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Research Report

Close facial emotions enhance physiological responses and facilitate perceptual discrimination

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ARTICLE INFO

Article history:
Received 11 February 2020
Reviewed 20 July 2020
Revised 22 September 2020
Accepted 26 January 2021
Action editor Holger Wiese
Published online 9 February 2021

Keywords:
Peripersonal space
Emotion
Sex
Virtual reality
Discrimination
Pupil diameter
Heart rate

ABSTRACT

Accumulating evidence indicates that the peripersonal space (PPS) constitutes a privileged area for efficient processing of proximal stimuli, allowing to flexibly adapt our behavior both to the physical and social environment. Whether and how behavioral and physiological signatures of PPS relate to each other in emotional contexts remains, though, elusive. Here, we addressed this question by having participants to discriminate male from female faces depicting different emotions (happiness, anger or neutral) and presented at different distances (50 cm–300 cm) while we measured the reaction time and accuracy of their responses, as well as pupillary diameter, heart rate and heart rate variability. Results showed facilitation of participants' performances (i.e., faster response time) when faces were presented close compared to far from the participants, even when controlling for retinal size across distances. These behavioral effects were accompanied by significant modulation of participants' physiological indexes when faces were presented in PPS. Interestingly, both PPS representation and physiological signals were affected by features of the seen faces such as the emotional valence, its sex and the participants' sex, revealing the profound impact of social context onto the autonomic state and behavior within PPS. Together, these findings suggest that both external and internal signals contribute in shaping PPS representation.

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https://doi.org/10.1016/j.cortex.2021.01.014

1. Introduction

Every day, we dynamically interact with the world around us. The space closely surrounding our body, termed peripersonal space (PPS, Rizzolatti et al., 1981), is where we physically interact with objects in the environment. Its representation depends on the activity of a cortical network including premotor-parietal regions and the putamen subcortically, which displays responses to tactile stimulation, as well as stimuli in other modalities (i.e., visual and auditory) provided they occur in close proximity to the body (Ben Hamed et al., 2001; Bremmer et al., 2013; Brozzoli et al., 2011; Colby et al., 1993; Duhamel et al., 1998; Fogassi et al., 1992; Graziano et al., 1997; Makin et al., 2007; Rizzolatti et al., 1981; Sereno & Huang, 2006). At the behavioral level, the processing of stimuli in PPS is often facilitated in both uni- and multi-sensory settings, with faster detection of touches while auditory or visual stimuli approach in close space (Canzoneri et al., 2012; Ferri et al., 2015; Maister et al., 2015; Spaccasassi et al., 2019) and faster and more accurate discrimination of visual shapes (Blini et al., 2018a).

PPS representation is also characterized by a high degree of plasticity that likely facilitates interactions with the outside world. It can be shaped by experience, for instance following tool use (Farnè & Làdavas, 2000; Maravita & Iriki, 2004; Serino et al., 2007), or depending on the social context (Heed et al., 2010; Iachini et al, 2014, 2015; Maravita & Iriki, 2004; Pellencin et al., 2017; Ruggiero et al., 2017; Teneggi et al., 2013). When assessed via multisensory paradigms, PPS representation shrinks in the presence of another person: the tactile detection facilitation observed in PPS is less extended in space, as if the presence of another person was modulating the extent of one's own PPS representation (Teneggi et al., 2013). When assessed via the distance at which an approaching person is reachable, participants are influenced by the sex or the emotion the person conveys: PPS representation expands in the presence of males, angry or immoral persons, whereas it shrinks in the presence of females, happy or moral persons (Iachini et al., 2016). By contrast, multisensory tasks have shown a shrinkage or an expansion of PPS representation when facing an angry or immoral person, or a happy or moral person, respectively (Pellencin et al., 2017). PPS representation also expands when participants play a cooperative game with a partner before the task, suggesting that cooperation reconfigures the participants' PPS representation to include the space around the partner (Teneggi et al., 2013). Personality traits also influence PPS representation (Bufacchi & Iannetti, 2018; de Vignemont & Iannetti, 2015; Iachini et al., 2015; Lourenco et al., 2011; Sambo & Iannetti, 2013). For example Sambo and Iannetti (2013), found an expansion of PPS representation depending on the participants' anxiety level. Altogether, these results highlight the highly flexible nature of PPS representation that is modulated both by environmental constraints and individuals' psychological traits but also by the way this part of space is measured: whether it involves subjective judgments of reachability or sensory decisions. A handful of recent studies further suggested that the plastic features of PPS, determined by social stimuli, are associated with enhanced physiological responses (Cartaud et al., 2018; Ferri et al., 2015; Ruggiero et al., 2017). For instance, electrodermal activity increases when participants are presented with close as compared to far angry faces (Cartaud et al., 2018). Such physiological responses preferentially evoked by close emotional stimuli may reflect an increase of arousal within PPS, resulting from an activation of the sympathetic branch of the autonomic nervous system (Critchley, 2002).

However, to date the relationships between the behavioral and physiological markers of social modulations of PPS remains poorly understood. Here, we aimed at characterizing behavioral and physiological signatures of PPS representation in emotional contexts, also considering the potential role of participants' psychological traits. We thus modified an immersive virtual reality paradigm (O'Connor et al., 2014) we previously used to show advantages in visual discrimination of geometrical shapes in close space (Blini et al., 2018a). To keep distance and emotion task irrelevant, participants had to discriminate male from female faces with stimuli that could vary both in spatial location (50–300 cm) and emotion (happiness, anger, neutral). We measured participants' reaction times (RTs) and accuracy and recorded pupillary responses and heart rate.

We performed three experiments. In Experiment 1, faces were presented at 6 different distances (50–300 cm way, in 50 cm steps) and their size was scaled as a function of distance, thus farther faces appeared smaller as in natural viewing conditions. In Experiment 2, the same face stimuli were presented at two distances (50 cm, close or 300 cm, far) and, to control for the potential confound of stimulus size, they were corrected for retinal size: this way, farther faces appeared bigger than closer ones. In both experiments, we measured the participants' behavioral performance and pupil diameter. We also assessed two personality traits: anxiety (using STAI-Y and SAS questionnaires), and claustrophobia (using the CLQ questionnaire). Experiment 3 was similar to experiment 2, but participants viewed the stimuli passively to allow us for the recording of heart rate frequency and variability (HRV). We predicted that face proximity would facilitate visual discriminative abilities and this facilitation would be modulated by the facial features (sex, emotional valence), as well as the participants' sex and psychological traits. We further predicted that these behavioral changes would be associated with enhanced physiological responses.

2. Material and methods

We report how we determined our sample size, all data exclusions (if any), all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

2.1. Participants

Participants were healthy volunteers recruited through web advertising. None had history of neurologic or psychiatric disorders, and their vision was normal or corrected to normal (through contact lenses). All gave written informed consent

Table 1 – Demographic information for the three experiments.

Experiment	Demographic Information	Tasks	Measure	Retinal Size	Distances from subject
1	- 40 Subjects (20 female) - 0 Left-handed - Age (M = 22.5, SD = 3.72)	- Male/female Discrimination task - Questionnaires	- Accuracy - RTs - Pupil diameter	No correction	6 distances: 50 cm, 100 cm, 150 cm, 200 cm, 250 cm and 300 cm
2	- 40 Subjects (20 female) - 4 Left-handed - Age (M = 21.5, SD = 2.47)	- Male/female Discrimination task - Validation task - Questionnaires	- Accuracy - RTs - Pupil diameter	Correction	2 distances: 50 cm and 300 cm
3	- 24 Subjects (7 female) - 0 Left-handed	- Passive viewing task	- HR - HRV	Correction	2 distances: 50 cm and 300 cm

and were payed for their participation. A summary of participants' demographic information for each experiment is reported in Table 1. For experiments 1 and 2, we established a priori our target sample size ranged between 20 and 40 participants on the basis of what is regarded as a common sample size in the field (see, e.g., our previous study, Blini et al., 2018a). Different groups of participants took part in these experiments. For experiment 3, we managed to recruit a subset of participants who had already carried out experiment 2. In total we were able to enroll 24 subjects on the 40 who carried out experiment 2. No part of the study procedures or analyses of the three experiments was preregistered prior to the research being conducted.

The study followed the Declaration of Helsinki standards and was approved by the Institut National de la Santé et de la Recherche Médicale (INSERM) Ethics Committee (IRB00003888, No. 16-341).

2.2. *Apparatus*

In all experiments, visual stimuli were presented in a virtual reality environment. In experiment 1, the scene was rendered in an HTC Vive™ Head-Mounted Display (HMD), with a resolution of 1200 × 1080 pixels per eye, a frequency of 90 Hz and a field of view of 110°. The HMD had an embedded 250 Hz eye-tracking system (SMI). In experiments 2 and 3, the scene was rendered in an Oculus Rift DK2 HMD, with a resolution of 960 × 1080 pixels per eye, a frequency of 75 Hz, a field of view equal to 106°. The Oculus had an embedded 75 Hz eye-tracking system (SMI). The augmented technology Unity software (Version 5.1.2; Unity Technologies, San Francisco, CA) was used to create the virtual environment, display the stimuli and record participants' responses as in Blini et al. (2018a). Visual stimuli (faces) were presented in the virtual environment at different distances (see Table 1) while pupil diameter was recorded using the eye-tracking system of the HMD. In experiments 1 and 2, participants provided responses using the index and middle fingers of the dominant hand by pressing the B and N buttons on a computer keyboard. In experiment 3, a photoplethysmogram transducer (PPG, TSD200, Biopac) was attached to the right index finger of the participants to measure heart rate (HR) and heart rate variability (HRV); the signal was recorded via a Biopac system (MP150, PPGED- EDA device) at a frequency of 1 kHz.

2.3. *Stimuli*

Visual stimuli consisted of 20 individuals' faces, 10 females and 10 males, each mimicking 3 emotions (happy, neutral, angry). Legal copyright restrictions prevent public archiving of the stimuli used in our study, which were drawn from the Karolinska Directed Emotional Faces database (KDEF, Goeleven et al., 2008). These stimuli can be obtained from [www.kdef.se]. In this database, individuals were all photographed at the same distance. In detail, they were seated at a distance of approximately three meters from the camera. This distance was adapted for each subject by adjusting the camera position until the subject's eyes and mouth were at specific, predefined vertical and horizontal positions on the camera's grid screen. Then, each picture was cropped to a size of 562 pixels width and 762 pixels height. We further processed these images in the following way: stimuli were cropped to an oval shape, to remove outline and external features (e.g., hairs); images were equated for luminance, such that the mean luminance did not differ across sex or emotion of the faces. For that, we calculated the mean luminance of the face images. We then tested if luminance was different with a repeated measure ANOVA with sex and emotion of the image faces as factors; we found no significant main effects or interactions between these variables.

