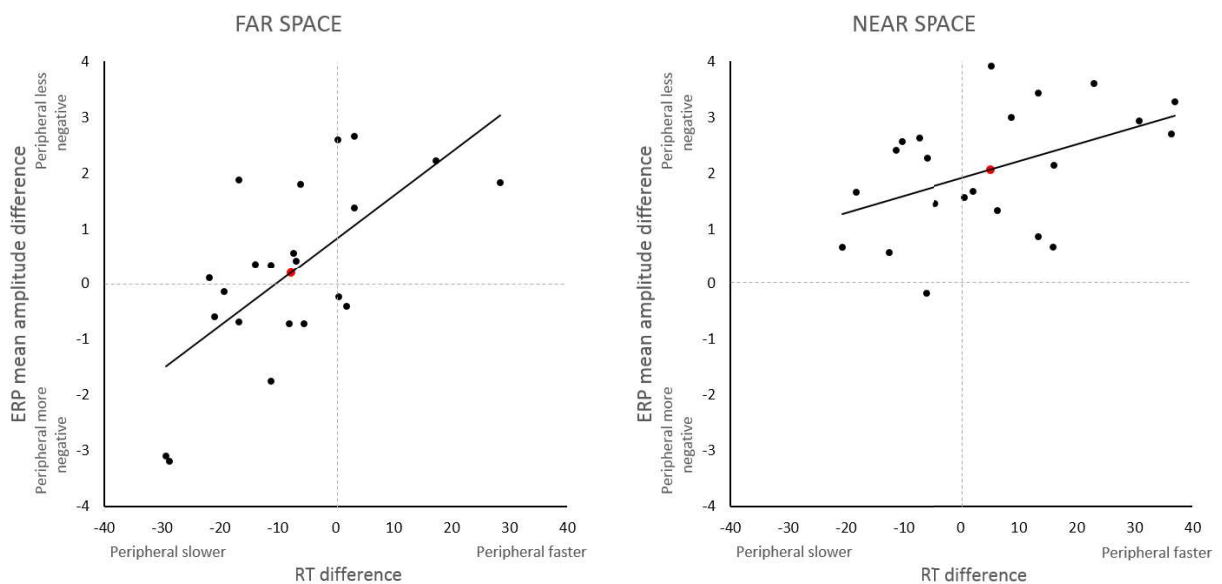
probe with fearful faces. In contrast, in near space, participants responded faster with fearful

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



803 **Figure 5.** ERP results. Panel A and panel B represent ERPs results in the far space condition.
 804
 805 In panel A, ERPs are plotted as a function of the probe position (central probe vs peripheral
 806 probe) in response to the emotion condition (fearful face vs neutral face). Bar plot on the
 807 rightmost part of panel A depicts averaged values of the **N1** amplitude in the far space

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



821 **Figure 6.** Correlation between the difference in RTs between the central and peripheral
 822 probe, and the difference in N1 mean amplitude between the peripheral and central probe for
 823 fearful faces presented in far space ($r=0.67$, $n=22$, $p<0.001$) and in near space ($r=0.46$, $n=22$,
 824 $p=0.032$). 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 Lådavas:** Conceptualization, Methodology, Resources, Writing - Review & Editing, Supervision