The size of each image was approximately 16 × 20 ° of visual angle except for the 1st experiment, in which images were scaled as a function of distance. In experiments 2 and 3, retinal size was kept constant across both distances (close and far). This was implemented in the Unity software by scaling up the far stimuli based on the size and distance of the close one, following the Basic Proportionality theorem: considering the size s of the closest stimulus displayed at a distance d, the size S of a stimulus displayed at distance D is: $S = s*D/d$. As such, in both experiments 2 and 3, the exact same 2D pictures, taken from the same position, were presented in either close or far conditions, allowing for similar object-specific spatial frequencies in both conditions. By presenting these images at different distances, they were not affected by perspective distortions, typically observed when pictures are taken from different distances (see for example Verhoff et al. (2008), Perona (2007) and Bryan et al. (2012)). Using the exact same pictures when applying retinal size correction (Experiments 2 and 3) to control for the potential confound of stimulus size, prevented the influence of implicit distance information potentially conveyed by such perspective distortions. The 2D face images were rendered onto a VR environment over a flat surface, using a Head-Mounted Display, where geometrical distortions are marginal, only appearing in the peripheral visual field and do not differ between distances (https://github.com/facebookarchive/RiftDK2/blob/master/Documentation/DK2FirmwareSpecification.pdf).

2.4. Procedure

2.4.1. *Male/female discrimination task (DT)*

Participants sat in a quiet room, wearing the virtual reality headset (HDM), their head on a chinrest. The virtual environment was the same as the one used in (Blini et al., 2018a), and consisted of an empty room, as to minimize the presence of distracting elements. Different conditions were obtained by presenting the pictures of faces at different positions from the observer (6 distances in the 1st experiment: from 50 cm to 300 cm and 2 distances in the 2nd experiment: 50 cm, close and 300 cm, far). In experiment 1, retinal size was naturally scaled, as in ecological conditions (closer faces appeared bigger than farther ones). In experiment 2, retinal size of the stimuli was kept constant across distances (farther faces appeared bigger than closer ones, see Fig. 1 and Table 1).

After a 5 points calibration of the eye-tracker, trials started with a white fixation cross, presented in the center of the visual field. If the subject correctly fixated the cross for 1000 msec, its color became blue, and it was followed by the presentation of one face stimulus randomly chosen among male or female faces, its identity (10 levels for each sex), its emotion (happy, neutral, angry), and the distance of presentation. Faces were presented for 1 sec and subjects had a time-limit of 750 msec to provide an answer. A feedback text was then presented for 1 sec. The feedback reported whether a response was correct, incorrect, too slow (>750 msec), or too fast (<100 msec), as to encourage compliance with task instructions and induce time-pressure. Subjects used their index and middle fingers to report the sex of the presented face (the response keys were counterbalanced across participants). The pupil size was recorded for each trial during the sex categorization task. At the beginning of the experiment, a practice block was administered. The goal of practice trials was to ensure a stable performance across blocks. Practice

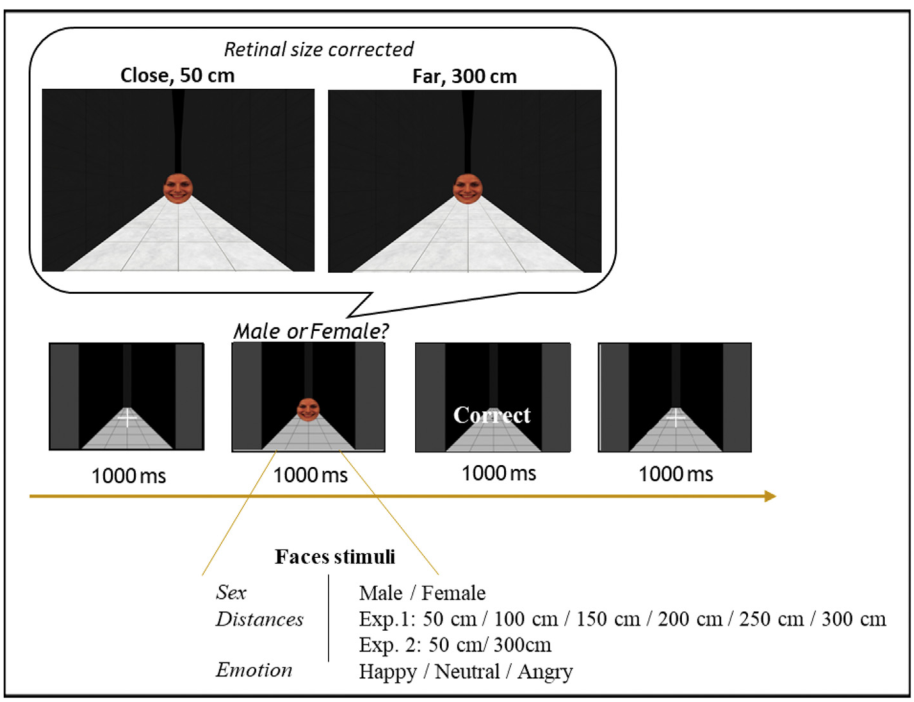

Fig. 1 – Experimental design for the male/female discrimination task in experiment 1 and 2. These experiments exploited a 3-D virtual-reality setting consisting in a simple empty room (same as the one used in Blini et al. (2018a). We used faces stimuli from the Karolinska Directed Emotional Faces database (KDEF, Goeleven et al., 2008, ID of the example face: AF06HAS). Faces stimuli with different emotions (happy, neutral, angry) were presented at different positions from participants. In the experiment 1, faces were presented at six different distances (50, 100, 150, 200, 250, and 300 cm) and retinal size was scaled as a function of distance. In the experiment 2, faces were presented at two distances (50 and 300 cm) and retinal size of the stimuli was kept constant across distances, resulting in the more distant faces appearing larger. Each trial started with a white fixation cross. If subjects correctly fixated the cross for 1000 msec, its color became blue, and it was followed by the presentation of the faces stimulus randomly chosen. Faces were presented for 1000 msec, then a feedback text was presented for 1000 msec. The feedback reported whether a response was correct, incorrect, too slow (>750 msec), or too fast (<100 msec). Participants used their index and middle fingers to report the sex of the presented face. Note that, due to lack of stereoscopic vision on 2D printing, these images do not bear any perceivable difference related to distance. Yet, their different position was clear in 3D.

blocks included 30 (experiment 1) or 24 (experiment 2) images that were also used in the ensuing experimental blocks. These stimuli were selected pseudo-randomly among the full images sample, thus including male or female faces, with various identities (10 levels for each sex), various emotions (happy, neutral, angry), and distances (6 distances from 50 to 300 cm for the experiment 1 or 2 distances for experiment 2). These categories were presented at least once in the practice trials. In addition, practice stimuli were selected randomly, according to these criteria, such that they differed for each participant.

Participants then performed 4 blocks of trials with a total of 576 trials for experiment 1, and 480 trials for experiment 2. After each block, subjects could rest and resume with the experiment by pressing the space key.

2.4.2. *Validation task (VT)*

At the end of experiment 2, we presented all the stimuli sequentially on a 2D monitor screen and asked subjects to judge whether the displayed emotion was neutral, happy or angry using a 9 points, Likert scale (range: −4–+4) presented below each face stimulus. In the scale, the minimum value (−4) indicated an angry face, the maximum (+4) a happy one, with intermediate values indicating neutral expressions. The open-source OpenSesame software (Mathôt et al., 2012) was used to display stimuli and collect responses. No time-limit was given. The aim of this task was to ensure that all the faces we presented could be correctly classified according to their emotional content.

2.4.3. *Passive viewing task*

Experiment 3 was designed to measure HR and HRV, which are typically estimated over several seconds (Shaffer & Ginsberg, 2017). Participants kept their right arm passively lying on the table in front of them with a photoplethysmogram transducer attached to their right index finger. Unlike in the first two experiments, participants had to merely look at the face stimuli. They viewed 6 blocks of 84 trials, each lasting about 4 min and followed by one-minute wash-out rest period. Also, at odds with experiment 1 and 2, here the same condition was presented within a given block. For each block, the condition was randomly selected among the different emotions (happy, neutral, angry), and distances (50 cm, close and 300 cm, far). As in experiments 1 and 2, the sex of the face stimuli (male or female), and identities (10 levels for each sex) were randomly presented in each trial within the block. The experiment started when the physiological signal (heart rate) appeared stable, typically from 5 sec to 1 min, based on the experimenter's visual inspection. At the beginning of each trial, participants had to fixate a white cross for 750 msec; then, one face stimuli appeared in the virtual environment for 2 sec and participants were instructed to look at them.

2.4.4. *Questionnaires*

At the end of experiments 1 and 2, participants filled the French versions of the following questionnaires, assessing personality traits supposedly related to PPS representation (Iachini et al., 2015; Lourenco et al., 2011; Sambo & Iannetti, 2013):

- STAI-Y questionnaire for assessing individual state and trait anxiety levels (i.e., two scores: STAY state and STAY trait scores; Gauthier & Bouchard, 1993; Spielberger & Sydeman, 1994).

- The sociality-avoidance questionnaire (SAS) for the measurement of anxiety for one own performance or for social situations, including the tendency to avoid them (i.e., six scores: Performance anxiety or fear, Social anxiety or fear, Total anxiety or fear, Performance avoidance, Social avoidance and Total avoidance scores; Radomsky et al., 2006).

- The Claustrophobia Questionnaire (CLQ), which includes two subscales assessing the specific fears of suffocation and restriction (i.e., three scores: Claustrophobia suffocation, Claustrophobia restriction and Total claustrophobia scores; Liebowitz, 1987).

The correlation between participants' scores in these questionnaires (i.e., a total of 11 different scores) and their performance on the DT was assessed by using Spearman correlations tests. The performance on the DT included RT variables for each emotion separately (i.e., angry, neutral and happy) and for all emotions regrouped. In experiment 1, we selected three variables: 1) the maximum (Max) RT and 2) the minimum (Min) RT among the 6 distances and 3) the difference between Min and Max RT (Delta RT). In addition, we computed differences in Delta RT between angry and neutral faces (Delta RTAngry-Neutral) and between happy and neutral faces (Delta RTHappy-Neutral), leading to a total of 14 variables for the correlation analysis. For experiment 2 with 2 distances (50 and 300 cm), we selected the difference between Close and Far RT for each emotion separately and for all emotion regrouped. Also, as in experiment 1, we computed differences in Delta RT between angry and neutral faces (Delta RTAngry-Neutral) and between happy and neutral faces (Delta RTHappy-Neutral), leading to a total of 6 variables for the correlation analysis. These analyses were explorative and resulted in a large number of correlation tests (exp. 1: 154 and exp. 2: 66) and as a consequence, we focused on correlations for which Bayes factors provided moderate ($3 < BF < 10$) or strong ($BF > 10$) evidence as to be more conservative with respect to false positives in the context of multiple tests (Blini et al., 2018; Gelman et al., 2012).

2.5. *Analyses*

In experiments 1 and 2, we measured accuracy, Reaction Times (RTs) and pupil diameter while the subjects performed the DT. At the end of experiment 2, we used the validation task to ensure that the emotions conveyed by the faces were correctly categorized by the participants. In experiment 3, we measured heart rate (HR) and computed heart rate variability (HRV) in the passive viewing task. Details about data processing, analyses and statistics for each variable are provided below.

2.5.1. *Behavioral performance in the male/female discrimination task (DT)*

Data were analyzed with the open-source software R (The R Core Team, 2013). Accuracy and RTs, in which both an accurate and timely response (>100 msec and <750 msec) was provided, were analyzed.

Table 2 – Psychometric functions fitted to the behavioral data (accuracy and RTs): linear, exponential, sigmoidal and gaussian. The N represents the number of participants displaying the same fitting function for all three emotions in Experiment 1. The models' goodness of fit was assessed using RMSE and AIC at the individual level. The greyed-out cells indicate that no participant presented the relative best-fitting function for all three emotions simultaneously using either goodness of fit measure (RMSE and AIC).

Curve	Equation	Measure	AIC	RMSE
Linear	y = a + b * x	Accuracy		
		RTs		
Exponential	y = a + b * exp(x/100)	Accuracy	N = 1/40	
		RTs		
Sigmoidal	y = a + b -a / 1+exp(c*(x-d))	Accuracy		N = 21/40
		RTs	N = 1/40	N = 7/40
Gaussian	y = a *exp(-1*(x-b)/c)+d	Accuracy		
		RTs	N = 4/40	N = 6/40

Experiment 1 was designed to study the spatial distribution of the effect by fitting psychometric functions: This approach is indeed well suited to study PPS, measuring performance of individuals along a continuum between far and near space. Importantly, this approach also allows for our results to be compared to several previous studies on peripersonal space, which made use of the same measures and analyses (e.g., Blini et al., 2018a; Canzoneri et al., 2012; Pellencin et al., 2017; Teneggi et al., 2013). Mean discrimination accuracy and RTs were calculated for each distance and emotion. These values were fitted at the group level and at the individual level, to four different psychometric functions: linear, exponential, sigmoidal and gaussian. The models' formulas are reported in Table 2. We performed non-linear least-squares estimations through the nls() function in R for every Emotion, using Distance as an independent predictor. We compared models' goodness of fit using both the root-mean-square error (RMSE) and the Akaike information criterion (AIC). The RMSE is a measure of dispersion of the residuals, whereas the AIC is best used for model comparison and accounts for models' complexity. The results of this analysis are provided in Tables 2 and 3. At the group level, for all emotions, the gaussian function provided the best fit for both accuracy and RTs (i.e., lower RMSE and AIC coefficients; see Table 3). At the individual level, the results indicated that the sigmoidal function best explained accuracy data for the largest number of participants while the gaussian function best explained RTs data for the largest number of participants (number of participants reported in parentheses in Table 3). Due to variability in the fitting of the four functions between individuals and emotions that lead to multiple convergence problems, we identified for each participant the best fitting function that was consistently found for the three facial expressions (Table 2). Results showed that the more consistent fitting was found for accuracy with 21 out of 40 participants, whose data were best fitted with the sigmoid function regardless of the emotion. Results were less conclusive for RTs, with <10 participants whose data were best fitted with the sigmoid or gaussian function. The inter-individual variability precluded further statistical analysis and we only provide a qualitative assessment of the results. Following previous studies (Canzoneri et al., 2012; Teneggi et al., 2013), we focused on the inflection point of the sigmoid function to identify the impact of a change in PPS representation according to facial emotions. Following the same reasoning for the gaussian fitting, we focused on the maximum peak of the gaussian curve as a putative analogous index.

In experiment 2, the results of the male/female discrimination task (i.e., Accuracy and RTs) were analyzed with mixed-effects multiple regression models (Baayen et al., 2008)

Table 3 – Results of models' goodness of fit using RMSE and AIC at the group level in Experiment 1. The number of participants who favored each model is reported in parentheses, based on analysis at the individual level.

Curve	Measure	Happy		Neutral		Angry	
		AIC	RMSE	AIC	RMSE	AIC	RMSE
Linear	Accuracy	−19.81 (N = 9)	.03 (N = 0)	−29.12 (N = 11)	.013 (N = 0)	−28.19 (N = 13)	.01 (N = 0)
	RTs	48.65 (N = 5)	8.46 (N = 0)	47.70 (N = 5)	7.82 (N = 0)	45.81 (N = 4)	6.68 (N = 0)
Exponential	Accuracy	−27.98 (N = 13)	.01 (N = 0)	−35 (N = 18)	.007 (N = 0)	−38.68 (N = 9)	.006 (N = 0)
	RTs	44.32 (N = 9)	5.90 (N = 0)	45.10 (N = 8)	6.29 (N = 0)	41.12 (N = 8)	4.52 (N = 0)
Sigmoidal	Accuracy	−30.84 (N = 7)	.008 (N = 28)	−32.60 (N = 5)	.007(N = 32)	−36.24 (N = 11)	.005(N = 33)
	RTs	44.84 (N = 9)	4.41 (N = 19)	47.42 (N = 9)	5.47 (N = 19)	39.67 (N = 12)	2.87 (N = 22)
Gaussian	Accuracy	−46.11 (N = 11)	.002 (N = 12)	−35 (N = 6)	.005 (N = 8)	−42.23 (N = 7)	.003 (N = 7)
	RTs	22.48 (N = 17)	.69 (N = 21)	37.27 (N = 18)	2.35 (N = 21)	27.36 (N = 16)	1.03 (N = 18)

using the lme4 package for R (Bates et al., 2015). These models had a logistic link-function, appropriate for binary variables, when assessing accuracy. We used Linear Mixed Effects Models (LMEM) because they allow to accommodate for both random effects of subjects and identities, most notably in this setting (e.g., Baayen et al., 2008). Thus, we could both generalize to individuals and different faces. The other advantages in the use of LMEM were that we used all the available data (trial basis, not collapsed), we could specify random effects appropriately to our design which therefore was more powerful (e.g., Jaeger, 2008).

As a first step, we defined a model containing the most appropriate random effects, striving for a parsimonious solution (Bates et al., 2015). We used an objective pipeline exposed in details elsewhere (Blini et al., 2018b). The simplest starting model included the random intercept for Subject (baseline level). We then tested: i) the random intercept for Identity (item); ii) possible nesting of the latter within Picture sex; iii) random slopes one by one. Random slopes testing started with introducing, for the random intercept of Subject, the following effects: 1) Distance; 2) Emotion; 3) Picture sex. Then, random slopes for Identity were tested in the following order: 1) Subject sex; 2) Distance; 3) Emotion. Procedures for testing fixed effects or for dealing with convergence problems were also unchanged with respect to our previous approaches (Blini et al., 2018b). We tested the role of the following four factors (fixed effects) and their interactions: Distance (2 levels: Close, Far), Emotion (3 levels: Happy, Neutral, Angry), Picture sex (2 levels: Male image, Female image) and Subject sex (2 levels: Male, Female participant). All post-hoc analyses for significant tests were computed on the basis of least-squares means (Lenth, 2016), using False Discovery Rate (FDR; Benjamini & Hochberg, 1995) correction for multiple tests.

In addition, a parametric bootstrap was used to obtain 95% confidence interval for the β coefficients, and thus to evaluate the distribution of estimated mean differences between the levels of a factor (Claridge-Chang & Assam, 2016).

2.5.2. *Pupil diameter*

Pupil diameter was retained for valid trials only, averaged across the left and right eye. A 'valid trial' corresponds to a trial in which the response was both accurate and timely (>100 msec and <750 msec). Each sample was first time-locked and aligned to the presentation of the face stimuli. To cope with inter-individuals variability, raw data were transformed in z values according to the subjects' specific distribution pattern. Z values exceeding ±2.5 SD were then treated as outliers/artifacts. We discarded trials in which more than 30% of the samples indicated such a corrupted signal, and linearly interpolated missing values in the remaining ones. Finally, each sample was normalized to (subtracted from) the first sample of each trial, which serves thus as baseline to better assess the time course of pupil dilation throughout the whole 1 sec window (corresponding to the presentation of face stimuli in each trial). To obtain a scalar index of pupil dilation/constriction for each trial, we then computed the temporal derivative (Van Den Brink et al., 2016) as the difference between the last and first sample of each epoch (submitted to statistical modelling and referred here as Gain). Positive values of Gain reflect overall pupil dilation since the beginning of the trial, negative values reflect overall constriction. Statistical modelling of the Gain followed the same pipeline of behavioral data, exposed above. For depiction purposes, smoothed curves were plotted. Since we did not correct for the influence of gaze position on pupil size measurement, results from this experiment are discussed taking into account the influence of gaze position on pupil size (see, for example, Hayes & Petrov, 2016).

2.5.3. *Heart rate and heart rate variability*

The heart rate signal was recorded and the inter-beat RR peaks were first detected with Spike2 software (Cambridge Electronic Design). The data were then imported in Kubios (Kubios software, version 2.1; Biosignal Analysis and Medical Imaging Group, Department of Applied Physics, University of Eastern Finland, Kupio, Finland) for following analysis. After extracting the HR signals, the R peaks were automatically identified. We visually inspected the automatic identification of the R peaks, and manually corrected for any missing peak. The number of R peaks during 1 min corresponds to the number of contractions (beats) of the heart per minute (bpm), i.e., heart rate frequency.

Time domain HRV indices included: 1) the number of adjacent normal to normal intervals (NN intervals or R–R interval; i.e., successive intervals between two heartbeats) differing by more than 50 msec in the entire recording (NN50, time, count); 2) mean of the standard deviations of all NN intervals for all 5-minute segments of the entire recording (SDNN, time, ms), informing about global variability and 3) the square root of the mean of the sum of the squares of differences between adjacent NN intervals (RMSSD, time, ms), expressing high frequency variability mainly of parasympathetic origin. Concerning the frequency domain analysis of the HRV, the power spectrum was obtained with a fast Fourier transform-based method (FFT; Welch's periodogram: 256 points windows with 50% overlap). The interpolation was used to resample RRi time series at 4 Hz. After the fast Fourier transform, HRV spectrum was then decomposed into two separate frequency bands: a low-frequency band (LF) with spectral components from .04 to .15 Hz and a high-frequency band (HF) comprising frequencies from .15 to .4 Hz. The ratio of LF power to HF power (LF/HF) was also calculated. We performed repeated measurement ANOVA on HR and HRV parameters, with FDR post-hoc correction ($p < .05$), with expressions (angry, happy and neutral) and distances (close and far) as factors. We ran an ANOVA instead of a LMEM approach because we didn't have multiple trials per cell, but only one value that corresponded to the mean HR and HRV parameters per block. In addition, a parametric bootstrap was used to obtain 95% confidence interval for the β coefficients, and thus to evaluate the distribution of estimated mean differences between the levels of a factor (Claridge-Chang & Assam, 2016).

3. Results

The supporting materials for this study are available on the Open Science Framework website (Supplementary Materials: https://osf.io/98mur/).

3.1. *Experiment 1: male/female discrimination task with face stimuli scaled as a function of distance*

In experiment 1, we modelled the subjects' DT performance (accuracy and RTs) as a function of depth (6 distances, from 50 to 300 cm). Due to inter-individual variability concerning the psychophysical modeling of subjects' performance and related convergence problems (see the Methods section), we reported in the part 3.1.1 only qualitative assessment of the results.

3.1.1. *Psychophysical modeling of behavioral data*

Psychophysical modeling of the subjects mean performance (accuracy and RTs) are illustrated in Fig. 2 and Table 3. Overall, visual inspection of the results show that the number of correct responses decreases (Fig. 2, on the top) while RTs increase as a function of the distance (Fig. 2, bottom), as previously reported with non-social stimuli (Blini et al., 2018a; Canzoneri et al., 2012; Ferri et al., 2015). Note that for close distances (in particular 50 cm), RTs seemed to be higher than those measured for more distant positions. At debrief, several subjects reported some 'difficulties' in focusing on stimuli at the closest distance, possibly due to the abrupt appearance of the faces in our experimental procedure.

Table 4 – Maximal peaks and of Gaussian curves and inflection points of Sigmoid curves in cm.

	Functions	Emotions		
		Happy	Neutral	Angry
Accuracy	Gaussian	122.584	95.087	96.151
	Sigmoid	255.971	266.999	268.672
RTs	Gaussian	136.530	145.576	133.452
	Sigmoid	247.191	264.581	242.383

3.1.1.1. Accuracy. Visual inspection of Fig. 2 suggests that the peak of the gaussian curve and the inflection point of the sigmoid curve change as a function of the emotional valence conveyed by the faces (Fig. 2 and Table 4). In particular, for happy faces, these parameters stand out from the other two emotions, namely neutral and angry faces, regardless of the fitting, suggesting higher accuracy for the former as compared to the latter.

3.1.1.2. Reaction times. As for accuracy, the peak of the gaussian curve and the inflexion point of the sigmoid curve for RTs seem to change as a function of the emotional valence conveyed by the faces (Fig. 2 and Table 4). Faster RTs are

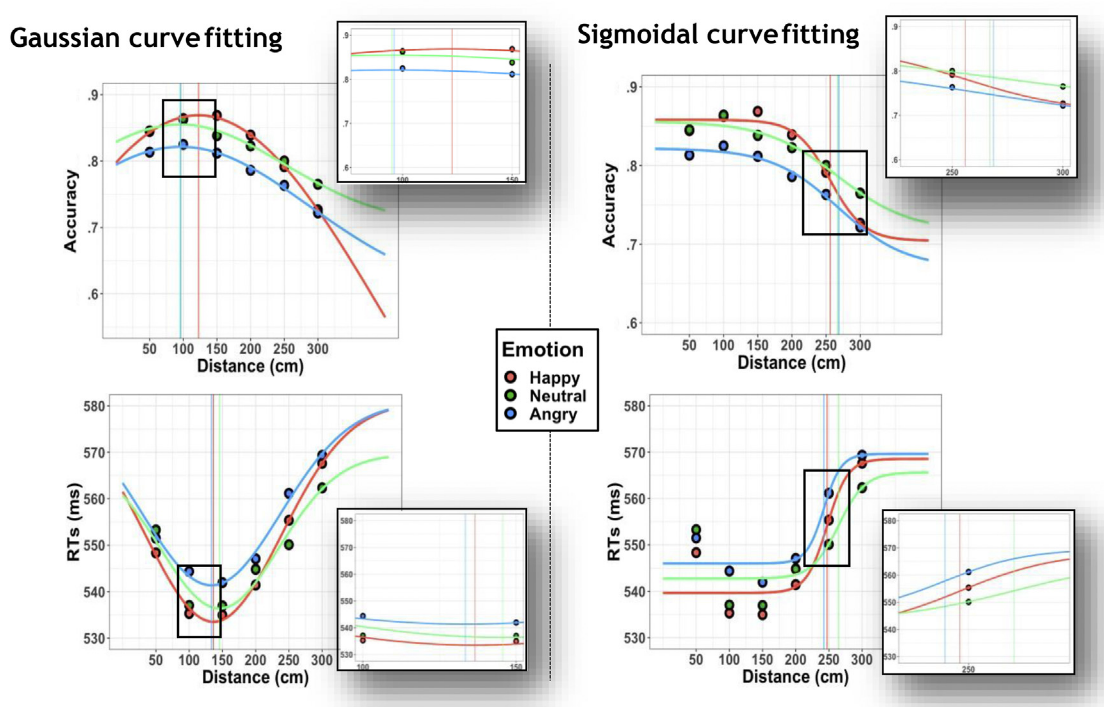

Fig. 2 – Psychophysical modeling of accuracy and RTs from Experiment 1. Fitting with gaussian (left) and sigmoidal (right) functions for the relationships between accuracy (top) or correct RTs (bottom) of the discrimination between male and female faces as a function of distance presented (in cm) with one color per emotion (red: happy faces, green: neutral faces and blue: angry faces). In each plot, the y-axis refer to the accuracy of participant's responses (correct responses) and RTs to discriminate. The x-axis refer to the distance where the stimuli were presented. The windows next to the main plot represent a zoom into the maximal peak and inflection points of the Gaussian and Sigmoidal curves, represented by the solid vertical lines for each emotion (red line: happy, green line: neutral, blue line: angry).

observed for happy faces compared to the two other emotions. Moreover, both gaussian and sigmoid fitting suggest a similar trend with a closer central point for both angry and happy faces compared to neutral faces, suggesting a modulation of PPS representation depending on the emotion conveyed by faces.

3.1.2. *Physiological analysis: pupil diameter*

The time-course of the pupil response, reflecting overall pupil dilation (positive values) or constriction (negative values) during the 1 sec time-window of stimulus presentation, is depicted in Fig. 4D Gain values for each trial were submitted to analyses with a random effect matrix which included: random slopes of Distance and Emotion for the random intercept of Subject; random intercept of Identity. We found a significant main effect of distance on pupil diameter ($\chi^2(5) = 99.98$, $p < .001$) with close faces inducing constriction and far faces inducing dilation ($\beta = 2.1$, 95% CI [1.89, 2.29]). A significant main effect was also observed for emotion (χ^2 (2) = 29.34, $p < .001$) with a difference in pupil dilation according to emotional faces. Pupil dilation was induced by the presentation of angry faces compared to the presentation of both neutral ($\beta = .05$, 95% CI [.03, .07]) and happy faces (all $|z| < 4$, all pfdr< .0001, $\beta = .05$, 95% CI [.02, .07]), while neutral and happy faces did not differ ($|z| = 1.845$, pfdr = .15, $\beta = -.007$, 95% CI [−.03, .01]). Finally, Distance and Emotion did not interact ($\chi^2(10) = 15.02$, $p = .13$).

3.1.3. *Psychological indexes and their correlation with behavioral responses*

We assessed the participants' anxiety, their sociality-avoidance and claustrophobia scores and estimated their relationship with their behavioral results on the DT. Due to large inter-individual variability in the fitting of the four functions between individuals and emotions that lead to multiple convergence problems, for the correlation analysis with personality traits, we focused on differences between the minimum and maximum RTs across the 6 distances for each participant rather than a mean RT at a fixed distance.

Our results found moderate evidence (3 < BF < 10) with a relation between differences between min and max RTs and claustrophobia levels. The measure of claustrophobia is composed of two separates but related items: fear of suffocation and fear of restriction (Radomsky et al., 2001). The global score and each individual item were positively correlated with the difference between min and max RTs for the neutral emotion: higher scores were associated with larger RTs differences (total.claustrophobia score: $r = .36$, $p = .024$; suffocation: $r = .34$, $p = .031$; restriction = .33, $p = .035$).

3.1.4. *Discussion*

We fitted the participants' accuracy and RTs with different theoretical curves as in previous studies (Blini et al., 2018a; Canzoneri et al., 2012; Ferri et al., 2015; Pellencin et al., 2017; Teneggi et al., 2013). When assessing gaussian and sigmoid functions fittings, our results suggest a shift of PPS representation depending on the emotional valence of the face to be discriminated. Specifically, both the maximal peak of the gaussian curve and the inflection point of the sigmoid curve occurred at closer distances for angry faces, followed by, in turn, happy and neutral faces. Emotion and distance modulated also pupil diameter. The pupillary response is tightly coupled with the vergence system (Feil et al., 2017). A decrease or increase in pupil diameter is observed when focusing the eyes from far to near distances (accommodation), or from near to far distances (disaccommodation), respectively (Kasthurirangan & Glasser, 2005). In our immersive setting, subjects moved their eyes from central fixation to either closer or farther positions, inducing a constriction and a dilation of the pupil when stimuli were presented in close and far space, respectively. In addition, we found that pupil size was larger with angry as compared to neutral, or happy faces, as in previous studies (Bradley et al., 2008; Libby et al., 1973). This increase likely reflects an activation of the sympathetic branch of the autonomic nervous system (Steinhauer et al., 2004), typically recruited to mobilize body's resources in threatening circumstances (Gordan et al., 2015).

Finally, we found a modulation of PPS that depended on participants' psychological traits and in particular their level of claustrophobia. We found that high claustrophobic fear was related to larger distance effect, suggesting that participants' psychological traits influence PPS representation.

3.2. *Experiment 2: male/female discrimination task with retinal-size corrected face stimuli*

In experiment 2, face stimuli were corrected for the retinal size and presented at either the closest or farthest distance (50 cm or 300 cm).

3.2.1. *Analysis of discrimination abilities in close and far space*

3.2.1.1. Accuracy. The mean accuracy of the 39 participants was 85.28% (SD = 6.15%). One subject was excluded from the analysis due to poor performance. Multiple convergence problems prompted us to use a matrix of random effects, which only included the random intercepts for Subject and Identity; no random slope was included. Fig. 3A illustrates the participants' accuracy depending on the distance (close/far) and the emotional valence conveyed by the faces (happy, neutral, angry). We found that accuracy was not modulated by Distance ($\chi^2(1) = .12$, $p = .73$). Emotion, on the other hand, did modulate participants' accuracy ($\chi^2(2) = 32.59$, $p < .001$). Indeed, happy faces were discriminated better than both neutral ($\beta = -.02$, 95% CI [−.03, −.008]) and angry ones (all $|z|$ >3.49, all pfdr < .001, $\beta = -.03$, 95% CI [−.04, −.02]), whereas the latter two did not differ ($|z| = .56$, pfdr = .58, $\beta = -.008$, 95% CI [−.02, .004]). There was no interaction between Distance and Emotion (χ^2 (2) = .07, $p = .97$). Three two-way interactions were also significant: Distance by Picture sex ($\chi^2(1) = 32.97$, $p < .001$); Emotion by Picture sex ($\chi^2(2) = 270.06$, $p < .001$); Picture sex by Subject sex ($\chi^2(1) = 12.54$, $p < .001$). The discrimination of male faces improved when images were presented far with respect to close ($\beta = .03$, 95% CI [.01, .04]), the pattern being reversed for female faces ($\beta = -.03$, 95% CI [-.05, −.009]). Within female faces, accuracy for the angry emotion was the lowest ($\beta_{Happy-} = -.08$, 95.0%CI [−.06, −.11], $\beta_{Neutral} = -.11$, 95.0%CI [−.08, −.13]); angry male faces were instead discriminated more

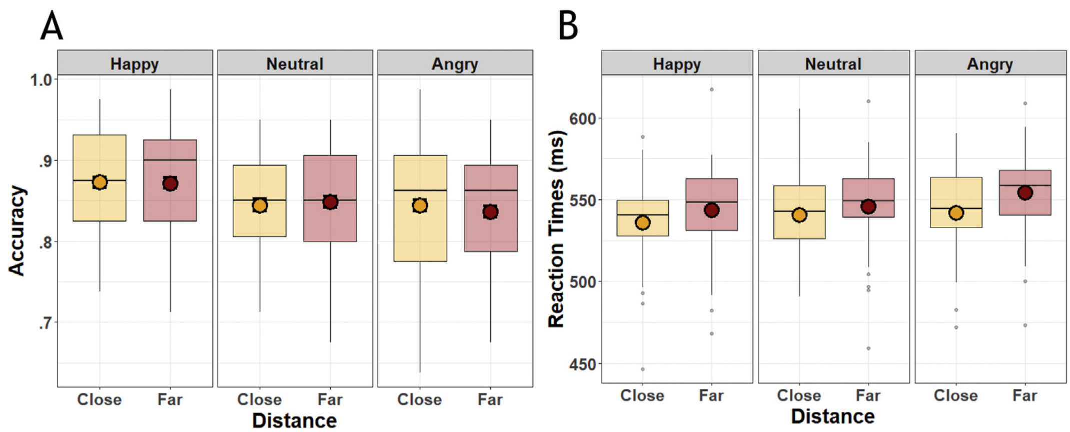

Fig. 3 – Results of male/female discrimination task from Experiment 2: A. Box-plots depicting participants' accuracy as a function of distance (close, 50 cm and far, 300 cm) and emotion depicted by faces. B. Box-plots depicting the participants' correct RTs as a function of distance (close, 50 cm and far, 300 cm) and emotion. In each plot, the vertical length of the box represents the interquartile range, the thick horizontal line represents the median, and the whiskers indicate the full range of values. Large dots inside the whiskers represent the mean. Dots outside the whiskers represent values exceeding 1.5 times the interquartile range.

accurately ($\beta_{Happy} = .02$, 95.0% CI [.003, .04], $\beta_{Neutral} = .09$, 95.0% CI [.07, .1]). Full results and graphical depictions of these tests are detailed in the supplementary materials.

3.2.1.2. Reaction times. The selected matrix of random effects included Emotion, Distance, Sex, and the Distance by Sex interaction as random slopes for Subject. No random slope was selected for the random intercept of Identity, which was included as well. Fig. 3B illustrates the participants' RTs depending on the distance (close/far) and the emotional valence conveyed by the faces (happy, neutral, angry). We found main effects of Distance ($\chi^2(1) = 25.45$, $p < .001$) and Emotion ($\chi^2(2) = 17.02$, $p < .001$). The first, as found in experiment 1 without retinal size correction, reflected faster responses for stimuli presented close with respect to far from participants (|z| = 6.17, $p < .001$, ($\beta = 8.75$, 95% CI [5.63, 11.4]). The second, also similar to experiment 1, reflected faster RTs for happy faces, which were discriminated faster than both neutral ($\beta = 3.48$, 95% CI [1.04, 5.92]) and angry ones (all |z|> 3.23, all pfdr < .002, $\beta = 7.65$, 95% CI [4.28, 11.2]); neutral faces were, in addition, discriminated faster than angry ones (|z| = 2.79, pfdr = .006, $\beta = 4.18$, 95% CI [.69, 7.86]). Moreover, these two effects were found to interact (Distance by Emotion: χ^2 (2) = 7.94, $p = .019$, depicted in Fig. 3). We thus compared the magnitude of the Distance effect between the three Emotions (i.e., the difference between RTs obtained in close and far space). We found that it was enhanced for angry faces with respect to neutral (|z| = 2.8, pfdr = .015, $\beta = 7.38$, 95% CI [.79, 14.2]) but not happy ones (|z| = 1.83, pfdr = .1, $\beta = -4.35$, 95% CI [−9.71, .85]); the magnitude of the advantage for close did not differ between neutral and happy faces (|z| = 1.01, pfdr = .31, $\beta = 3.03$, 95% CI [−4.02, 9.89]). As a complementary approach to post-hoc contrasts, we examined RTs for Emotion for each Distance. When images were presented close, happy faces were discriminated faster than both neutral ($\beta = 5.1$, 95% CI [1.45, 9.42]) and angry ones (all |z|> 3.04, all pfdr< .004, $\beta = 6.09$, 95% CI [1.62, 10.5]); when images were presented far, angry faces were discriminated slower than both happy ($\beta = -10.4$, 95% CI [−14.4, −6.7] and neutral (all |z|> 5.48, all pfdr< .001, $\beta = -8.37$, 95% CI [−13.5, −3.28]). Finally, three two-way interactions and one three-way interactions were significant: Distance by Picture Sex ($\chi^2(1) = 9.29$, $p = .002$); Emotion by Picture Sex ($\chi^2(2) = 292.66$, $p < .001$); Emotion by Subject Sex ($\chi^2(2) = 7.49$, $p = .023$) and Distance by Emotion by Subject Sex ($\chi^2(2) = 7.40$, $p = .024$). Concerning the two-way interactions, the first refers to female faces being discriminated faster than male ones when presented close ($\beta = 14.4$, 95% CI [8.92, 20.1]), but not far (and thus an enhanced distance effect for the discrimination of females, $\beta = 5.75$, 95% CI [−.66, 12.8]). The second indicates that female faces were consistently discriminated faster when displaying happy (~30 msec, 95% CI [27.5, 38.3]) or neutral (~23 msec, 95% CI [19.6, 30.2]) expressions with respect to angry, whereas male faces where discriminated faster if displaying angry expressions (~15 msec, 95% CI [10.3, 19.6] $_{Neutral}$, 95% CI [9.77, 19.8] $_{Happy}$). Finally, female participants were consistently faster in discriminating happy faces ($\beta_{Neutral} = 4.52$, 95% CI [2.41, 7.09], $\beta_{Angry} = 4.2$, 95.0% CI [.315, 10.1]), but there were no differences between neutral and angry faces ($\beta = -.32$, 95% CI [−3.97, 4.86]); male participants, on the contrary, showed a full gradient also indicating that angry faces were discriminated particularly slower ($\beta_{Happy} = -12.5$, 95.0% CI [−16.3, −8.95], $\beta_{Neutral} = -9.62$, 95.0% CI [−13.4, −4.92,]). The three-way interaction refers to a larger distance effect (advantage for Close) for Females for Neutral with respect to Happy faces and a larger Distance effect for Males for Happy than Neutral. All post-hoc results and graphical depictions for the last tests can be retrieved in the supplementary materials.

3.2.2. *Physiological analysis: pupil diameter*

As for experiment 1, the time-course pupil response during the whole 1 sec time-window of stimulus presentation, is depicted in Fig. 4E. Gain values for each trial were submitted to analyses using a random effect matrix, which included:

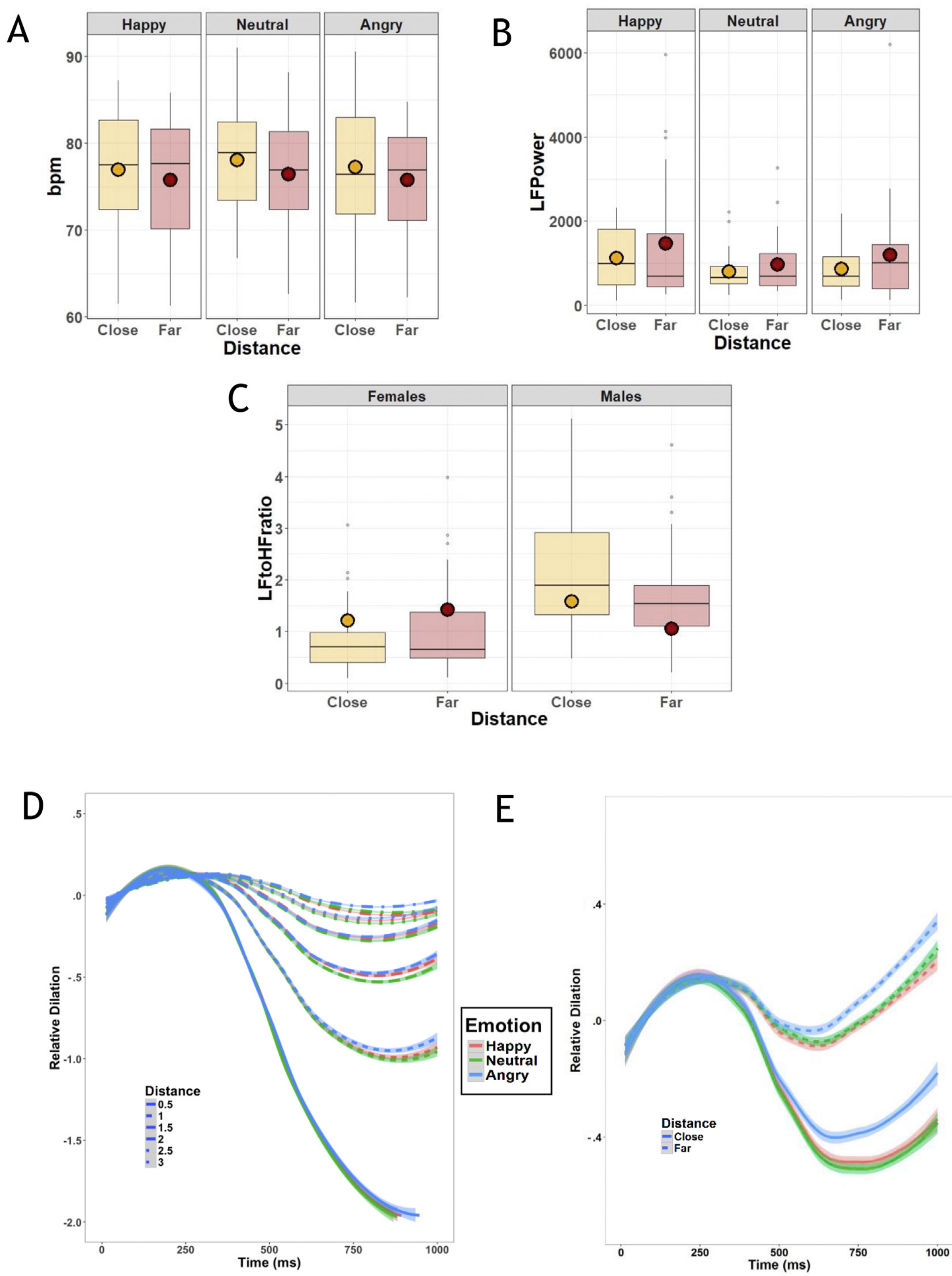

Fig. 4 – Physiological responses: A. Heart Rate results from Experiment 3. Box-plots depicting the participants' Heart Rate as a function of distance (close, 50 cm and far, 300 cm) and the emotion depicted by faces. B. and C. HRV results from Experiment 3. Box-plots depicting the LF power component of HRV as a function of distance (close, 50 cm and far, 300 cm) and the emotion depicted by faces (B) and LF to HR ratio of HRV as a function of distance (close, 50 cm and far, 300 cm) and the participants' sex (C). In each plot, the vertical length of the box represents the interquartile range, the thick horizontal line represents the median, and the whiskers indicate the full range of values. Large dots inside the whiskers represent the mean. Dots outside the whiskers represent values exceeding 1.5 times the interquartile range. D and E. Pupil diameter results from Experiment 1 and 2, respectively. Time-course of changes in pupil size, reflecting dilation or constriction during the whole 1 sec time-window of stimulus presentation represented as a function of distance and emotion depicted by faces. The lines and dashed lines correspond to the different distances where face stimuli were presented from 50 cm to 300 cm in panel C.; close, 50 cm and far, 300 cm in panel D. Locally weighted smoothing (LOESS) was applied to curves for depiction purposes.

random slopes of Distance, Emotion, and Sex for the random intercept of Subject; random slopes of Emotion and Subject Sex for the random intercept of Identity. Similarly to experiment 1, we found an effect of Distance on pupil diameter ($\chi^2(1) = 27.55$, $p < .001$) when retinal size was controlled for. Close stimuli induced pupil constriction, whereas far stimuli induced pupil dilation ($|z| = 6.53$, pfdr< .0001, $\beta = .54$, 95% CI [.39, .71]). Emotion had a strong effect as well ($\chi^2(2) = 34.64$, $p < .001$); angry faces caused pupil dilation with respect to both neutral ($\beta = -.12$, 95% CI [−.15, −.09]) and happy faces (all $|z|>$ 6.97, all pfdr< .0001, $\beta = -.13$, 95% CI [−.17, −.09]), while the latter two conditions did not differ ($|z| = .54$, pfdr = .59, $\beta = .01$, 95% CI [−.01, .05]). Distance and Emotion did not interact ($\chi^2(2) = 2.38$, $p = .30$). The three-way interaction Distance by Subject Sex by Picture Sex was significant ($\chi^2(1) = 6.19$, $p = .01$). When viewing female faces presented far, male participants showed less dilation compared to female participants.

3.2.3. *Validation task*

We found significant main effects of Sex [F(1, 38) = 40.63, $p < .001$] and Emotion [F(2, 76) = 982.94, $p < .001$]. The first indicates that images of males were ranked on average towards the “angry” side of the continuum ($\beta = -.19$, 95% CI [−.246, −.131]). The second effect, which was the core test for this section, confirms that Emotions were clearly clustered such that angry faces obtained strongly negative rankings, happy faces strongly positive rankings, and neutral ones clustered around zero ($\beta_{\text{Happy-Angry}} = -4.94$, 95% CI [-4.66, −5.24], $\beta_{\text{Happy-Neutral}} = -2.8$, 95% CI [−2.64, −2.96], $\beta_{\text{Neutral-Angry}} = -2.14$, 95% CI [−1.99, −2.32]). However, Emotion and Sex interacted [F (2, 76) = 8.52, $p < .001$], such that males were indeed classified more often towards the “angry” side of the continuum, but only for neutral ($\beta = .17$, 95% CI [.08, .26] and angry expressions ($\beta = .34$, 95% CI [.23, .45]; rankings did not differ between male and female images for happy emotions ($\beta = .07$, 95% CI [−.008, .15].

3.2.4. *Psychological indexes and their correlation with behavioral responses*

In particular, we found strong evidence (BF > 10) for a correlation between the distance effect observed for happy faces and sociality-avoidance: the more self-reported avoidance for social situations, the smaller the deltas for happy faces ($r = -.4$, $p = .011$). This support, again, the notion that participants’ personality traits influence PPS representation. Full details can be found in the supplementary materials.

3.2.5. *Discussion*

First, in Experiment 2, despite the retinal size was kept constant, we observed an advantage in responding to faces presented in near space, as previously found for geometrical objects shape discrimination (Blini et al., 2018a). Interestingly, this effect was modulated by the emotion conveyed by the face. Participants were fastest and more accurate in discriminating happy faces when these were presented close to them, while the slowest responses were obtained with angry faces presented far. Noteworthy, the distance effect (i.e., difference in RTs for close *vs* far faces) was more important for angry faces compared to other emotions (neutral and happy). Finally, we also observed a modulation of accuracy and RTs according to the Sex of the face stimuli (i.e., angry males were recognized faster and better than happy males, and inversely for females) and according to the participants’ Sex (i.e., females were faster to discriminate happy faces, males were slower to discriminate angry faces) confirming that the impact of emotion on PPS representation may differ between males and females (Gigliotti, Soares Coelho, Coutinho, & Coello, 2019 ;Iachini et al., 2016; Ruggiero et al., 2017; Wingenbach et al., 2018).

Second, we found changes in pupil size depending on distance, emotion of the face stimulus and participant sex. The emotional- and distance-dependent modulation replicated the findings of Experiment 1, where retinal size varied as a function of distance: 1) pupil dilates for far faces and constricts for close faces, which likely reflects the tight coupling between pupil size and eye vergence and, 2) pupil dilates with angry faces, which likely reflects an increased level of arousal (Bradley et al., 2008; Steinhauer et al., 2004). In addition, we found an interaction between distance, participants’ sex and the sex of the face stimuli, supporting the view that females and males process social stimuli differently in PPS, as reported in previous studies (Iachini et al., 2016; Ruggiero et al., 2017).

Third, we found that distance effect (i.e., far-close RTs) for happy faces was related to participants’ self-reported avoidance scores in social situations, with larger distance effect related to smaller avoidance scores.

3.3. *Experiment 3: HR indices when viewing close and far faces*

In experiment 3, participants were merely exposed to the same emotional faces presented in the DT. Similar to experiment 2, they viewed retinal-size corrected stimuli at two distances (close: 50 cm and far: 300 cm) while we measured HR frequency and HRV.

3.3.1. *Heart rate and heart rate variability as a function of distance and emotion*

3.3.1.1. Heart rate frequency. Fig. 4A illustrates the participants’ HR frequency as a function of Distance (close/far) and Emotions (happy, neutral, angry). We found a main effect of Distance [F (1, 21) = 6.94, $p = .02$], that reflected higher HR frequency for faces presented close with respect to far from participants ($|t| = 2.63$, $p = .015$, $\beta = 1.4$, 95% CI [.64, 2.92,]). Emotion did not modulate participants’ HR [F (1.97, 41.29) = 1.31, $p = .28$] and there was no interaction between Distance and Emotion [F (1.83, 38.40) = .13, $p = .86$].

3.3.1.2. Heart Rate Variability. ANOVA tests were performed on the time domain (NN50, SDNN and RMSSD components) and the frequency domain (HF and LF components). Results on the time domain revealed no effect of Distance (NN50: F(1, 21) = .15, $p = .70$; SDNN: F(1, 21) = 1.41, $p = .25$; RMSSD: F(1, 21) = 1.61, $p = .22$), nor Emotion (NN50: F(1.72, 36.02) = .09, $p = .89$; SDNN: F(1.80, 37.76) = .004, $p = .65$; RMSSD:F(1.99, 41.74) = .06, $p = .94$). Results on the frequency domain revealed a main effect of Emotion for the LF component [F (1.46, 30.75) = 5.38, $p = .02$], but no effect of Distance [F (1, 21) = 2.67, $p = .12$], nor any interaction [F (1.98, 41.67) = .50, $p = .61$]. Fig. 4B illustrates the participant’s LF component for HRV depending on the distance (close/far) and the face emotional valence (happy, neutral, angry). Post-hoc analysis revealed that LF component was enhanced for happy faces with respect to neutral ($|t| = 3.245$, $p = .007$, $\beta = 415$, 95% CI [113, 779]), but not angry ones ($|t| = 2.028$, $p = .073$, $\beta = -264$, 95% CI [−583, 26.5]) and the latter two did not differ ($|t| = 1.217$, $p = .23$, $\beta = 151$, 95% CI [−9.31, 354]). Analysis of the LF to HF ratio showed no effect of Distance [$F(1, 21) = 3.49$, $p = .08$] nor Emotion [$F(1.88, 39.55) = .64$, $p = .52$], but there was a significant two-way interaction of Distance by Subject Sex [$F(1, 21) = 18.38$, $p = .0003$], showing that males presented larger ratios when images were presented close with respect to far ($\beta = .54$, 95% CI [.29, .85]) (Fig. 4C).

3.3.2. *Discussion*

We found higher HR when faces were presented close (50 cm), as compared to far (300 cm), from the participants. These results extend previous findings reporting changes of skin conductance with emotional faces within PPS (Cartaud et al., 2018), or HR in conditions involving a stimulated hand approaching the face (Chillura et al., 2018). Altogether, these findings demonstrate that emotional faces enhance physiological responses and these responses are potentiated within PPS. The increase in physiological responses typically signifies an aroused state, through the activation of the sympathetic branch of the peripheral nervous system (Gordan et al., 2015; Kreibig, 2010). In addition, our results demonstrate that distance also modulated HRV depending on the participants' sex. We found a selective increase of LF/HF ratio when faces were presented close to male participants. The ratio between the high- and low-frequency oscillations in HRV is viewed as reflecting the balance in activity between the parasympathetic and sympathetic systems. An increase of this ratio is thought to represent a sympathetic effect on the heart (Shaffer & Ginsberg, 2017). We found also that the HRV is sensitive to the emotion displayed: LF component was increased for happy faces compared to neutral faces. Both parasympathetic and sympathetic peripheral nervous system contribute to LF power (Shaffer & Ginsberg, 2017), however in some conditions sympathetic activity may dominate over parasympathetic activity (Pagani et al., 1984). The HR and HRV responses suggest an activation of the sympathetic system depending on the emotion perceived by the subject (happy faces), by the distance at which these stimuli were presented (close compared to far) and by the sex of the participants.

4. General discussion

In the present study, we investigated the impact of social stimuli (i.e., faces with emotional expressions) on the PPS advantage in visual discrimination abilities reported recently (Blini et al., 2018a) and its physiological markers. We presented emotionally connotated faces close or far from participants in an immersive virtual reality environment. Across experiments, we consistently observed a facilitation in facial discrimination within PPS. In absence of any speed accuracy trade off, participants performed sex categorization faster in close compared to far space (Exp. 1), even when retinal size was equated for close and far images (Exp. 2). Most relevant for this study's purpose, this distance-related modulation depended on the face emotional valence, its' sex, and the participant's sex, providing new evidence that PPS representation is finely tuned to both external and internal constraints. In addition, two physiological responses were also modulated by distance: the pupil size and HR indexes (frequency and variability). Interestingly, and similar to the behavioral findings, these distance-related physiological changes (pupil diameter, HR and HRV) also depended on the participant's sex and the sex of the face stimuli.

4.1. *Close emotional faces facilitate visual discriminative abilities*

We found that participants were faster in categorizing sex when faces were presented close as compared to far (8.6 msec advantage). This advantage was found even when stimuli in close and far space were equated in retinal size, without any speed accuracy trade off, as found for object shape discrimination (Blini et al., 2018a), suggesting that the faster processing in PPS, previously reported for neutral objects, extends to social stimuli.

Humans faces share the same basic prototypic structure with subtle idiosyncratic differences in the position, shape and characteristics of the elements that constitute an individual face (Logan et al., 2017). Despite these complexities, humans can extract seemingly effortlessly an important number of information such as sex. Here, we further show that the depth at which a face is presented affects this fine discrimination ability, facilitating such an ability within close space. This effect was present with unfamiliar, cropped faces, that is hair and any other external features were lacking and with faces expressing emotions that could potentially increase the difficulty in discriminating the sex of the face image. As accumulating evidence suggest that "what" and "where" information can coexist in the dorsal pathway (Freud et al., 2017), it is tempting to suggest that the PPS network seems ideally suited to subserve the advantage in discriminating close versus far objects and faces. Yet, recent evidence also demonstrates that category-selective regions in the visual ventral stream are also engaged in the processing of depth information (Nag et al., 2019). The specific contribution of these different networks in the behavioral facilitation that we report here is beyond the scope of the current study and future neuroimaging studies are needed to provide insights about the brain processes involved. Importantly, the present study provides new evidence that male/female discrimination, a fine perceptual ability, is facilitated in close space, within PPS. Interestingly, Smith and Schyns (2009) reported that changes in viewing distance affect the spatial frequency (SF) content of the stimuli and performance was differently affected across distances depending on the facial expressions. The recognition of neutral facial expressions tended to be more impaired than happy and angry across several distances. Although we report here performance related to sex discrimination, instead of emotions, we also observed that performance was differently affected depending on the emotions across the different distances. Specifically, we found that performance with angry faces tended to be more impaired than that of happy or neutral faces across several physical distances. We did not determine the SF range of the face images depending on the emotion and viewing distance in our set of stimuli as this was beyond the scope of our current experiment, but it is possible that differences in SF across emotion and viewing distances may impact performance differently depending on the task at hand (discrimination of emotional facial expressions *vs* sex of faces). Noteworthy, Aguado et al. (2010) found both common and specific effects of SF content on sex and emotional expression discrimination in faces, suggesting that they rely on a set of features that are in part overlapping and in part independent. This is also consistent with Rotshtein et al. (2010) findings demonstrating specific effects of SF content depending on the task demand. Importantly, in experiments 2 and 3 where retinal size was equated across close and far conditions, the SF content of the images were similar across both distances and therefore did not affect our results.

Second, within PPS, participants were faster to discriminate happy faces compared to both neutral and angry ones whereas, outside PPS, participants were slower in discriminating angry faces compared to both happy and neutral ones. The psychophysical modeling (gaussian and sigmoidal fittings specifically) of accuracy and RTs as a function of distance indicates that performance is modulated according to emotions. In particular, up to 150 cm from the observer happy faces lead to faster and more accurate performance compared to the other emotions. Such a perceptual facilitation with happy faces could result from salient information extracted from the mouth region, that may speed up the processing (Calvo et al., 2010). This finding concurs in suggesting that complex stimuli appearing in PPS benefit of a much finer visual processing than previously thought. In addition, a comparison between the maximum peak of the gaussian fitting and the inflection point of sigmoid fitting for RTs, a canonical signature of PPS representation (Canzoneri et al., 2012; Pellencin et al., 2017; Teneggi et al., 2013), suggests a similar shift in representation of PPS depending on the facial emotions. These parameters are typically taken to indicate a change or a shift in PPS representation 'border', which comes closer to the body facing angry compared to happy and neutral faces. Our results are in keeping with previous work assessing PPS with multi-sensory tasks whereby, as here, distance is not relevant to the task (Pellencin et al., 2017). Together, these findings suggest a shrinkage of PPS representation in the presence of faces with negative connotations. Yet, faces with negative connotations are not always associated with a shrinkage of PPS representation. For instance, in reachability judgement task, participants favored larger distance from faces with negative connotations (Iachini et al., 2015; Ruggiero et al., 2016). This task, on the contrary, directly involves a distance judgment (participants press a button when an approaching avatar is reachable). Altogether, these results denote the highly flexible, context-dependent nature of PPS representation. This representation of the space close to the body allows us to adapt our behavioral response and interact toward and away from the different elements of our environment depending on the context, in an unconscious and automatic manner. Noteworthy, the differences observed on the flexibility of PPS representation (shrinking or enlargement with negative emotions) suggest that different methods to assess PPS representation (Iachini et al., 2015; Pellencin et al., 2017; Ruggiero et al., 2016; Teneggi et al., 2013) may refer to different concepts of PPS (de Vignemont & Iannetti, 2015). In this regard, the unisensory visual approach developed in the present study seems to capture PPS features that are typically observed in multisensory tasks (Pellencin et al., 2017; Teneggi et al., 2013).

Finally, our exploratory correlation analyses suggest that PPS representation depends also on the participants' psychological traits and in particular on their level of claustrophobia and social avoidance. In Experiment 1, high claustrophobic fear (fear of restriction or suffocation) were related to larger RT differences. Our results are in line with those of Lourenco et al. (2011) and Hunley et al. (2017) who found larger PPS representation in individuals with high claustrophobic fear and suggested that this distortion in the representation of near space might be linked to the defensive function of PPS (Graziano & Cooke, 2006). In experiment 2, we found that higher avoidance scores in social situations were related to smaller distance effect for happy faces. In both experiments with different groups of participants, the results seem to indicate that PPS representation is influenced by personality traits. Yet, it is difficult to draw strong conclusions about the specificity of this influence due the degree of subjectivity and variability associated with these types of questionnaires. Future studies – including a larger number of participants and testing more systematically psychological traits – are necessary to understand the complex relationship between psychological traits and PPS representation depending on the context at hand.

4.2. *Emotional faces in PPS enhance physiological responses*

Stimuli presented in PPS tend to be processed faster; the processing of objects conveying a potential threat, whether social or not, are even more prioritized when approaching the body (Bufacchi, 2017; Coello et al., 2012). A few recent studies suggested that physiological responses are also modulated as a function of distance (Meyer et al., 2019). For instance, Rossetti et al. (2015) reported an increase of electrodermal activity to incoming threatening stimuli (a needle) in the space close to the hand. Cartaud et al. (2018) also reported an increase of electrodermal activity for angry facial emotions presented in PPS using human-like point-light displays. Other studies investigated the relationship between interoceptive accuracy, a proxy for trait-like sensitivity to one's visceral signal determined by heartbeat tracking, and the modulation of participants' autonomic response (Ferri et al., 2013) and PPS representation (Ardizzi & Ferri, 2018). Ferri et al. (2013) found a positive correlation between heartbeat perception scores and respiratory sinus arrhythmia (RSA) responses in PPS in a social task, suggesting that high interoceptive sensitivity contribute to more efficient body-related information occurring in PPS. In addition, Ardizzi and Ferri (2018) found that higher interoceptive accuracy predicts sharper PPS boundary. These studies suggest that the level of arousal is differentially affected by the position of stimuli in space, with an increase of interoceptive accuracy (i.e., heartbeat perception) or physiological responses in close space.

Our results add to these findings by providing novel evidence of distance-dependent modulation of pupil diameter and heart rate indexes (frequency and variability). We found a constriction of the pupil size when faces were presented in close space and a dilation when faces were presented in far space. This finding fits nicely with the modulation of the pupil diameter that is generally observed during accommodation and disaccommodation: focusing the eyes at different distances is associated with a decrease in pupil diameter when focusing from far to near (accommodation) and an increase when focusing from near to far (disaccommodation) (Kasthurirangan & Glasser, 2005), reflecting the tight coupling between pupil size the vergence system (Feil et al., 2017). Such internal signals could therefore contribute to or result from the behavioral facilitation within PPS. In addition to this general modulation though, the pupil diameter was selectively modulated by the facial emotion: angry faces induced pupil dilation, as previously reported (Bradley et al., 2008; Libby et al., 1973). The pupil diameter is controlled by two muscles, the dilator and the sphincter, differentially influenced by the sympathetic and parasympathetic nervous systems. Increased sympathetic activity leads to pupil dilation whereas increased parasympathetic activity leads to pupil constriction (Steinhauer et al., 2004). The increase in pupil diameter in response to angry faces thus suggests a stimulation of the sympathetic branch of the autonomic nervous system, preparing the body for a rapid reaction to face environmental changes, which is especially important for near-space situated stimuli (Ebitz & Moore, 2019). Although in the present study this effect did not appear to vary as a function of the distance, we prefer cautiously not excluding this possibility on this sole basis. Further, a study by Schurgin et al. (2014) on eye movements during facial emotion recognition reported an eye-gaze distinctive pattern for each type of emotional face. For example, the eyes region is less explored in expressions of happiness and disgust, as compared to faces expressing fear and shame. When additionally considering that changes in pupil size according to close and far presentation of stimuli are highly coupled with the vergence system (Feil et al., 2017), it is possible that the difference in eye movements between different facial expressions and face sizes might have affected the pupil diameter results. Yet, in the light of the similar, distance dependent pattern we observed across emotions when faces were presented either without or with retinal size correction (Exps 1 and 2, respectively) we deem this possibility is unlikely.

We also measured the heart rate (HR) and its variability (HRV) while the subjects observed the faces. As previously described, these variables were modulated by facial expressions (Appelhans & Luecken, 2006). In addition, we found that closer faces evoked significant increase of the HR, together with a modulation of its variability, which depended on the sex of the face stimuli or of the participants. As for the pupil size, sympathetic and parasympathetic systems exert antagonistic effects on the heart, either preparing the body for emergency or stressful situations (sympathetic system), or restoring the body to a restful state (parasympathetic system) (Ziegler, 2004). Both the pupil dilation and the HR/HRV increase suggest a sympathetic activation in the presence of emotional stimuli (i.e., increase of HRV for happy faces and pupil dilation with angry faces) and by their proximity to the body (i.e., increase of HR in close space compared to far). The physiological changes induced by emotional faces in PPS likely reflect an increase of the level of arousal when stimuli approach the body. Neither for the heart rate nor the pupil size, we observed any interaction between the type of emotion and distance from the body. This might suggest that they reflect a generalized arousing response when a stimulus approach the body, prompting a defensive response to protect from a potential danger (Cléry et al., 2015; Graziano & Cooke, 2006; di Pellegrino & Làdavas, 2015).

4.3. *Sex matters to the space around us*

The emotional content of a face influences both people's visual discrimination and their physiological responses and our results concur showing the profound impact that emotions can have on PPS. In addition, we also found that the sex of the face stimuli and/or that of the participants could influence behavioral and physiological responses. First, as previously reported (Hess et al., 2009), we found that male participants are slower to discriminate the sex of angry faces, when compared to other emotions. Second, the sex of the seen face influences the observer's accuracy and RT: sex categorization was better (higher accuracy) and faster (smaller RTs) for close female images (compared to far ones) and, conversely, it was better for far male images (compared to close ones). Third, the sex of the face and/or that of the participants influenced pupil size and HRV. Male participants showed less pupil dilation when female images were presented far (compared to close ones). In addition, here we report a larger LF/HF ratio for male participants exposed to closer faces. Pagani et al. (1984, 1986) have proposed that LF/HF ratio could be considered an estimate of the balance between sympathetic and parasympathetic nervous system activity. An increase in LF/HF ratio could thus be viewed as increase in sympathetic activity (Billman, 2013). According to this interpretation, our results suggest that the level of arousal in male participants is higher when emotional faces are presented next to them. Thus, both the sex of the viewer and that of the nearby conspecifics matters. These variables modulate the level of arousal, with changes that can be measured from the pupil and the heart and may also influence behavioral responses. Our results support the notion that PPS representation is highly sensitive to both external and internal milieu aspects (Bufacchi & Iannetti, 2018).

4.4. *How can interoceptive signals influence PPS brain network activity?*

The present study shows that when social elements enter the PPS, they induce a variety of specific effects at the behavioral and physiological level. Several neurophysiological and neuroimaging studies have identified a set of neural substrates with selective activity in response to stimuli presented in PPS, including premotor-putamen-parietal regions. How is this network involved in behavioral and physiological regulations when stimuli approach the body? While future neuroimaging studies are needed to tackle this question directly, we believe it should at least be tentatively addressed here. We wish discussing the speculation that peripheral physiological changes could contribute to behavioral effects by modulating activity of this network. The central nervous system receives inputs from the internal body by ascending visceral signals (Azzalini et al., 2019; Critchley & Garfinkel, 2017). Visceral inputs reach the brain via vagal and spinal pathways targeting brainstems relay nuclei (nucleus tractus solitarius, NTS; and parabrachial nucleus, PBN). Ascending sensory fibers represent 80% of the vagus nerve (Agostoni et al., 1957). From NTS and PBN nuclei, projections are sent to noradrenergic and serotonergic pathways in the brainstem acting as relays to subcortical regions (Azzalini et al., 2019). Then, via thalamic relays, numerous cortical areas receive visceral signals, including the PPS network. Emotionally connotated stimuli in close proximity of our body may increase the level of arousal (heart rate) and this interoceptive information may be transferred via thalamo-cortical pathways and other subcortical regions (e.g., hippocampus, amygdala, insula), which are connected to cortical PPS brain regions. In particular, strong thalamic projections are sent to premotor and prefrontal areas including ventral premotor cortex (PMV) (Fang et al., 2006). Strong anatomic connections also exist between the amygdala and the granular frontal operculum, an adjacent and connected region to the PMv (Gerbella et al., 2014). Amygdala activation could leads to heart rate increases and HRV decreases through activation or disinhibition of sympatho-excitatory neurons in the rostral ventrolateral medulla, and inhibition of vagal activity through the nucleus ambiguous (Thayer & Sternberg, 2009). Therefore, these routes could relay visceral/sensory inputs to brain regions coding for PPS representation and shape the behavioral responses depending on the context (i.e., faster RTs and higher accuracy).

Author contributions

Audrey Dureux: Conceptualization; Methodology; Validation; Formal analysis; Investigation; Data curation; Original draft; Review & editing; Visualization; Project administration.

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Laura Clara Grandi: Conceptualization; Methodology; Formal analysis; Investigation; Review & editing.

Olena Bogdanova: Resources; Writing - Review & Editing.

Clément Desoche: Software; Resources.

Alessandro Farné: Conceptualization; Methodology; Validation; Review & editing; Project administration; Supervision.

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Open practices

The study in this article earned Open Materials and Open Data badges for transparent practices. Materials and data for the study are available at https://osf.io/98mur/.

Declaration of competing interest

The authors declare that they have no conflict of interest.

Acknowledgements

This work was supported by the French National Research Agency ANR-15-CE37-0003 grant MySpace to FHB and ANR-10-IBHU-000 Neuro-Immersion to AF. EB was supported by: the European Union's Horizon 2020 research and innovation programme (Marie Curie Actions) under grant agreement MSCA-IF-2016-746154; a grant from MIUR (Departments of Excellence DM 11/05/2017 n. 262) to the Department of General Psychology, University of Padova. The study was performed within the framework of the LABEX CORTEX (ANR-11-LABX-0042) of Lyon University within the program "Investissements d'Avenir" (ANR-11-IDEX-0007) operated by the ANR. We thank S. Alouche, JL. Borach, S. Terrones for administrative and informatics support, A. Belle and R. Salemme for engineering support.

Funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

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